2. Application of uniformitarian thinking has lead to intensive studies of Recent reefs which provide the opportunity to observe progressive reef formation from initial growth to completely lithified and even partly altered reef rock. Field observations are being supplemented by laboratory experiments. Results, criteria, and concepts obtained in this way need to be tested with respect to their general application by regional comparison, and with respect to their validity in geologic history by comparing reefs of various ages. Work on fossil reefs, in addition, provides further questions to be answered.

It is hoped that this symposium contributes to the understanding of reef formation and stimulates further studies.

Acknowledgements

We wish to extend our thanks and appreciation to

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Pacific Coral Reefs of Panamá: Structure, Distribution and Predators

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With 15 figures and 7 tables

Zusammenfassung

Die rezenten Korallenriffstrukturen an der östlichen Pazifikküste von Panamá zeigen starkes Wachstum. Von den 20 vorhandenen Arten hermatypischer Coelenteraten gehören 3 zu der Gattung *Millepora*, die erstmals im ostpazifischen Raum beobachtet

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wurde. Die häufigeren Scleractinia sind *Pocillopora* (4 Arten), *Pavona* (6 Arten) und *Porites* (5 Arten). *Pocillopora* ist der wichtigste Gerüstbildner in Kuppen- und Saumriffen, während die massigen Kolonien von *Pavona* und *Porites* an der Basis der Riffe wichtig werden können. Für einige Saumriffe ist ununterbrochenes *Pocillopora*-Wachstum charakteristisch, das zum Bau eines vertikalen Gerüstes von maximal 6 m Höhe führt. Der Verbund von Korallen durch inkrustierende koralline Algen gibt der Struktur an Ober- und Außenseiten Festigkeit und Zusammenhalt. Die Sedimente innerhalb und außerhalb der Riffstrukturen bestehen zu 90% aus Karbonaten; die häufigsten Komponenten sind Bruchstücke von *Pocillopora,* Cirrepediern und Mollusken. Die Riffentwicklung erreicht ihren Höhepunkt im Golf von Chiriquí, vermutlich weil in diesem Gebiet die Temperaturen hoch und gleichmäßig sind. Radiometrische Altersbestimmungen haben ein Vertikalwachstum von 1 m/250 Jahre oder 4000 Bubnoff-Einheiten ergeben.

Fische, ein Gastropode und Dekapoden (Paguren) sowie — in bestimmten Gegenden — *Acanthaster* sind wichtige Gegner der Korallen. Quantitative Erfassung von Nahrungsmengen und Bevölkerungsdichten der „Corallivoren" ergab, daß diese etwa ein Drittel des jährlichen Zuwachses von *Pocillopora* zerstören.

Abstract

Structural coral reefs of Recent age are undergoing vigorous growth on the eastern Pacific continental shores of Panamá. Coelenterate hermatypes include 20 species; 3 are hydrocorals in the genus *Millepora,* a notable new record for the eastern Pacific region; the abundant scleractinians are *Pocillopora* (4 spp.), *Pavona* (6 spp.) and *Porites* (5 spp.). *Pocillopora* is the chief constructor of mound and fringing reefs with massive *Pavona* and *Porites* sometimes important at the reef base. Uninterrupted *Pocillopora* growth characterizes some fringing reefs, forming a vertical framework with observed maximum thickness of 6 m. Binding of coral by encrusting coralline algae imparts a more rigid and coherent structure to the reef crest and peripheral faces. Intra-reef and flanking sediments contain over 90% calcareous matter; the predominant grain constituents are *Pocillopora,* cirriped and mollusk fragments. Reefs attain their greatest development in the Gulf of Chiriquí; the reason for this is sought in the high and stable thermal conditions of this area. Radiometric dating indicates that net vertical reef growth may approach 1 m/250 years or 4000 B.

Important coral predators include fishes, a gastropod, paguran decapods and *Acanthaster* (in certain areas). Quantitative measurements of the feeding rates and population densities of corallivores indicate that predators may destroy approximately one-third of the annual growth of a *Pocillopora* coral community.

Résumé

Les récifs structuraux récents de coraux de la côte Panamienne du Pacifique orientale présentent une croissance importante. Pour la première fois it fut possible d'observer dans le Pacifique orientale, parmi les 20 espèces de Coelentérés hermatypiques, 3 espèces appartenant au gènre *Millepora.* Les Scleractinia les plus fréquents sont les *Pocillopora* (4 espèces), les *Pavona* (6 espèces) et les *Porites* (5 espèces). Les *Pocillopora* sont l'élément le plus important de charpente des pitons sous-marins et des récifs frangeants, tandis que des colonies massives de *Pavona* et de *Porites* sont parfois importantes à la base des récifs. La caractéristique des récifs frangeants est en partie représentée par la croissance ininterrompue de *Pocillopora* conduisant à la construction d'une charpente verticale d'une hauteur maximale de 6 m. Une liaison des coraux par des algues corallines crouteuses forme une structure plus forte et cohérente du sommet et du peripherie des récifs. Les sédiments structuraux interieurs et exterieurs des récifs sont constitués à 90% par des carbonates. Les composants les plus fréquents sont des fragments de *Pocillopora,* de cirripèdes et de mollusques. Le dévelopement du récif atteint sont maximum dans le golfe du Chiriquí. La cause est cherchée dans les températures élevées et stables de cette région. Des précisions radiométriques sur l'âge donnent, pour la croissance verticale, une hauteur d'un mètre pour 250 années ou 4000 unités Bubnoff.

Des poissons, un gastéropode, des décapodes (pagures) ainsi que — dans quelques endroits — des *Acanthaster* sont des ennemis importants des coraux. Des récensements quantitatifs du nourriture et de la densite des populations des corallivores démontrent qu'ils détruisent a peu près un tiers de l'accroissement annuel des *Pocillopora.*

Краткое содержание

На восточном побережье Тихого океана (Панама) наблюдают интенсивный рост современных коралловых рифов. Из 20 имеющихся видов рифообразующих организмов, 3 принадлежащие к роду **Millepora**, обнаружены в восточной части Тихого океана впервые. Чаще всего встречаются **Scleractinia,** именно: **Pocillopora** 4 вида, **Pavona** 6 видов и **Porites** 5 видов. **Pocillopora** является ведущим видом ири образовании ствола и верхней части рифов различной формы, в то время, как основание его представлено умеренно растущими колониями **Pavona** и **Porites.** Для барьерных рифов характерен непрерывный рост **Pocillopora,** при котором создается вертикальная постройка до 6 м высоты. — Отложения внутри и во вне рифовых образований состоят на $90^0/_0$ из карбонатов. Наиболее частыми компонентами здесь являются обломки **Pocillopora, Cirrepedier,** и мягкотелых. Самое интенсивное рифообразование наблюдают в заливе **Chiriquí.** С помощью радиометрических измерений установили, что рост коралла происходит со скоростью 1 м в 250 лет. Обычно на кораллах и в них поселяется большое количество животных (рыбы, гастроподы, декаподы, а в некоторых областях и **Acanthaster**). По количественному соотношению имеющихся запасов питательных веществ и по плотности населения ,,кораллоядов‘‘ утсановили, что последние разрушают 1/3 годового прироста **Pocillopora.**

Contents

A. Introduction

In the literature it has generally been held that coral reefs are absent from the eastern Pacific region (Vaughan, 1919; Yonge, 1940). It has also been concluded that predators of living corals are unimportant to coral survival and reef growth (Yonge, 1968; Stoddart, 1969). We wish to devote attention to these topics in order to demonstrate a. that large, actively accreting structural coral reefs do occur in the Pacific coastal waters of Panamá and b. that corallivores have significant effects on coral reef growth as shown by quantitative measurements of these activities.

That coral reefs have not previously been reported from this region is probably a result of several factors. First, an early correct observation — that unfavorable hydrographic conditions greatly restrict coral reef development off the western coasts of continents — may have directed the efforts of workers away from this region. Very little has in fact been published on the littoral communities of the Pacific coast of America as well as the central west African region. Another factor concerns the largely subtidal character of the reefs and the often poor clarity of the sea. Usually SCUBA diving or aerial reconnaissance are the most efficient means of locating the position of coral formations, but these methods have been developed only relatively recently. In addition, the areas supporting greatest reef development are located offshore in comparatively remote sectors of the country.

The most thorough field study of corals in the eastern Pacific region was that of Squires (1959) in the Gulf of California. He found thriving coral communities, but no Recent structural reefs as he points out, in this marginal subtropical area. Despite the early reconnaissance by Crossland (1927) in Panamá, and his conclusion that reef corals were developed very meagerly in this area, Durham and Barnard (1952) and Durham (1966) suspected that true modern coral reefs would eventually be found somewhere along the eastern Pacific coast. This conclusion was derived from the frequently encountered coral growth in the Gulf of California (Durham, 1947; Squires, 1959), the rich communities of *Pocillopora* reported off the western coast of México (Palmer, 1928) and the abundant coral collections obtained incidentally by the VELERO expeditions to the eastern Pacific region. Joubin's (1912) atlas of the distribution of coral reefs in Panamá has thus far proved largely inaccurate. Clipperton Island, well off the Mexican coast, has long been regarded as a coral atoll (e. g. Hertlein & Emerson, 1957; Allison, 1959; Sachet, 1962), but little information is available on the nature of the coral formations.

The evidence presented in this paper for vigorous coral growth and the development of structural coral reefs (sensu Wainwright, 1965) along Pacific Panamic shores comes from a detailed study of surface reef morphology and coral zonation, dissection of the reef framework with explosives, radiometric dating of corals from the reef core and study of the sedimentological characteristics of surrounding reef deposits. The best developed coral reefs were found to occur in the Gulf of Chiriquí. An explanation for this is sought in terms of the high stenothermic conditions characteristic of this region.

While the depredations of *Acanthaster* on certain reefs is now well known (e. g. Chesher, 1969; Talbot & Talbot, 1971) it is still assumed by many that the feeding activities of other corallivores are inconsequential (WELLS, 1957; YONGE, 1963, 1968; STODDART, 1969). The results of our analysis indicate that these activities can be great in terms of their trophic and geologic effects, probably enough to result in the destruction of significant amounts of the annual growth of *Pocillopora* reef corals. Some concluding remarks are made in this context on the contribution of corallivores to sediment production and coral reef progression.

B. Hermatypic Coral and Hydrocoral Fauna

The present preliminary inventory of coelenterate hermatypes in Panamá includes 20 recognized species (Table 1). Three of these are hydrocorals in the genus *Millepora* while the remaining 17 species are scleractinian corals distributed among 5 genera. Except for *Pocillopora robusta,* all of the species have been collected from the Gulf of Chiriquí in southwestern Panamá and the majority of them can be found cohabiting single reef complexes. Additional recent information on species distributions along Panamic shores can be found in PORTER (in press).

Discovery of the Order Milleporina in the eastern Pacific region was made during the course of these studies and was referred to briefly by GLYNN (in press a). The scleractinian corals comprise possibly two undescribed species and three new records for the American continental coastal region, the latter formerly reported from the Galápagos Islands. While not included in the present list, ahermatypic scleractinians were also present at all localities visited. Among these, *Tubastrea tenuilamellosa* (MILNE EDWARDS & HAIME) was especially abundant in the shaded recesses of reefs.

It should be cautioned that the inventory of species herein reported must be accepted on a provisional basis at this time. Many of the taxonomic problems posed by species of *Pavona, Porites* and *Pocillopora* have not yet been resolved. In addition, field collections have until now been confined to a limited number of localities.

C. Reef Morphology and Species Zonation

I. Description of Reef Morphology

The structural coral reefs in the Gulf of Chiriquí are exposed only at extreme low water; subaerial structures of bioclastic materials or fossiliferous deposits are not present on these reefs. Reef-derived sediments are scattered widely around the reef base and beyond, and frequently entire beaches contain a preponderance of bioclastic calcareous sands. At shallow depth, species of *Pocillopora* usually predominate in terms of biomass, whether they occur as a veneer on the underlying substratum (the base rock in the littoral zone of south-western Panamá is an ancient submarine basalt flow) or comprise the chief framebuilding component of reefs. The shoal sections of some reefs contain live *Pocillopora* which is awash briefly during extreme exposures. Massive coral species such as *Porites* and *Pavona* assume a more important role peripheral to *Pocillopora* or around the reef base at greater depth.

