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CORAL REEFS OF GORGONA ISLAND, COLOMBIA, WITH SPECIAL REFERENCE TO CORALLIVORES AND THEIR INFLUENCE ON COMMUNITY STRUCTURE AND REEF DEVELOPMENT

By

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RESUMEN

Este estudio presenta un breve resumen de la estructura y distribución de los arrecifes coralinos de la Isla de Gorgona. Se investigaron los organismos coralívoros, comparándolos con los de otras localidades del Pacífico Americano; de esta forma se establece un criterio, para conocer las diferencias regionales y las interacciones bióticas sobre las diferentes comunidades coralinas.

La Isla de Gorgona se localiza hacia el extremo sur de la provincia de Panamá (Panamá Bight), distante unos 30 km de la franja costera aluvial, lo que la aleja considerablemente del efecto directo de afloramientos y derrames de agua dulce, provenientes de los ríos costeros.

El equinodermo asteroideo, *Acanthaster,* que es uno de los coralívoros que más estragos causa en las comunidades coralinas del Pacífico, no se ha detectado en la Isla de Gorgona. La ausencia de *Acanthaster,* parece estar determinada por un frente de baja salinidad que se forma hacia la región norte del Pacífico colombiano y que seguramente impide, con sus condiciones desfavorables la migración de las formas larvales de esta estrella. Las formaciones coralinas de Gorgona, corresponden a arrecifes verdaderos, los cuales presentan un gran desarrollo en la franja costera de Sotavento (costa oriental), aunque en la franja costera de Barlovento (occidental), también aparecen formaciones. El arrecife de La Azufrada es el más extenso y mide aproximadamente 1000 m de largo, por 150 m de ancho y unos 8 m de espesor. En este arrecife, las masas de corales vivos se presentan hasta unos 15 m de profundidad. La cresta y demás zonas altas del arrecife están dominadas por corales del género *Pocillopora* mientras que los flancos y hacia el borde expuesto al mar, se presentan otras formas, generalmente masivas.

Entre los organismos coralívoros de Gorgona, hay que destacar a los "tamboreros" y a un gasterópodo de la familia Ovulidae. De los coralívoros conocidos en otros lugares, tenemos que notar en el bajo número de cangrejos ermitaños coralívoros, lo mismo que del erizo *Eucidaris,* el cual se encontró en la isla, pero no comiendo corales. Los daños causados por un pez de la familia Pomacentridae en los corales masivos son considerables y hacen que sobre las zonas afectadas se fijen algas bentónicas, las cuales afectan considerablemente el desarrollo de los corales, especialmente hacia las zonas poco profundas del arrecife.

Al comparar la estructura arrecifal de Gorgona, con arrecifes de Panamá afectados por *Acanthaster,* se encontró que en zonas libres de esta estrella, las colonias coralinas diferentes de *Pocillopora,* como *Porites, Pavona, Gardineroseris* y *Psammocora* (las preferidas por este coralívoro), son mucho más abundantes.

SUMMARY

This study offers an overview of the distribution and structure of coral reefs and coral communities at Gorgona Island, off the Pacific coast of Colombia. Biotic interactions, mainly the effects of corallivores, are examined and compared with coral communities elsewhere in the eastern Pacific in order to provide a basis for understanding regional differences in community structure.

Located at the south end of the Panamá Bight and ca. 30 km offshore, Gorgona is largely removed from the influence of upwelling and freshwater dilution. The key corallivore *Acanthaster,* which is widely distributed in the tropical eastern Pacific, is absent from Gorgona, probably a result of unfavorable physical conditions (low temperatures and low salinites) for larval development in the Panamá Bight area. True fringing coral reefs are present at Gorgona and are best developed on the eastern or leeward side, but they also occur in one area on the western and exposed side of the island. The La Azufrada reef, the largest of the fringing reefs, was about 1 km long and 150 m wide, had a minimum thickness of 8 m and supported live corals to a depth of 15 m. Pocilloporid corals predominated on the reef crest and upper to mid forereef slope, and massive and small species increased in relative abundance in the deep forereef and sand plain zones.

A corallivorous pufferfish and ovulid gastropod were abundant, but other known corallivores (e. g., *Acanthaster,* hermit crabs and *Eucidaris*) were either absent, uncommon or not feeding on live coral. Damage inflicted on live massive colonies by a damselfish, in order to "farm" algae, could play an important role in altering the relative abundances of corals in shallow reef zones. A comparison of coral reefs at Gorgona and Panamá, in areas with and without *Acanthaster,* show that nonpocilloporid corals, which are preferred prey items, have a higher relative abundance on reefs where the predatory sea star is absent.