Structural reefs are most commonly developed as mounds of irregular configuration in plan view. These can spread laterally to cover a bottom area of 1 to

Table 1. Provisional list of coelenterate hermatypes collected from the Pacific shores of Panamá. Asterisks denote new records for the continental eastern Pacific region.

Species	Collecting locality	Disposition of material	Remarks
Order Milleporina			
Family Milleporidae			
* 1. *Millepora intricata* Milne Edwards	Contreras Is.	Rijksmus. Nat. Hist. 1)	Formerly known from East Indies and Caroline Is.
* 2. *Millepora platyphylla* Hemprich & Ehrenberg	Coiba Is.	do.	Formerly known from Red Sea, Indian Ocean and western Pacific east to Tuamotu Archipelago
* 3. *Millepora* n. sp. 1	Contreras Is.	do.	
Order Scleractinia			
Family Thamnasteriidae			
4. *Psammocora (Stephanaria) brighami* (Vaughan)	Contreras Is.	UCMP 2) loc. D-4136 hypotype no. 10762	
Family Pocilloporidae			
5. *Pocillopora capitata* Verrill	Secas Is.	UCMP loc. D-4137, hypotype no. 10763	Previously placed in synonymy with *P. robusta* and *P. elegans* Dana 3)
6. *Pocillopora damicornis* var. *bulbosa* Ehrenberg	Perlas Is.	UCMP loc. D-5493, hypotype no. 10764	
Pocillopora damicornis var. *cespitosa*	Secas Is.	UCMP loc. D-5500, hypotype no. 10765	
7. *Pocillopora lacera* Verrill	Secas Is.	UCMP loc. D-4137, hypotype no. 10766	Previously placed in synonymy with *P. damicornis* (Linnaeus) 3)
8. *Pocillopora robusta* Verrill	Jaqué 78° 10′ W 7° 31′ N	UCMP loc. D-4135, hypotype no. 10767	Not *P. palmata* Palmer. Previously placed in synonymy with *P. elegans* 3)
Family Agiriciidae			
9. *Pavona clivosa* Verrill	Secas Is.	UCMP loc. D-4137, hypotype no. 10768	
10. *Pavona (Pseudocolumnastrea) galapagensis* Durham & Barnard (?)	Perlas Is.	UCMP loc. D-4134, hypotype no. 10769	Identity uncertain. Calices slightly larger than in type. Previously placed in synonymy with *P. clivosa* 3)
11. *Pavona gigantea* Verrill	Secas Is.	UCMP loc. D-4137, hypotype no. 10770	

Table I (contd.)

Species	Collecting locality	Disposition of material	Remarks
* 12. *Pavona ponderosa* Gardiner	Secas Is.	UCMP loc. D-4137, hypotype no. 10771	Formerly known in eastern Pacific from Galápagos Is.
13. *Pavona varians* Verrill	Secas Is	UCMP loc. D-4137, hypotype no. 10772	
* 14. *Pavona* n. sp. 1	Contreras & Secas Is.	UCMP loc. D-4136, hypotype no. 10773 & loc. D-4137, hypotype no. 10774	Also known from Galápagos Is.
15. *Leptoseris* (?) n. sp.	Contreras Is.	UCMP loc. D-4136, hypotype no. 10775	Possibly an unifacial form of *Pavona*
Family Poritidae			
16. *Porites californica* Verrill	Secas Is.	UCMP loc. D-4138, hypotype no. 10776	
17. *Porites excavata* Verrill	Perlas Is.	UCMP loc. D-5497, hypotype no. 10777	
* 18. *Porites lobata* Dana (?)	Secas Is.	UCMP loc. D-4137, hypotype no. 10778	Formerly known in eastern Pacific from Galápagos Is.
19. *Porites panamensis* Verrill (?)	Secas Is.	UCMP loc. D-4137, hypotype no. 10779	
20. *Porites paschalensis* Vaughan (?)	Perlas Is.	UCMP loc. D-5496, hypotype no. 10780	

¹) Rijksmuseum van Natuurlijke Historie, Leiden, The Netherlands.

²) University of California Museum of Paleontology, Department of Paleontology, Berkeley, California 94720.

³) Cf. Squires, 1959.

2 hectares (ha.) in extent. The central sections of such reefs often extend upwards to the spring low water level; large areas of the reef crest tend to be uniformly flat. Coral growth assumes a lower elevation peripherally where at the reef base (ca. 5—8 m depth) only single colonies of low stature are present. The principal framebuilder of these reefs is *Pocillopora*. Other hermatypes occurring in the reef core among *Pocillopora* often include *Millepora intricata, Pavona ponderosa, P. varians* and *P. clivosa*. Large massive colonies of *Pavona varians, P. clivosa, Porites panamensis* and *P. paschalensis* are also common at the reef base. Maximum thickness of the reef mounds, estimated from their relief above the bottom, examination of eroded sections and dissection with explosives, is about 3 m.

Pocillopora also forms fringing reefs. A structural reef of such morphology, nearly 500 m in length, was studied in detail in the Secas Islands (Fig. 1). The frame of this kind of reef, consisting of a broad linear elevation of *Pocillopora* 50 to 60 m wide, is welded together as a rigid interlocking lattice of erect coral branches (Fig. 2). Along its southern end the reef abuts directly against the sloping basaltic rock shore. However, at the eastern end the reef is located farther from shore (ca. 40 m), separated from the latter by a 3 m deep basin (Figs. 3

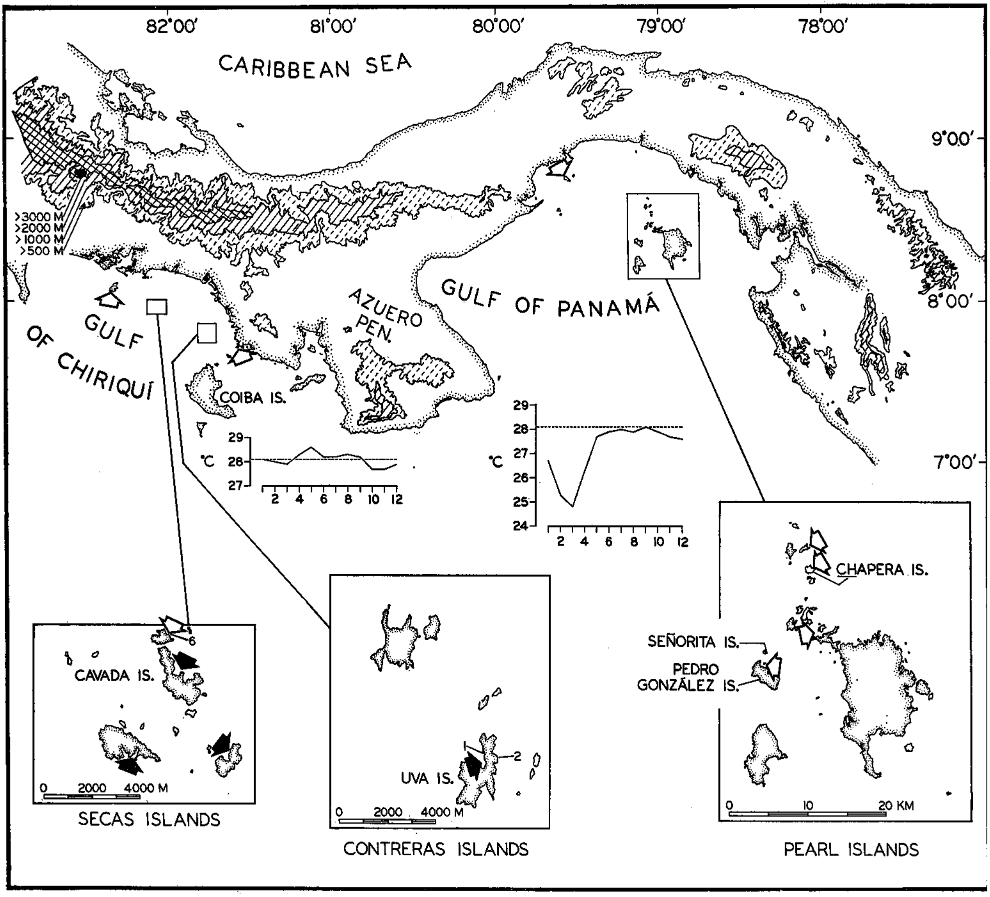

Fig. 1. Map of Panamá showing the Talamanca and Central mountain ranges in the west and the distribution of known coral formations on the Pacific side of the Isthmus. The locations of true structural reefs (framework ≧ 3 M) are indicated by solid arrows; open arrows denote incipient reef devolopment (framework ≦ 2 M). The locations of transects in the Secas and Contreras Islands are also shown. Plots of the annual variations in mean sea surface temperatures are indicated for the Gulf of Chiriquí (80°—84° W, 6°—8° N) and the Gulf of Panamá (78°—80° W, 6°—8° N), after RENNER (1963). Mainland Panamá from Special Map No. 2, sheets 1, 2 and 3, USARCARIB Engineer, Canal Zone, scale 1 : 500,000. Secas and Contreras Islands from U.S. Army topographic sheets 3739 I and 3839 II, respectively, series E 762, scale 1 : 50,000. Pearl Islands from H. O. chart 5584, scale 1 : 145,130.

and 4). The fathograms in Fig. 5 illustrate the surface relief across five sections of the reef. The steep sides of the reef are particularly well illustrated in these profiles and the accompanying photographs in Figs. 3 and 4. The reef crest is 0.2 m below the MLWS (mean low water spring) level and in some places slopes precipitously from this elevation to 2—3 m depth. Vigorous coral growth also appears to be taking place deeper, at 7 m to 8 m depth, along the seaward face.

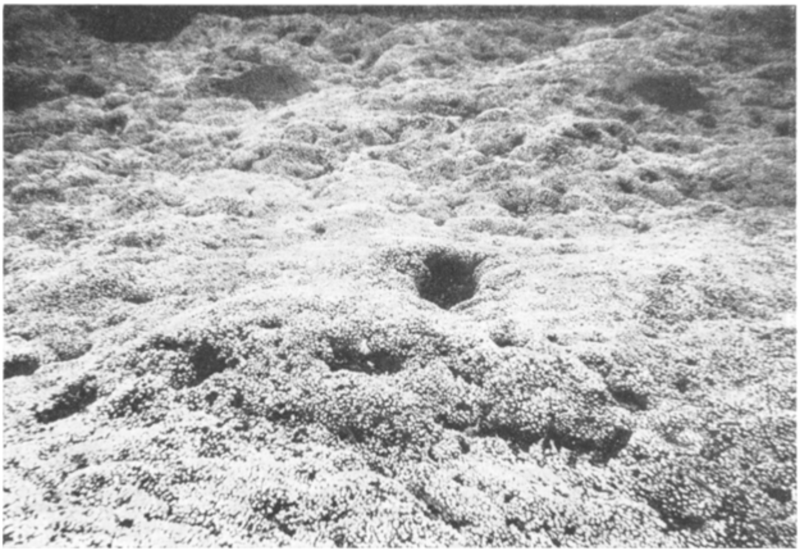

Fig. 2. Underwater view of crest of *Pocillopora* fringing reef illustrating uniform flat surface near extreme low water level. SE-most island in the Secas group, March 24, 1971.

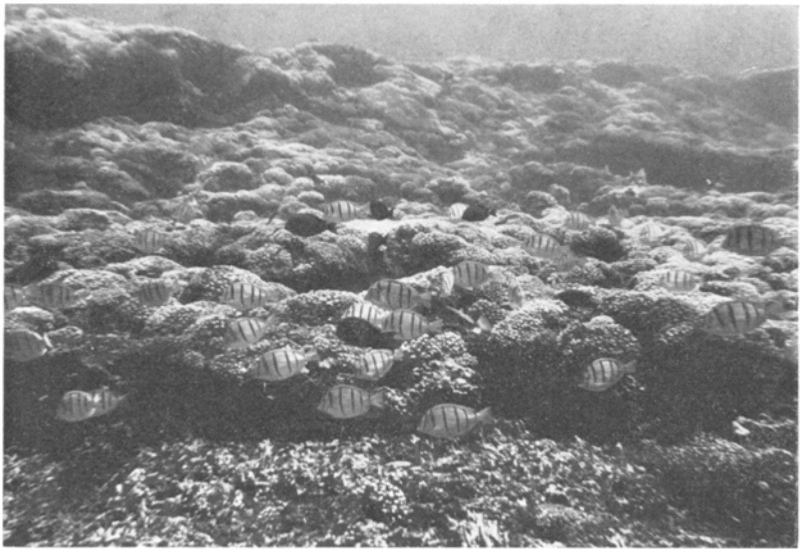

Fig. 3. *Pocillopora* fringing reef illustrating abundant coral growth in basin shoreward of reef crest, 3 M depth. SE-most island in the Secas group, March 24, 1971. Trans-Pacific fishes in foreground include *Acanthurus triostegus* (Linnaeus), *A. xanthopterus* Valenciennes, *Ctenochaetus cyanoguttatus* RANDALL and *Scarus rubroviolaceus* BLEEKER.

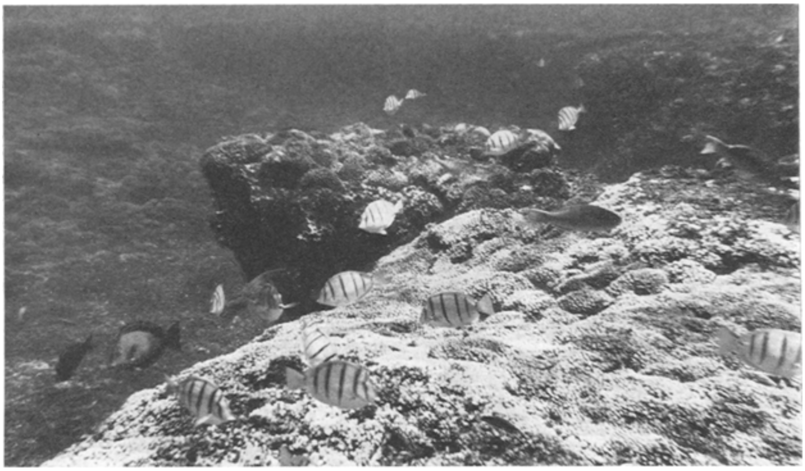

Fig. 4. Underwater view of shoreward basin (left) and reef crest (foreground and right) of *Pocillopora* fringing reef, maximum depth 3.5 m. The deeper sections of the basin floor contain mostly coral rubble sediment. SE-most island in the Secas group, March 24, 1971.

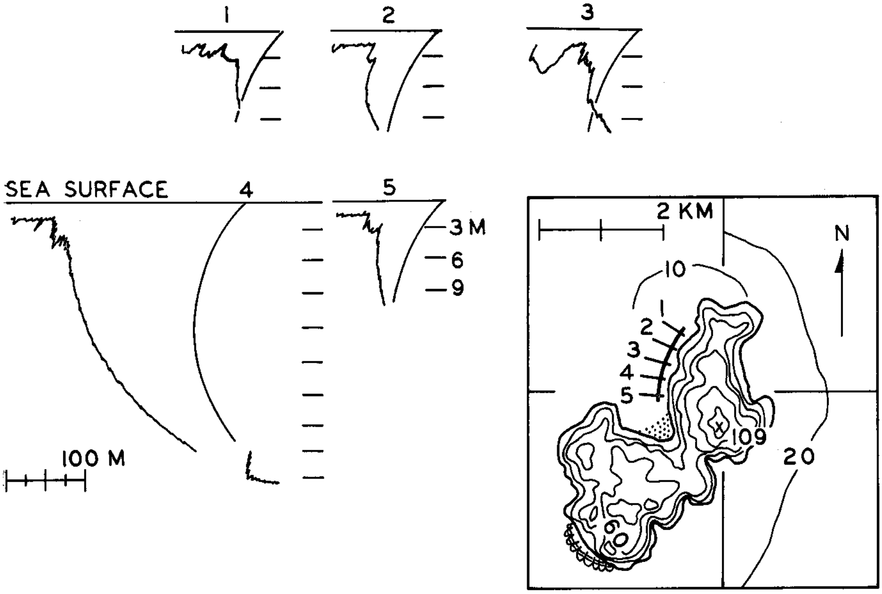

Fig. 5. Vertical profiles of *Pocillopora* fringing reef, SE-most island in the Secas group, March 24, 1971. The five sections surveyed were oriented normal to the long axis of the reef as indicated. The profile at position 4 indicates an abrupt decrease in slope at 27 M depth approximately 300 M west of the shore. Reef crest 0.2 M below MLWS. Fathograms obtained with portable Raytheon Explorer 11 recording fathometer, DE-725 B. Arcs indicate true vertical. Map from U.S. Army topographic sheet 3739 I, series E 762. Contour interval 20 meters; vertical datum mean sea level; scale 1 : 50,000.

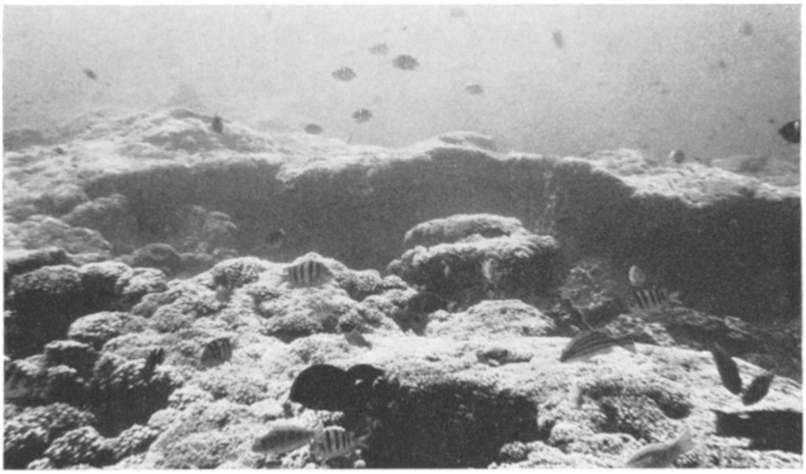

Fig. 6. Underwater view of crest of *Pocillopora* fringing reef illustrating deep holes and depressions with slumping of large coral blocks. *Scarus ghobban,* a trans-Pacific species, is present in the foreground.

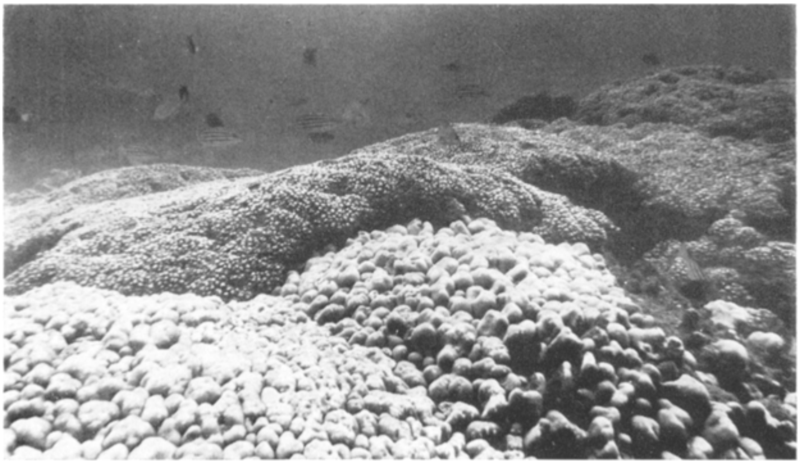

Fig. 7. Underwater view of coral reef rise showing *Pocillopora* coverage at 2 m to 3 m growing on and presumably spreading over a massive colony of *Pavona clivosa* slightly deeper in the foreground. SW-most island in the Secas group, March 24, 1971.

The bottom below this level, to depths of 8 m to 14 m, is a talus slope composed chiefly of *Pocillopora* rubble. Deep holes, pits and basins, particularly on the reef crest, indicate that the reef has undergone recent extensive erosion (Fig. 6). This particular reef appears to have attained a maximum thickness of 6 m.

Until now the discussion has been confined to reef formations situated in relatively protected areas, *i. e.* along shores oriented toward the north or in bays and coves. However, large structural reefs have also been found on the seaward or south-facing sides of islands. These appear to be best developed in the central portions of mouths of coves and not along the adjacent exposed headlands. Expansive patches of *Pocillopora,* often forming steep-sided elevations, again dominate the shallower sections of these reefs and extend to about 5 m depth (Fig. 7). Large colonies of *Pavona clivosa* begin to appear at 5 m where they become intermingled with *Pocillopora.* In this zone of co-habitation the surface relief of live *Pocillopora* growth suggests that dead *Pavona* heads provide the underlying substratum. The deeper sections of the reef, from 7 m to 10 m, is comprised of nearly a pure stand of *P. clivosa,* some of which attain 2 m in height and 3 m to 4 m in diameter. Abundant coral growth has not been found deeper than about 10 m. The bottom adjacent to the reef base contains coral rubble and numerous coralline algal nodules.

II. Coral Zonation

Quantitative sampling to determine the abundance and bathymetric distribution of coral populations was carried out at 7 localities in the Gulf of Chiriquí. The results of 3 of these censuses are presented here in order to provide some impression of the distributional patterns of species across the depth gradient.

Census procedures were as follows. The positions of transects were selected from U.S. Army topographic maps and were random in the sense that no prior knowledge of the biotic character of the site was available. The only restrictions in site selection included the availability of a rock substratum and sea conditions compatible with small boat operations. The transect was established by positioning a wire measure normal to the shoreline from the MLW level to the deepest limit of coral growth. A 1 m^2 quadrat frame was moved along the center of the transect within which all discrete coral colonies present were enumerated.

The most abundant corals at shallow depth included three species of *Pocillopora* and small encrusting colonies of *Porites californica* (Fig. 8), the latter usually covering a surface area no larger than 50 cm^2. *Pocillopora damicornis* was usually the most abundant species but *P. capitata* and *P. lacera* were also quite common. Unfortunately, these species could not be readily distinguished from one another in the field. *Pocillopora* spp. often exhibited densities of 10 colonies per m^2 and in one area attained an abundance exceeding 40 colonies per m^2 (Fig. 8, Transect 6). Here coverage was continuous with the coral frame elevated in some places about 1 m above the bottom. *Pavona varians* and *Millepora intricata* were also sometimes fairly common at shallow depth (Fig. 8, Transect 2) where they appear to compete for space with *Pocillopora* spp. and *Porites californica.* Large massive colonies of *Porites paschalensis, P. panamensis, Pavona gigantea* and *P. clivosa,* which commonly attain 2 m in diameter, occurred as a rule in deeper water, beyond 5 m depth (Fig. 8, Transect 1).

Generally, the above named species present on structural reefs demonstrated similar patterns of distribution. However, where shallow sections of reefs contained uniformly dense populations of *Pocillopora,* other hermatypes normally present elsewhere under less crowded conditions were either absent or markedly reduced in abundance. The incipient reef development at Cavada Island (Fig. 8, Transect 6) illustrates this condition. *Porites californica* co-occurs with *Pocillo-*