INTRODUCTION

Information on the nature of coral reef communities at Gorgona Island is of interest because this area lies near the southernmost limit of coral reef development in the eastern Pacific region. Gorgona's geographic position (Fig. 1), at the south end of the Panamá Bight, places the island (including Gorgonilla Islet and associated rocks) beyond the influence of the strong upwelling system in the Gulf of Panamá (ABBOTT, 1966; FORSBERGH, 1969; GLYNN, 1974). Gorgona Island is also far enough north and east to avoid the cool coastal Perú Current system which moves away (in a westerly direction) from continental South América in the vicinity of Cabo Blanco (ca. 4° S), Perú Thus, although the Gorgona area lies within the tropical Panamic Province, it is to some extent bounded north and south by marginally tropical conditions.

While the coral communities of Gorgona are diverse and relatively mature compared with other eastern Pacific areas (PRAHL *et al.,* 1979), some species present elsewhere are notably absent from Gorgona (GLYNN *et al.,* 7972). One of these, a key corallivore, is the crown-of-thorns sea star *Acanthaster planci* (Linnaeus). This study focuses on the ecology

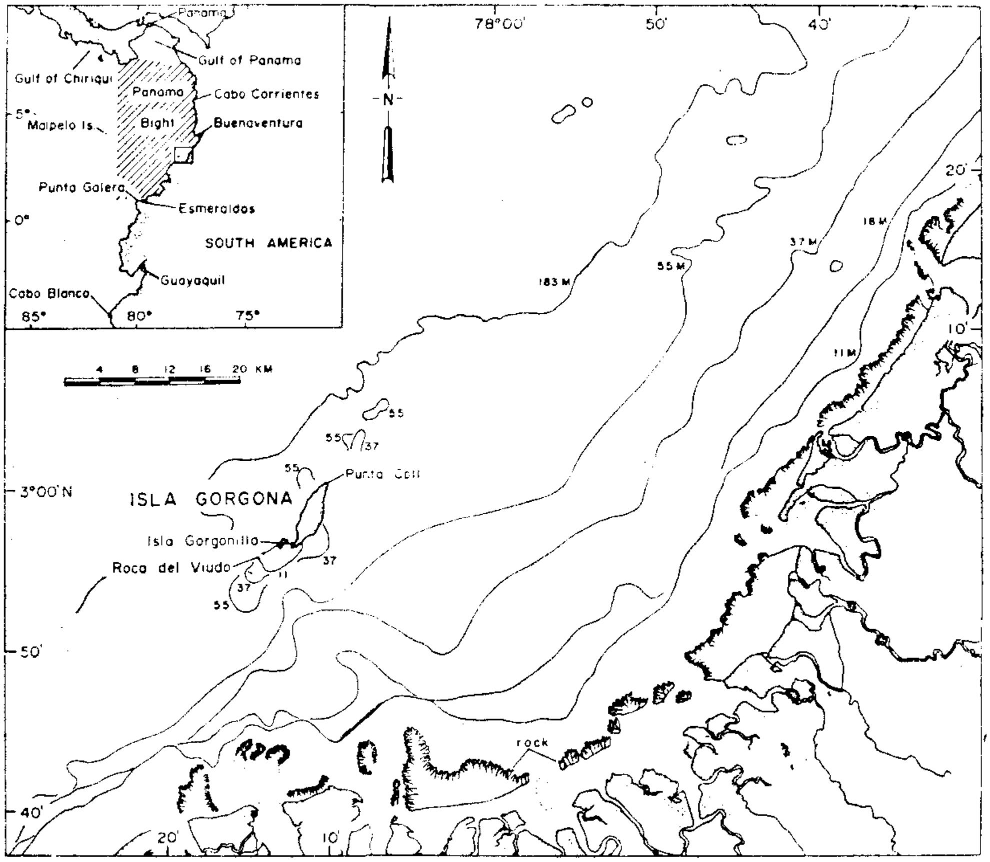

Figure 1. Location of Gorgona Island off the SW Colombian coast and in relation to the Panamá Bight area. From chart number 22050, Cabo Corrientes to Isla Gorgona, 2nd ed., April 7, 1979, Defense Mapping Agency, Washington, D.C.