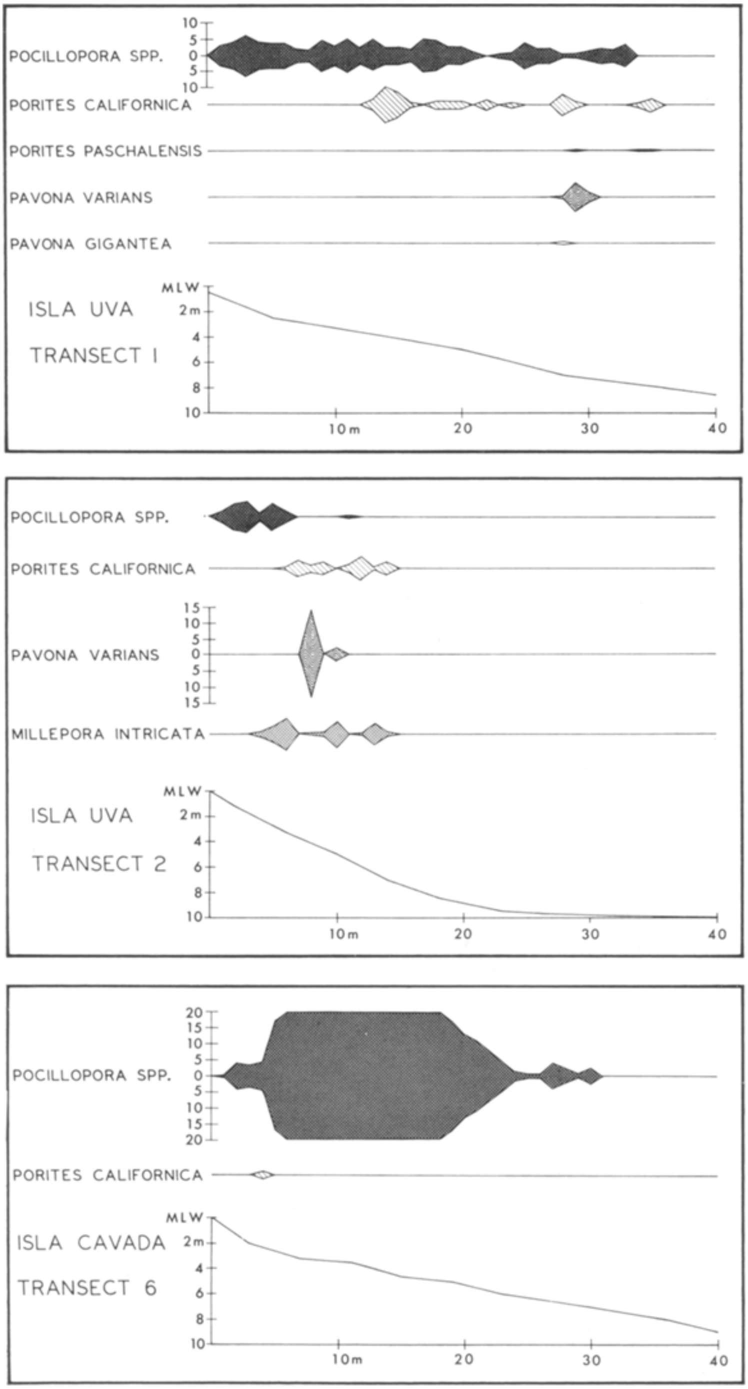

Fig. 8. Population densities (number of colonies per m^2) of coral and hydrocoral hermatypes over bathymetric range of distribution from selected shore sampling stations in the Gulf of Chiriquí. The bottom relief is shown along each transect. Transect 1, Isla Uva, Islas Contreras, April 29, 1970; Transect 2, Isla Uva, Islas Contreras, April 30, 1970; Transect 6, Isla Cavada, Islas Secas, May 2, 1970. The locations of sampling sites are indicated in Fig. 1.

pora at relatively low density, but is absent, as are other corals, where *Pocillopora* forms a continuous cover.

Clear signs of interspecific aggressive interactions, similar to the extracoelenteric feeding aggression described by LANG (1970) in the Caribbean, are evident in eastern Pacific scleractinian populations. *Pavona clivosa,* growing in juxtaposition with *Pocillopora* sp., often exhibited damaged surfaces, from freshly produced lesions to areas overgrown with algae, where these species came into contact. It is suspected that the apparent encroachment of *Pocillopora* over *Pavona* illustrated in Fig. 7 is a result of this kind of interaction. A tentative hierarchical classification developed from field observations follows: *Pocillopora* spp. > *Pavona gigantea, P. clivosa* > *Porites panamensis, P. paschalensis.* This dominance series is possibly an important factor in determining the structural character of coral communities. It would explain the peripheral occurrence of *Pavona* and *Porites* where *Pocillopora* is abundant, and the presence of other species at shallow depth when *Pocillopora* is present at low densities.

Among the Caribbean corals first investigated by LANG (op. cit.), it was generally found that the more aggressive species tended toward small size or massive growth form. Field studies indicated that these species can compete successfully for space with more rapidly growing subordinate corals of ramose growth habit. Our observations demonstrate that the fast-growing ramose species are also the superior aggressors. It is not unreasonable to suspect that *Pocillopora* largely owes its success in the eastern Pacific to the possession of these two kinds of competitive strategies.

Two further comments are necessary. No corals were found deeper than 8 m in the transects. Several surveys beyond the transects, to 30 m depth, showed that isolated colonies of *Pavona* and *Porites* usually occur no deeper than 15 m. The deepest hermatypic coral populations thus far reported in the eastern Pacific are at Clipperton Island, where major reef growth is taking place between 12 m and 18 m (ALLISON, 1959). Finally, the random selection of sampling sites resulted in the finding of only a single incipient coral reef. Thus it can be tentatively concluded that reef coral populations are confined to very shallow depths and that coral reef formations show a marked patchy distribution.

III. Coralline Algae

While only brief mention is made here of the coralline algae, it is obvious from the abundance and binding properties of some species in this group that they must be regarded as an important constructional component of reefs.

The reef crest, which is periodically exposed for brief periods, often contains a greater surface coverage of calcareous algae than any other group of organisms. *Mesophyllum* sp. and an apparent *Archeolithothamnium* or possibly a *Lithothamnium* occur abundantly in this habitat. These algae often form a pavement-like cover over the surface of the reef crest, binding and imparting rigidity to the dead coral structures present here.

The chief element encrusting the vertical branches of *Pocillopora* on fringing reefs was a *Porolithon,* closely allied to *P. cocosicum* LEMOINE. In addition, some *Polystrata ?compacta* (Foslie) Denizot, a fleshy crust, and a *Mesophyllum* sp.

were found in association with *Porolithon*. These algae bind and stabilize the *Pocillopora* framework which forms the periphery of steep-sided reef faces.

Algal nodules are sometimes abundant in deposits flanking the reef base. The principal species constructing these nodules in the Secas Islands is *Polystrata ?compacta*. In addition, approximately in order of surface abundance, the following corallines can be found in these structures: *Lithophyllum* sp., *Lithophyllum ?imitans* Foslie, and *Mesophyllum* sp. (probably the same species as found on the reef crest).

D. Sedimentological Characteristics

Where sizeable coral communities or reefs occur the adjacent beach sands usually reflect the proximity of the source area in their overall whitish appearance and high composition of bioclastic materials. Such beaches and the genetically related sub-littoral bottom deposits occur commonly in the Gulf of Chiriquí and in the Pearl Islands Archipelago in the Gulf of Panamá. The present discussion is based on a study of the sedimentological characteristics of the Chapera Island reef, Pearl Islands. This site was selected because it contains a relatively well developed reef formation with the usual compliment of coral predators and it is easily accessible.

Sampling was carried out on bottom areas of suspected contrasting environmental character along a transect located normal to the shore and bisecting the reef formation. Surface sediments (upper 20 cm stratum) were collected from the mean high water line seaward to a depth of 8 m as indicated in the bathymetric profile in Fig. 9. All grain size data were obtained from mechanical (sieve) analyses. Replicate sampling spanning a one month period failed to show any significant departures from the data herein reported.

The most prominent sublittoral topographic feature is the fringing *Pocillopora* reef (Fig. 9 C) which extends for about 200 m along the shore. It was observed to develop a thickness of 2 m along its seaward edge. Also present are well bedded, seaward dipping outcrops of tuffaceous sandstone; these are most evident near the extreme low water level. Farther seaward there are additional ridges of tuffaceous sandstone cropping out parallel to the shore. The remainder of the bottom is composed of sedimentary deposits.

Some trends are evident in the grain size characteristics of sediments relative to their position across the shore (Fig. 9 A). The graphic mean (M_z) and inclusive graphic standard deviation (σ_I) indicate that these parameters attain minimum and maximum values, respectively, in intra-reef deposits. The skewness statistic (SK_I) shows that the distribution of reef sediments is fine-skewed, becoming coarse-skewed in deposits flanking the reef and nearly symmetrical in the intertidal zone and farther seaward. Intra-reef and shore sediments near the MLW level demonstrated leptokurtic (K_g) distributions. Another palpable shoreward trend, although not illustrated, was the decreasing angularity of the grains. It is assumed that these sedimentary properties are a result of the generation of relatively fine, well graded skeletal materials in the reef, which retain much of their original character due to the baffling effect of the coral framework. Progressive alteration of sediments away from the reef is believed due to erosion and the winnowing and sorting effects of water turbulence, especially wave action and tidal currents.

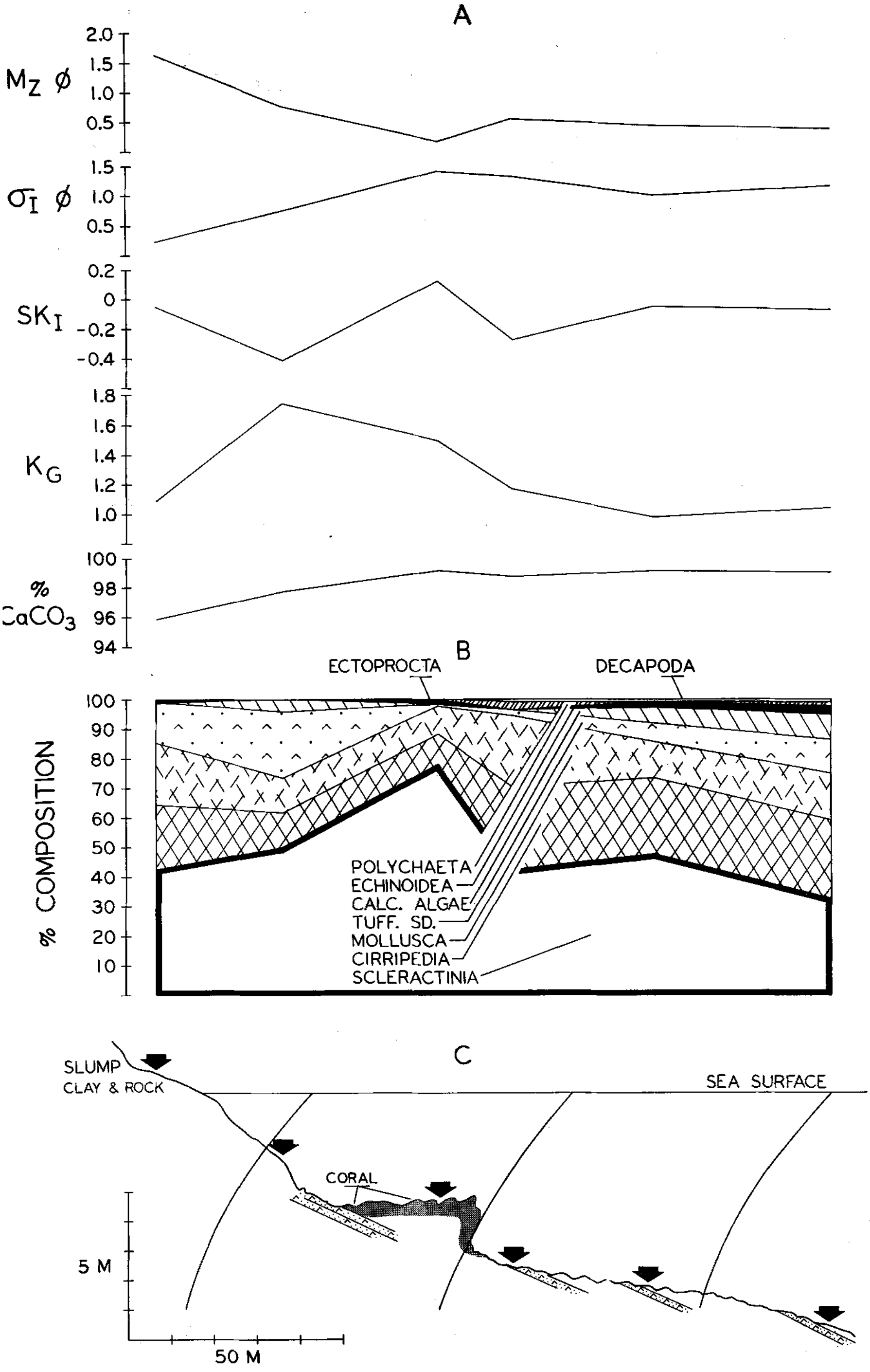

Fig. 9. Sedimentological characteristics of bottom deposits in and adjacent to the Chapera Island *Pocillopora* reef, Pearl Islands, June 19, 1971. A Grain size characteristics — M_Z graphic mean, σ_I inclusive graphic standard deviation, SK_I inclusive skewness, K_G graphic kurtosis (as defined by Folk, 1968), % $CaCO_3$ determined by repeated treatment with conc. HCL. B Per cent composition of 1.19 mm size grade. C Bathymetric profile of reef formation and adjacent bottom areas and intertidal sand beach. Reconstructed from fathogram obtained with portable Raytheon Explorer 11 recording fathometer (DE-725 B). Arcs indicate true vertical.

Also indicated in Fig. 9 A is the per cent composition of calcareous matter. This ranged between about 96% to 99% and was highest in the intra-reef deposits, namely 99.18%. The composition of the sediments revealed a preponderance of skeletal reef-derived materials.

Grain mounts in the 1.19 mm size grade were prepared and identified according to form and structure as revealed under a binocular microscope. Thin sections were also examined and compared with grains of known identity for purposes of verification. The results of these analyses are summarized in Fig. 9 B.

Coral fragments represented the largest component present with a mean contribution to all samples of 48.9%. Intra-reef deposits contained 78.1% of coral skeletal remains, showing a diminution in values away from the source area. Species of *Pocillopora* formed the bulk of this material. Skeletal fragments of cirripeds (balanomorph thoracicans) and bivalve and gastropod mollusks were next in importance, showing somewhat greater abundances away from the reef. Tuffaceous sandstone was most common near the MLW level, where extensive outcrops of this rock are present. Minor sedimentary constituents included the skeletal remains of calcareous red algae, echinoids, cheilostomatous ectoprocts, serpulid polychaetes and decapod crustaceans.

Unexpectedly, the Cirripedia were found to constitute as much as 20.6% of all samples. Living barnacles occur abundantly on dead in situ coral heads as well as on skeletal debris some distance from the reef. Conversely calcareous algae, which are often abundant in reef sediments elsewhere in tropical seas (STODDART, 1969), contributed only 3.0% to the samples examined. The abundant calcareous algae in the study area form hard crusts over the substratum and thus are not easily fragmented as are species with branching and segmented thalli.

E. Distributional Considerations

I. Thermal Conditions

As early as 1931 SCHOTT drew attention to the marked temperature front (attributed to the convergence of warm water from the NW and cold water from the Panamá Bight) usually located south of the Azuero Peninsula in February and March. GALTSOFF (1950) also observed pronounced differences in sea surface temperatures in the Gulf of Panamá and in the Gulf of Chiriquí, west of the Azuero Peninsula; he noted that such contrasting conditions must have considerable biological significance. The thermal conditions reported by GALTSOFF, again observed in February, ranged between 22°—24° C in the western sector of the Gulf of Panamá and between 28°—30° C in the Gulf of Chiriquí. SCHAEFER et al. (1958) and FORSBERGH (1963) demonstrated that the observed seasonal decline in temperature in the Gulf of Panamá is due to upwelling induced by strong northerly Trade Winds which blow across the Isthmus during the dry season (approx. from mid-December through April). Significant variations in the surface thermal structure of the Gulf of Chiriquí have not been detected. It is believed this is a result of the location of this area in the lee of the high mountain ranges of western Panamá (Fig. 1). The long-term temperature data summarized by RENNER (1963) show a mean difference between the two areas of 3.1° C.

in the month of March. Seasonal variations are compared in Fig. 1 with reference to the Gulf of Chiriquí annual mean of 28.1° C.

Preliminary observations of subsurface temperature conditions in the Gulf of Chiriquí show the 25° C isotherm to vary in depth from 5 m to 30 m in the wet season (Newman and Dana, 1970) and from 15 m to 25 m in the dry season (Dana, pers. com.). Thus, while conditions at the surface appear stable it is quite probable that rather wide variations in temperature exist at comparatively shallow depth.

While many physical factors are involved in the control of reef development — some evidence indicates that sedimentation and fresh-water dilution are the limiting factors in certain areas — we wish to emphasize the effects of the thermal environment which offers such a wide range of conditions in this region. The following examples of the distribution and development of coral reefs in Panamá and the occurrence and abundance of the associated reef biota are offered as evidence for this view.

II. Distribution and Extent of Development of Reefs

A synoptic view is given in Fig. 1 of our current information on the distribution of incipient structural reefs and true structural reefs in the eastern Pacific region of Panamá. Since many areas have not yet been explored, these records at present represent an incomplete inventory. Already, important new marginal reef formations have been discovered in the Pearl Islands since April, 1971, requiring alteration of the distributional records given by Glynn (in press a).

Considering first reefs in the Gulf of Chiriquí, the largest of these (indicated by solid arrows) have been found at Uva Island in the Contreras group and at the three localities indicated in the Secas Islands. These are all structural reefs, in some cases attaining a buildup of 6 m (Fig. 5). The location of smaller reefs is also indicated; one of these at Parida Island, occurs close to the coast near the Chiriquí River mouth.

Radiocarbon dates of two different coral samples obtained 1 m deep in the reef core at Uva Island gave ages of 210 ± 100 yrs. B.P. and 280 ± 120 yrs. B.P. This is good evidence of very rapid net reef growth, approaching 4000 *B*1). This compares favorably with one of the highest reported net rates of accretion for coral reefs, namely the Yucatán shelf reefs which according to Logan et al. (1969) have formed at the rate of 2000 *B* to 4000 *B*.

The location of coral reefs relative to the seaward or windward sides of islands does not appear to follow any clear pattern. While most of our field work has been confined to the off-shore islands in the Gulf of Chiriquí, it is thought likely that continuing exploration along the isthmian coast will disclose true onshore structural reef formations. A brief reconnaissance of one segment of the coastline near Bahía Honda (81° 32′ W; 7° 45′ N) revealed rich coral communities with *Millepora, Acanthaster* and other elements typical of the island faunas.

In the Pearl Islands, Gulf of Panamá, incipient structural reefs, *i.e.* raised approximately 2 m off the bottom, are known from the various areas indicated

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1) The Bubnoff unit **B**, proposed as a standard measure of geological time-distance rates by Fischer (1969), is defined as 1 μ/yr.

in Fig. 1. These reef formations are largely located on the north-eastern sides of islands. Although few temperature data are presently available from the shallow shelf areas of the Pearl Islands, we wish to hypothesize that this apparent directional distribution pattern may be due to a greater influence of upwelling along the western shores of the islands. Smayda (1966) and Forsbergh (1969) may be consulted for information on proposed upwelling circulation systems in the Gulf. Sund (in Forsbergh, *op. cit.*) concluded that "Cool water apparently enters the Gulf along and above a trough in the western side, about half-way between the western coast of Panamá and the Archipiélago de las Perlas."

Furthermore, it is seen that the coral reefs present in the warmer waters of the Gulf of Chiriquí attain a greater topographic relief. While no marked difference in the depth penetration of coral communities is evident, there does exist an additional important difference in the species composition of the reefs in the two regions. For example, large massive colonies of *Pavona clivosa* are common on reefs in the Gulf of Chiriquí but occur only rarely in the Pearl Islands. *Pavona ponderosa* and *Millepora,* while common in the Gulf of Chiriquí, are not yet known from the Gulf of Panamá. Also, individual colonies of *Pavona clivosa* and *Porites paschalensis* may attain enormous dimensions in the Gulf of Chiriquí, the latter reaching 4 m—5 m in height; these species do not exceed 2 m—3 m in height at the Pearl Islands.

III. Distribution of Associated Coral Reef Biota

In addition to the evident regional differences which exist in the hermatypic coelenterate fauna, there is ample evidence to suggest that the two areas also show differences in the occurrence of other taxonomic groups. *Acanthaster planci* L. occurs abundantly in the Gulf of Chiriquí. A population of at least 29 individuals was observed on the Uva Island reef, slightly greater than 1 ha. in area. *Acanthaster* has not been observed in the Gulf of Panamá. The gnathophyllid decapod crustacean *Hymenocera,* which we assume to be conspecific with the Indo-Pacific form *H. picta* Dana, has also been found at two localities in the Gulf of Chiriquí. It was known only from the latter area until a single specimen was collected at Pedro González Island, Pearl Islands, in July, 1971.

Rosenblatt et al. (in press) have called attention to the significant Indo-Pacific element (24% of 128 reef associated species) in the ichthyofauna of the Gulf of Chiriquí. All of these fishes are associated with reef corals and their presence and abundance in this region is attributed to this fact. A comparison of the fish faunas of the Gulfs of Panamá and Chiriquí would show the latter to dominate clearly both in the number of Indo-Pacific species and in their proportion of the ichthyofauna. Consequently, it is believed that the biotic character of these two contrasting marine environments, *i. e.* species composition, population sizes, growth rates, etc., will be found to differ on a quantitative scale as do the hydrographic conditions.

It would be premature to conclude that the coral formations of the Gulf of Chiriquí represent an isolated example of true reef development within the eastern Pacific region. Brief reference to rich coral communities and coral sand beach deposits off the western coasts of México (Palmer, 1928; Greenfield et al., 1970) and Colombia (Murphy, 1939, p. 32) invite further critical study.

F. Coral Predators

Even though the significant role of coral predators has been brought into better perspective in recent years (BAKUS, 1969; ROBERTSON, 1970), their influence as ecologic and geologic agents modifying reef structure and growth has not been given due consideration by many current authors. Our experience off the coast of Panamá indicates clearly that a variety of predators are consuming large quantities of nearly all the principal hermatypic reef elements (Fig. 10). The effects of predation by fishes are particularly evident (Figs. 11 and 12). Consideration will be given here to the animals presently known to consume corals and hydrocorals in the eastern Pacific region and to estimates of their abundances and feeding rates. In the next section a synthesis of these data will be examined with respect to a coral community in the Pearl Islands in order to provide a measure of reef attrition through these activities.

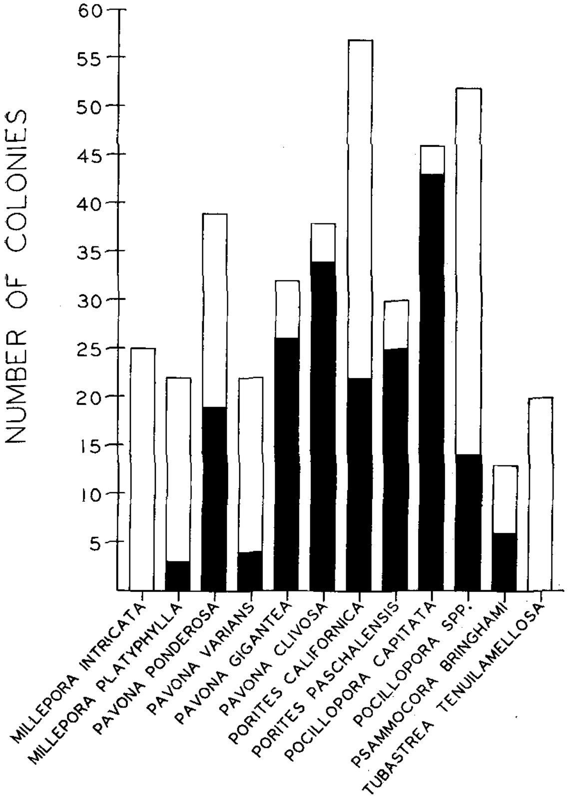

Fig. 10. Scleractinian coral and hydrocoral species showing evidence of destruction by predators (darkened sections of bars). Bulk of data from Gulf of Chiriquí, March 30—April 3, 1970.

I. Species

1. Pisces *(Teleostei)*

Several species of fishes destroy living corals either directly by feeding on the corallum or incidentally by breaking into coral colonies in order to expose animals dwelling within. The following observations indicate that these feeding activities are important in bioerosive processes, in the retardation of coral growth and to the invasion of corals by alien growth through damaged surfaces.

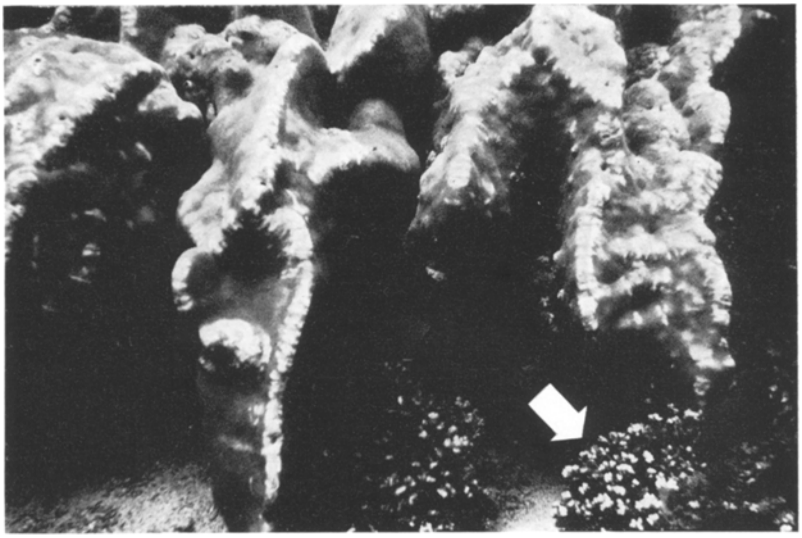

Fig. 11. Underwater view of a large colony of *Pavona clivosa* showing 2 to 3 cm long nicks concentrated along the edges of the plate-like extensions, the result presumably of scarid predators. Below (arrow) *Pocillopora* also shows evidence of cropping by *Arothron*. Isla Uva, Contreras Islands, 5 M depth, April 29, 1970.

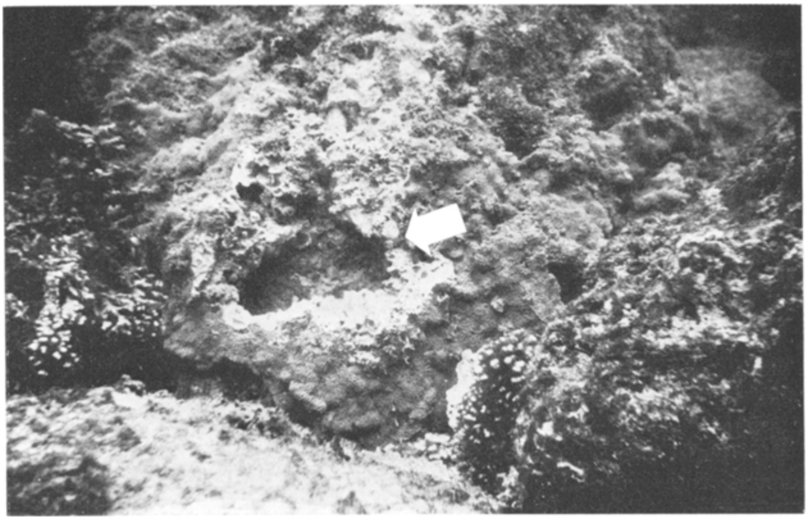

Fig. 12. Underwater view of a large colony of *Pavona varians* showing destruction of a central 800 cm^2 area (arrow) by the triggerfish *Balistes polylepis*. Taboga Island, 4 M depth, May 13, 1970.

Scaridae. — Coral species scraped most commonly by scarids are *Porites paschalensis, P. panamensis* and *Pavona clivosa.* The preferred feeding sites are the exposed edges and prominences of *Porites* and the rims of plate-like outgrowths of *Pavona clivosa* (Fig. 11). The feeding marks produced are most often nicks 1 cm to 3 cm in length. It appears that the normal feeding behavior of scarids is easily disturbed because feeding was observed on only a single occasion. Several individuals in a school of approximately 60 young of *Scarus ghobban* FORSSKÅL were observed biting into a living colony of *Porites panamensis* at the Pearl Islands. Feeding ceased and the school moved away as soon as the fish became aware of the observer (GLYNN). This single observation is apparently the only one known in this region (ROSENBLATT & HOBSON, 1969) although BAKUS (1969) did draw attention to the prevalence of scarid feeding marks on corals in Panamá. In addition, a large collection of corals from the Galápagos Islands (courtesy of V. & T. WILLIAMS) disclosed numerous nicks in massive species of *Pavona* and *Porites,* indicating a similar feeding behavior in another eastern Pacific locality. It is also possible that other species of the six eastern Pacific scarids feed on corals. The only other evidence now available, however, is the large fragment of *Pocillopora* found among the gut contents of *Scarus perrico* JORDAN & GILBERT (Table 2).

Evidence that serious damage to corals may result was seen in several colonies of *Pavona* where lesions, presumably produced by scarids, were invaded by a variety of algae. The dominant alga, a green siphonaceous plant of creeping and penetraing filaments, is probably a species of *Derbesia.* This plant and other species of algae were attached deep in the skeleton and showed signs of lateral spreading over the coral surface.

Tetraodontidae. — *Arothron hispidus* (LINNAEUS) and *Arothron meleagris* (LACÉPÈDE) ²) have been observed on several occasions to bite off the branch tips of *Pocillopora.* An apparent preference for the apical branches often results in a uniform peripheral cropping of the coral. Both species are also known to feed on corals in the Marshall Islands (HIATT & STRASBURG, 1960). The diet of *A. hispidus* appears to be quite varied with sponges comprising a major component (Table 2). Five species of scleractinian corals have been found in the gut contents of *A. meleagris,* equal to a combined total of 91.3% of the mass of food items ingested (Fig. 13). Field observations and gut analyses indicate that *Pocillopora* is the preferred natural diet of this fish.

Balistidae. — *Balistes polylepis* STEINDACHNER was observed on several occasions to bite the protruding surfaces of *Porites paschalensis* and *Pavona varians* in order to wrench loose large sections (3 cm to 8 cm lengths) of the coral. The fish then searches through the fragments and parent colony for bivalves, gastropods, crustaceans and other exposed forms. The coral is not normally ingested. Numerous large colonies of *Porites paschalensis* and *P. panamensis* were observed to suffer extensive damage. It is relatively easy to associate this damage with the feeding of *B. polylepis* because the unique pattern of dentition is permanently impressed upon the parent corallum as well as the

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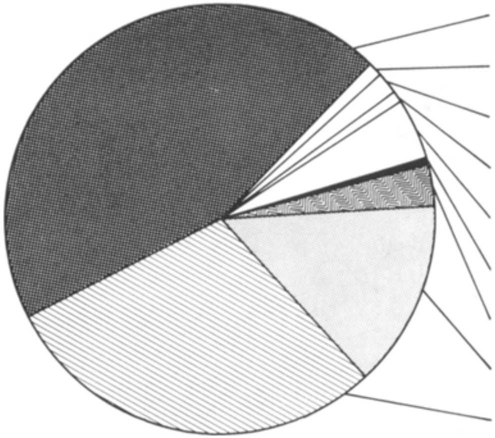
²) J. C. TYLER, J. E. RANDALL and J. E. MCCOSKER (in prep.) have found that *Arothron meleagris* and *A. setosus* (SMITH) are conspecific. The nominal species *A. setosus* is a junior synonym of *A. meleagris* and has been used in the past for the eastern Pacific population.

Table 2. Gut contents of fishes from various localities along the Pacific coast of Panamá.

Species	Number	Size (SL, mm)	Gut contents	Collecting data
Scaridae				
Scarus perrico Jordan & Gilbert	1	394	*Pocillopora* sp., 3.4 cm apical branch in pharyngeal mill.	Taboga Is., 8-V-70
Scarus ghobban Forsskål	14	125—220	Fragments of rock and dead coral; filamentous and crustose red algae; sponges	Secas Islands, 25-III-71
Scarus rubroviolaceus Bleeker	5	110—230	do.	do.
Tetraodontidae				
Arothron meleagris (Lacépède)	14	131—180	See Fig. 13	See Fig. 13
Arothron hispidus (Linnaeus)	5	112—190	Total combined dry mass: sponges, 19.31 gm; hydroids, 0.04 gm; polychaetes, 0.22 gm; bryozoa, < 0.01 gm; crustaceans, 0.13 gm; mollusks, 2.10 gm	Paitilla Pt., Panamá City, 25-VII-66. Hermatypic corals absent from this locality
	1	241	*Pocillopora* sp., 0.25 gm; shell frag., 0.25 gm; gravel, 0.48 gm; sponges, 19.76 gm	Taboga Is., 11-V-70
	1	216	*Pocillopora* sp., 15.05 gm; gravel, 0.03 gm; unident. animal tissue, 0.07 gm; sponges, 3.40 gm	do.
	1	150	Gravel, decapods, gastropods, filamentous algae	Montuosa Is., 18-IX-70
	1	190	*Pocillopora lacera*, 0.74 gm; gastropods, 0.19 gm; bivalves, 0.04 gm; amphineurans, 1.70 gm	Secas Islands, 25-III-71
Balistidae				
Balistes polylepis Steindachner	1	229	*Lithophaga (Leiosolenus) hancocki* Soot-Ryen; fragments of gastropods and crustaceans	Taboga Is., 11-V-70
	1	241	Fragments of *Lithophaga*, gastropods, decapods, and cirripeds	do.
Sufflamen verres (Gilbert&Starks)	1	260	Fragments of bivalves and crustaceans	Taboga Is., 11-V-70
	4	78—103	*Pocillopora* sp., sponge spicules, gastropods, caridean and brachyuran crustaceans, echinoid spines and test frag.	Contreras Is., 25-VIII-70
	1	200	*Pocillopora lacera* and *Porites californica*, total mass 10.40 gm	do.



FOOD ITEM	%	NO.	GM/INDIVID.
POCILLOPORA LACERA	45.0	6	17.32 (10.98-25.77)
OPHIUROIDEA	1.1	2	1.25 (0.50-2.00)
CALCAREOUS RED ALGAE	1.9	3	1.50 (0.50-2.00)
BIVALVIA	0.9	1	2.13
DIADEMA MEXICANUM	4.8	1	10.98
PAVONA SP.	0.4	1	1.00
PORITES CALIFORNICA	2.9	4	1.74 (0.20-5.20)
POCILLOPORA SPP.	13.8	5	6.36 (0.85-13.77)
POCILLOPORA CAPITATA	29.2	3	22.06 (15.20-25.79)

Fig. 13. Summary of gut content data from *Arothron meleagris*. Calculated from dry weight biomass of 14 individuals, size range (SL) 13.1 cm to 18.0 cm. Thirteen fish from Gulf of Chiriquí, one from Pearl Islands. Collected over period August 25, 1970 — March 27, 1971.

broken fragments. Approximately one-third of the colony of *Pavona varians* shown in Fig. 12 was destroyed by *Balistes.*

The gut contents of *Sufflamen verres* (GILBERT & STARKS) indicate that this balistid also feeds on hermatypic corals (Table 2). One individual contained a total combined mass of 10.40 gm of *Pocillopora lacera* and *Porites californica.* Also, in the field an adult was observed scraping *Pavona gigantea* (Señorita Is., Pearl Islands, July 19, 1971, McCOSKER). Since the remaining scars were very similar to those produced by scarids, it is impossible at this time to distinguish between the relative importance of this balistid and the scarids.

2. Echinodermata *(Asteroidea)*

Acanthaster planci L. has been found to be an important predator of corals and hydrocorals at many localities in the Gulf of Chiriquí (GLYNN, in press a). All species in Table 1, excluding *Millepora* n. sp., *Pavona galapagensis* and *Pocillopora robusta,* have been observed to be eaten by *Acanthaster.* Feeding occurs during the day as well as at night. Preliminary feeding rate data from field measurements indicate that individual adult *Acanthaster* normally destroy around 0.5 m^2 of continuous coral growth monthly.

Pharia pyramidata (GRAY), while commonly associated with reef corals in Panamá, has not yet been seen feeding on corals as reported in the Gulf of California (DANA & WOLFSON, 1970).

3. Mollusca *(Gastropoda)*

Jenneria pustulata (Solander), a monotypic genus in the Superfamily Cypraeacea, was first noted to feed on corals by D'ASARO (1969). He found that *Jenneria* would eat Atlantic reef corals in captivity. *Pocillopora* appears to be the preferred diet where *Jenneria* lives among corals. An indication of this is seen in animals which move from the basal area of colonies onto peripheral live branches to feed. Large populations of *Jenneria* do occur, however, on rock bottoms where corals are absent. *Pocillopora* colonies of 1 kg to 2 kg, completely stripped of their tissues by this predator, are found commonly on reefs and in the coral communities of Panamá. The field evidence implicating the gastropod is excellent since during the daylight hours they remain clustered around the coral being consumed. Feeding is nocturnal, at which time animals have been seen actively grazing on *Pocillopora.* Because large amounts of coral are consumed, regeneration is not possible and the grazed surfaces are quickly invaded by algae and other alien species.

While it is often asserted that the coralliophilid *Quoyula madreporarum* (SOWERBY) feeds upon corals (*e. g.* KEEN, 1958), very little specific information seems to be known about this aspect of its biology. This species is widely distributed and common in the Indo-Pacific, and also attains high population densities on *Pocillopora* in the eastern Pacific. Twenty-nine individuals were observed in a $^1/_8$ m^2 area of *Pocillopora* (Chapera Is., Pearl Islands, Aug. 24, 1971, BIRKELAND). The only evident coral damage, however, is in the area of attachment.

4. Crustacea *(Decapoda)*

Two species of pagurans employ their chelae to scrape the branch tips of *Pocillopora.* These are *Trizopagurus magnificus* (BOUVIER) and *Aniculus elegans* STIMPSON, both distributed along the tropical eastern Pacific coast. All species of *Pocillopora* are attacked and the soft parts and skeletal material are removed. Calicinal grains are ingested along with the coral tissue. Large amounts of uningested fine and coarse-grained sediment also settle to the bottom. Since large quantities of coral can be removed, it is possible that branch tips of *Pocillopora* invaded by algae, commonly observed in the field, result in part from the wounds inflicted by these predators.

Xanthid, alpheid and pontonid symbionts are also found on *Pocillopora.* At least one of the xanthid crabs, *Trapezia ferruginea* LATREILLE, appears to gain some nutriment from the coral (YOUNGBLUTH, unpubl. ms). Like *Trapezia f. ferruginea* at Eniwetok, it is likely that the Panamá species is also a well adapted ectoparasite, feeding on mucus, debris, etc., and thereby effecting little damage to its host (KNUDSEN, 1967).

II. Abundances and Activity Patterns

Observations on the population abundance and diel activities of corallivores will be confined to species which were found to have a significant impact on the coral community at Señora Islet (also known as Señorita Island), Pearl Islands. All sampling data of the population size of the various species are summarized in Table 3.

The population size of *Arothron meleagris* is considered highly reliable because it is based on a census of the entire coral community (see discussion in section F. IV). The 33 fish present at the Señora Islet study site compares favorably

Table 3. Estimates of the population densities of predators of *Pocillopora* in the coral community at Señora Islet, Pearl Islands (March 15 — July 19, 1971). Data from various sampling methods are pooled since no statistically demonstrable difference was evident.

Species	Numerical density estimates No./M² Mean	Median	Range	Total No. in study area	Total No. per ha.	Comments on sampling
Arothron meleagris	0.004	—	—	33	40	Based on census of entire study area
Jenneria pustulata	1.8	1.4	0—6	15,000	18,000	Censused in a. bleached corals, b. visibly undamaged corals and c. 5 M² quadrats
Trizopagurus magnificus	27.5	24.2	13—54	228,000	275,000	Censused in a. peripheral branches of 20 different corals, b. 6 M² quadrats
Aniculus elegans	0.02	0.01	0—0.06	170	200	Censused in a. peripheral branches of corals in 10 different 100 M² areas, b. 6 M² quadrats

with the numbers observed in the Gulf of Chiriquí. However, *A. meleagris* does not appear to be common in some areas of the Pearl Islands with abundant coral growth.

Jenneria demonstrated a mean abundance of 1.8 individuals per m^2 with an estimated total of 15,000 in the study area. The secretive habits of this species during the day require careful quantitative sampling to account for all animals present. *Jenneria* feeds actively at night, often moving out among the peripheral branches of *Pocillopora.* Broken *Jenneria* shells were found in the sediments, suggesting that the species is subject to some degree of predation.

Trizopagurus was by far the most abundant coral predator with an estimated mean density of 27.5 individuals per m^2 and a total of 228,000 in the study area. This species is inactive during the day and feeds at night. Large individuals usually nestle among the branch tips of corals during the day, but the smaller crabs often descend toward the basal branches.

Aniculus is a much less abundant paguran. An estimate of the population density in the study area amounted to only 170 individuals. Like *Trizopagurus,* this species also feeds at night and is usually quiescent during the light hours.

III. Feeding Rates

All feeding rate data were obtained from animals maintained in outdoor aquaria supplied with continuously flowing sea water or filtered sea water replenished frequently and aerated. Field observations indicate that the feeding behavior of the captive animals was not significantly altered. That reef corals and their associated biota survive indefinitely in the aquaria lend confidence to the validity of the following findings. The experimental animals were selected to represent as close as possible the size ranges observed in the wild.

Four adult *Arothron meleagris* supplied with an excess of whole living *Pocillopora* colonies ingested a mean dry mass (both tissue and skeleton) of 10.13 gm/day (Table 4). A slightly greater amount, 12.88 gm, was broken away from the

Table 4. Rate of coral destruction and sediment production by *Arothron meleagris* feeding on *Pocillopora.* Observed April 17 — July 23, 1971.

Individ. No.	Color phase	Size (cm) standard length	Mean live coral mass destroyed (gm dry wt/day [1], [2])		Combined mean sediment production (gm dry wt/day)	No. Obs.
			Ingested [3]	Not ingested		
1	yellow	20	11.87 ± 4.41	19.82 ± 9.6	28.36	17
2	yellow	23	5.60 ± 4.28	14.19 ± 11.70	16.81	11
3	black spotted	25	10.09 ± 3.38	8.27 ± 5.57	16.52	12
4	black spotted	24	12.96 ± 2.23	9.23 ± 10.40	19.97	8
Mean of all observations			10.13	12.88	20.42	

[1]) Coral mass includes entire living branch weight, i. e. superficial polyp zone plus inner calicinal core.

[2]) Confidence limits at 0.95 level.

[3]) Ingestion = mass coral defecated/% unassimilated coral.

parent colony but not ingested. Assimilation of tissue was determined from the difference in mass between equal numbers of digested and undigested coral grains resulting from the feeding activities of the fish. Parity of grain size was achieved by screening the coral fragments through standard sieve mesh ranging from 1.19 mm to 4.00 mm. This method indicates that *Arothron* assimilates 10.5% of the mass of ingested coral.

The mean sediment production resulting from defecation and the skeletal mass of uningested fragments amounted to 20.42 gm/day. This should be viewed as a maximum figure since some of the larger dislodged branches may continue to live.

No obvious preference for the different species of *Pocillopora* was evident. Also, the yellow and black spotted color phases appeared to consume equal amounts of coral.

An estimate of the grazing rate of *Jenneria* was determined from the time required to destroy half of a coral branch of known mass. Because the extent of coral destruction was estimated visually, these data are not free from subjective error. The actual mass differences in corals before and after feeding by *Jenneria* were obtained to provide information on the amount of soft parts consumed. Procedure involved gentle blotting with absorbant paper towel over a standard period of drying (not exceeding 10 minutes). Controls indicated that this treatment did not increase the susceptibility of corals to predation. Only corals eaten rapidly, *i. e.* within 3 to 4 days, were utilized for this purpose so as to avoid any mass gain from fouling algal growths, etc.

Observations on nine test animals showed that *Jenneria* destroys a mean dry mass (both tissue and skeleton) of 0.80 gm/day (Table 5). The organic matter consumed amounted to 3.7% of the coral mass. Repeated treatment of portions of grazed branches with hot (60° C) 20% H_2O_2 showed an inconsequential loss in mass, indicating an efficient feeding mechanism. The apparent lower tissue consumption by *Jenneria,* relative to the total coral mass, is believed due to a

Table 5. Rate of coral destruction and sediment production by *Jenneria pustulata* feeding on *Pocillopora.* Observed May 19 — July 8, 1971.

Individ. No.	Size (mm) l. x w.	Mass of coral destroyed (gm dry wt/day) [1] Mean	Range	Mean sediment production (gm dry wt/day)	No. Obs.
1	21 × 13	0.66	0.61—0.70	0.64	3
2	21 × 12	0.69	—	0.66	1
3	23 × 14	0.51	—	0.49	1
4	22 × 13	0.44	—	0.42	1
5	22 × 14	0.78	0.76—0.80	0.75	2
6	21 × 14	0.65	0.58—0.73	0.63	2
7	22 × 14	0.16	—	0.15	1
8	23 × 14	1.02	1.02—1.03	0.98	2
9	24 × 14	2.26	0.80—3.24	2.18	4
Mean of all observations		0.80		0.77	

[1]) Coral mass includes entire living branch weight, i. e. superficial polyp zone plus inner calicinal core.

lower surface area to mass ratio of the branches eaten. Whereas *Arothron* feeds preferentially on the branch tips, *Jenneria* grazes all branch surfaces.

No preference was noted for any one particular species of *Pocillopora*.

No decline in feeding rate was detected in known individuals observed for periods of up to 30 days. For example, one animal grazed surface areas of nearly equal size for 21 days, resulting in the total destruction of a 13.44 gm branch.

The techniques employed to measure the rates of feeding and coral destruction in the two paguran species were nearly identical. Feeding was confined to closed system, outdoor aquaria provided with filtered sea water and constant aeration. The fecal matter and uningested coral fragments were collected every 3 days from *Trizopagurus* and daily from *Aniculus*. Sediment production from other causes, *e.g.* endolithic boring organisms, was ruled out by a series of controls in the absence of predators. The rate of destruction of live coral was calculated from the combined mass of both fractions. The procedure involved repeated treatment with hot (60° C) 20% H_2O_2 to determine the inorganic sediment mass. Uningested coral fragments, collected daily, were treated similarly to determine the loss in mass due to the removal of organic matter; this mass was found to equal 7.9% of the ingested fragments for *Trizopagurus* and 7.3% for *Aniculus*. Because of the difficulty in distinguishing between all ingested and uningested materials from the total removed, it is not possible to determine accurately the quantity of organic matter actually consumed.

The mean mass of coral (both tissue and skeleton) destroyed daily by *Trizopagurus* was found to equal 10.3 mg; 9.6 mg of this represents inorganic skeletal material (Table 6). To the extent that feces and uningested material could be recognized, it is estimated that approximately 50% of the coral mass destroyed was ingested.

Table 6. Rate of coral destruction and sediment production by *Trizopagurus magnificus* feeding on *Pocillopora*. Observed May 15 — July 8, 1971.

Individ. No.	Size (mm) carapace width	Mean mass of coral destroyed (mg dry wt./day)	Sediment production (mg dry wt./day) Mean	Range	No. Obs.
1	5.5	1.6	1.5	0.6— 2.2	3
2	6.9	3.1	2.9	0.8— 5.2	5
3	7.3	3.4	3.2	0.7— 5.8	4
4	8.0	31.8	29.5	16.3—49.4	4
5	7.4	5.8	5.4	1.3—11.1	4
6	6.1	16.0	14.8	2.3—29.7	4
Mean of all observations		10.3	9.6		

The data on *Aniculus* are far more tenuous; however, the two largest individuals examined are in the size range of animals censused in the study area (Table 7). The mean mass of coral destroyed by large *Aniculus* was 1.24 gm dry wt./day; mean sediment production was equal to 1.16 gm dry wt./day. Coral destruction by one small individual was considerably less, equal to 0.08 gm dry wt./day. Ingestion of live coral is estimated to approximate 50% of the coral mass destroyed.

Table 7. Rate of coral destruction and sediment production by *Aniculus elegans* feeding on *Pocillopora*. Observed June 27 — August 23, 1971.

Individ. No.	Size (mm) carapace width	Mean mass of coral destroyed (gm dry wt./day)	Sediment production (gm dry wt./day)		No. Obs.
			Mean	Range	
1	18	0.94	0.88	0.07—4.76	8
2	14	1.54	1.44	0.36—2.87	6
3	8	0.08	0.07	0—0.24	18
Mean of 1 & 2 only		1.24	1.16		

On several occasions the pagurans were offered *Pocillopora* whose dead basal branches were encrusted with coralline algae, sponges, tunicates, etc. They frequently scraped this material and presumably ingested a certain amount of it. The main food preferred, however, was the living branch tips of coral. All of the data presented above refer only to this component of the diet.

Compared with *Arothron* and *Jenneria* the pagurans displayed considerable variability in feeding rate, within as well as between individuals. No explanation for this can be offered.

IV. Effects of Predation on a Coral Community

An analysis of the effects of coral predators was performed on Señora Islet for the following reasons: a. it is of convenient size, 8300 m^2 in area; b. *Pocillopora* is the dominant coral in the community; c. the island is relatively isolated from adjacent coral communities, thus limiting population movements; d. the location of the island is easily accessible.

Coral populations were censused by diving teams employing SCUBA. Transects were located normal to the shore and spaced at 10 m intervals. The per cent coral coverage within 1 m^2 quadrat samples was estimated visually. This information was grouped into four equal classes on a 100% scale. For example, continuous coral growth comparable to that in Fig. 2 or colonies growing in close contact as in Fig. 3, were assigned a coverage value of 75—100%. Further quantitative sampling allowed translation of areal coverage data into coral biomass units. This involved the collection of $^1/_4$ m^2 samples of coral from the four coverage classes. The mass measurements obtained were of the living branches only which were dried (max. temp. 105° C) to a constant weight. The organic matter content was found by pulverizing whole coral colonies and treating samples repeatedly with hot (60° C) 20% H_2O_2. The difference in mass before and after treatment was assumed equal to the organic matter removed through oxidation.

From the above procedure it is concluded that the *Pocillopora* community at Señora Islet is characterized mainly by sparse coral growth. About 64% of the bottom area has a coverage of less than 25%. Only about 10% of the coral community contains framework construction. Estimates of the standing crop biomass indicate that this is probably in the neighborhood of 105 metric tons per ha. with an organic matter content of 8.8 metric tons. The results of this analysis are summarized in Fig. 14.

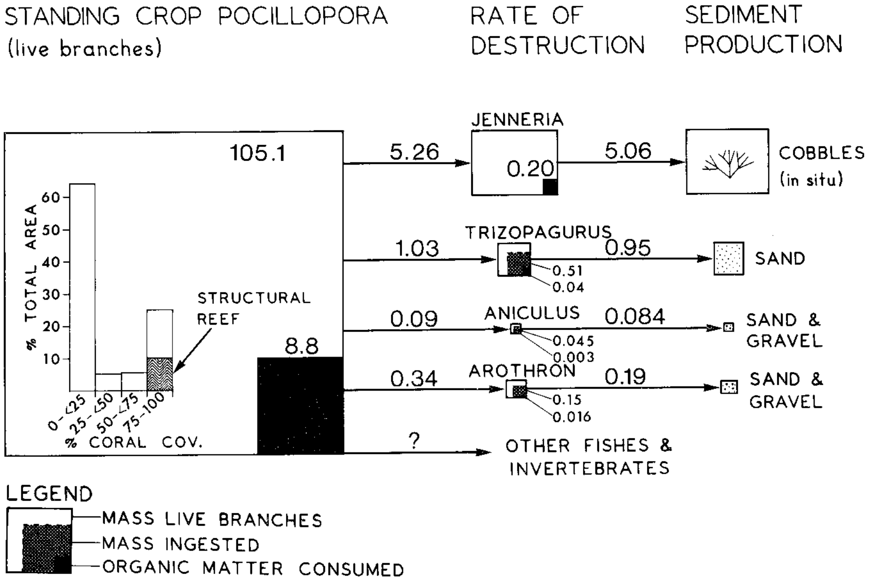


Fig. 14. Preliminary block diagram of the rates of destruction, feeding and sediment production by four predators of *Pocillopora* spp. in the coral community of Isleta Señora, Pearl Islands. Units are in dry mass of coral (metric tons) per ha. per annum. Block areas are proportionately equivalent. The frequency distribution of per cent coral coverage is included in the standing crop compartment.

Relating now the numerical density and feeding rate measurements of predators to this food resource, the following annual rates of coral destruction and sediment production emerge (Fig. 14). The combined coral destruction effected by the four predators herein examined amounted to 6.72 tons/annum, with *Jenneria* responsible for nearly 79% of the damage. Thus, the chief initial impact results in the partial or complete death of colonies which often remain intact and are subsequently overgrown by largely non-scleractinian species. Later invasion by bioerosional agents such as boring sponges, mollusks, etc. will lead to further alterations. This magnitude of coral destruction amounts to 6.4% of the standing crop of *Pocillopora;* the consumption and incidental destruction of organic matter involves a loss of 3.6%. The generation of sediments amounts to over 6 tons/ha./yr. with abundant fractions being produced in the sand *(Trizopagurus,* 1 ϕ), granule (*Aniculus,* —1 to —2 ϕ) and pebble (*Arothron,* —3 ϕ) size grades (Fig. 15).

As indicated in Fig. 14, effects due to other species are either known or suspected but cannot be accurately quantified at present. Included in this category are large fish which occasionally move *Pocillopora* while feeding, such as the carangid *Gnathanodon speciosus* (Forskål), or others like *Balistes polylepis* that uproot corals during their nest-building activities. The more direct effects through feeding of other fishes, *Quoyula,* juvenile *Aniculus,* etc. are unknown and will require further study.

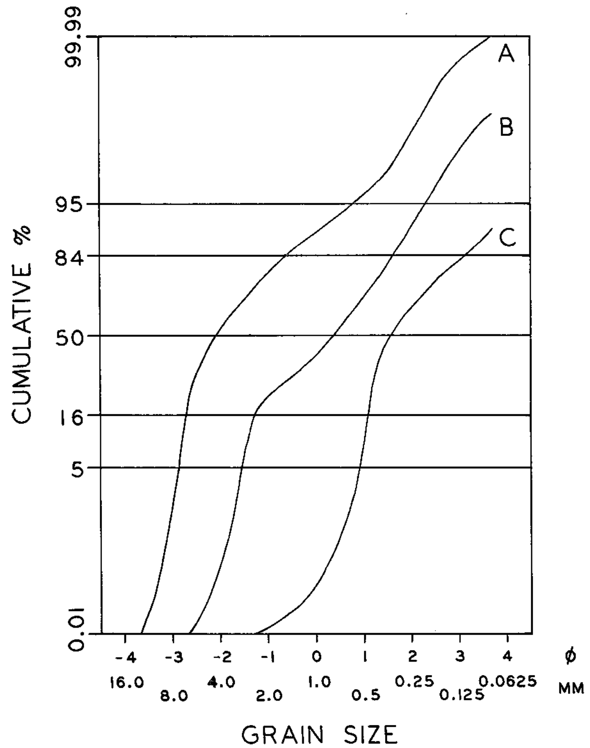


Fig. 15. Grain size distributions of sediments produced by *Arothron meleagris* (A), *Aniculus elegans* (B) and *Trizopagurus magnificus* (C). The sediments are from fecal remains (A), and fecal remains plus broken uningested coral fragments (B & C).

From the standpoint of community growth dynamics, it is necessary to relate the rates of attrition and accretion on an equal time basis. The standing crop of coral is the result of cumulative skeletal growth spanning several years. In this context it is of interest to know to what extent predators modify the annual growth of reef corals and thereby influence the progression of coral communities.

Unfortunately, growth rate data for corals are not yet available from the eastern Pacific region. For present purposes, EDMONDSON's (1929) growth measurements on *Pocillopora* in Hawaii — the average annual thermal conditions are quite similar to those in the Gulf of Panamá (H. O. Pub., 1954; RENNER, 1963) — can be used as a fair approximation of *Pocillopora* growth in the Pearl Islands. Three species of *Pocillopora* were shown to have a mean annual growth increment (vertical branches) of approximately 15 mm. In order to estimate the annual accrual of *Pocillopora* from this value, the peripheral branch tips of 15 mm length were removed and compared with the total standing crop of all live corals in samples of $^1/_4$ m^2 area. This procedure indicates that the mean annual growth is probably in the neighborhood of 19.5% of the standing crop biomass.

Further calculation shows that a growth increment of 19.5% would result in the annual accrual of 20.5 tons of *Pocillopora* (19.5% of a standing crop of 105.1

tons). Thus, it follows that attrition due to predation, equal to 6.7 tons of coral per annum, could lead to the destruction of nearly one-third of the annual growth (6.7/20.5 × 100). This we believe is convincing evidence of the significant role of corallivores as geologic agents affecting coral growth and in turn the progression of structural reef formations.

V. Discussion

Although careful attention was given to several of the major sources of error possible in this kind of analysis, it is important to underscore areas of uncertainty that will require further study and verification. The validity of the estimated population abundances should be examined quantitatively in other coral communites as well as seasonally. The search for new bioerosive agents must continue along with the development of techniques to evaluate their effects.

Growth rate data are urgently needed to assess with precision the impact of corallivores on the annual accretion of coral communities. It would be desirable to measure coral growth simultaneously in the Gulf of Panamá and the Gulf of Chiriquí to test further the hypothesis that a high thermal regime in the latter region permits more vigorous reef growth.

All field studies lent confidence to the conclusions reached regarding feeding behavior, food preferences and rates of consumption among animals observed in captivity. However, mobility may be an important factor in limiting the feeding range of *Jenneria*. It is conceivable that *Jenneria* remains in circumscribed areas and switches to another food resource after the depletion of coral. This possibility will require attention for it could lead to an over-estimate of the influence of this species as a predator of living coral.

In addition, most observations were made after the upwelling season[3]), which raises the question of the effects of a sudden temperature change on the feeding activities. If such an influence is found, it will also be necessary to relate this to the effects of temperature on reef coral growth.

Considering the fate of sediments produced by corallivores, it is seen that these will lead to deposition along both vertical and horizontal axes. In situ deposition of cobbles are produced by *Jenneria;* pagurans and fishes produce finer sediment which settles through the coral lattice to accumulate on the bottom. All corallivores were also observed to prey on isolated corals located away from framework structures. The subsequent transport and alteration of sediments from these sources are expected to occur relatively more rapidly. Also contributing to the lateral spreading of reefs are vagile predators which defecate away from the areas in which they feed.

The larger uningested fragments of *Pocillopora* and *Porites* often continue to live after separation from the parent colonies. In *Arothron meleagris,* it was found that broken, uningested *Pocillopora* amounted to 56% of the total coral destroyed. While it is possible that the amount of incidental destruction is less in the field, disturbances of this nature must play some role in the dispersal and lateral progression of reefs.

If predator-induced erosion can amount to one-third of the annual coral growth,

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[3]) Our data, mostly taken during 1970 and 1971, are representative of a mild upwelling season. Strong upwelling which results in cold water transport over wide areas of the Gulf of Panamá is an exceptional but re-occurring condition.

it is appreciated that large quantities of sediment can accumulate from this cause alone. Therefore, this example of the significant effects of bioerosion indicates that the genesis of clastic deposits can take place in reef environments outside the influence of high energy physical processes, such as strong wave action, tropical storms, etc.

While several sources can be cited giving evidence of the important role of fishes as sedimentary agents, not once have the quantities of live coral consumed been identified, though this component is usually conceded to be substantial. Cloud (1959) estimated that reef fishes in Saipan produce between 4.25 and 6.18 metric tons/ha./yr. Bermudian reef fishes were found to ingest and redeposit 2.3 metric tons of calcareous materials on a ha./yr. basis. In terms of sediment production, the higher rate reported for Saipan is close to the eastern Pacific rate of 6.29 metric tons/ha./yr. Since the data in the present study refer only to living coral, it appears that this food resource is utilized more in Panamá.

From the above it is clear that too few data are available to allow a comparison of the degree of utilization of corals on a regional basis. An analysis of the food habits of fishes on an east African reef indicates that this trophic pathway involves 20% of the species (Talbot, 1965). In Panamá only 5% (6 of 128 species) of the reef fishes are known to consume live coral, indicating that this group may have a greater impact on reef corals in some other regions. Moreover, the widely accepted view that Pacific (Marshall Islands) scarids prey more intensively on corals than in the West Indies will require tempering in the light of more recent evidence (Glynn, in press b; Gygi, 1969).

There is no reason to suspect that the effects of corallivores in the Gulf of Chiriquí are any less than that observed at Señora Islet in the Pearl Islands. In fact, there are excellent indications that coral destruction in certain areas is even more widespread due to the presence of *Acanthaster*. For example, at the Uva Island reef, *Acanthaster* has remained stable at a population density of 22 individuals/ha. over a one year period (March, 1970—1971). Relating the observed mean feeding rate, approximately 0.5 m^2 of continuous coral growth per individual per month, to the standing crop of reef corals indicates that this predator is destroying between 5% and 10% of the reef standing crop every year. This is in the same range of influence as *Jenneria*, which was found to consume 5% of the corals at Señora Islet.

Goreau (1964) first suggested the possibility that *Acanthaster* may be responsible for the complete destruction of coral reefs. Later Chesher (1969), Endean (1969) and others gave direct evidence for this on some reefs in the western Pacific Ocean. While it is evident that coral destruction by *Acanthaster* in Panamá is very significant, no evidence for total reef devastation has been found. To the contrary, radiometric dating of the Uva Island reef disclosed one of the highest rates of accretion known (see p. 500). This poses the intriguing question: Can accelerated reef growth and significant coral destruction occur contemporaneously?

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