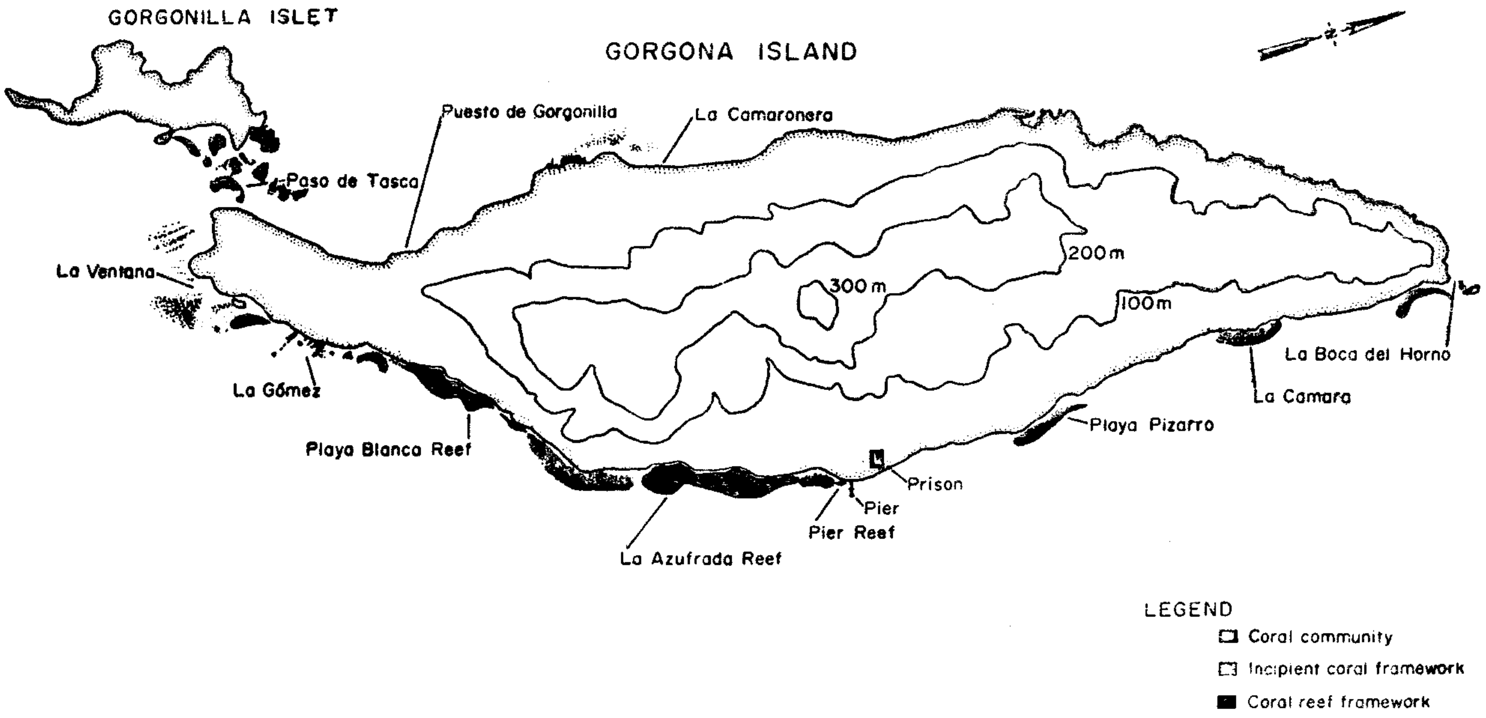

Figure 2. Distribution of coral reefs at Gorgona Island. Base map courtesy Instituto Geográfico "Agustín Codazzi", Bogotá (1959), scale 1: 7,700. El Viudo and some rocks and shoals present on the base map but not confirmed in our survey were omitted. Coral communities illustrated in Prahl et al. (1979), are also shown here in relation to coral framework development.

of the Gorgona coral formations, especially that aspect dealing with the effects of corallivores on coral community structure and reef growth. The field work was carried out under the auspices of the Sula III Expedition which permitted an intensive study of Gorgona over the period 18-23 May 1979.

Until the recent work of PRAHL *et al.* (1979), the coral formations and reefs of Gorgona were only incompletely known (see CROSSLAND, 1927; MURPHY, 1939; ABBOTT & EVANS, 1968; COSEL, 1977). PRAHL and co-workers published the first detailed information on the distribution and structure of Gorgona reefs. They further considered the effects of thermal conditions, sedimentation, and corallivores on the distribution and growth of corals. The present study is an attempt to extend and amplify the latter work. Here we reexamine and slightly amend the distributional patterns of coral reefs at Gorgona. Reef morphology is examined and preliminary results of reef probing are presented as an indication of reef frame thickness. Coral zonation and community structure (relative abundance, live coral cover and diversity) are also considered and new sampling data are presented to assess the abundance of corallivore populations. These results will serve as a basis for comparing Gorgona coral communities with other areas in the eastern Pacific region. A comparison that will receive special attention involves coral communities free of *Acanthaster* (Gorgona and the Gulf of Panamá) with reefs where the effects of *Acanthaster* have been monitored for several years (Gulf of Chiriquí, western Panamá).

MATERIALS AND METHODS

An aerial reconnaissance of the shallow shelves of Gorgona and Gorgonilla islands was carried out on 28 March 1975 between 1030-1130 aboard a light, fixed-wing aircraft. Color photographs taken at an angle of approximately 45°, employing a polaroid filter to reduce glare, were obtained of the entire island shores at an elevation of 760 m. The flight was timed to coincide with the dry season (cloud cover was about 10%) and an extreme low stand of the tide. Coral reef formations were sketched on a large-scale map (Fig. 2) of the Gorgona Island group based on the aerial photographs and information obtained from *in situ* inspection.

Coral abundance was measured with a chain transect 10 m in length and containing 78 links per meter (PORTER, 1972; GLYNN, 1976). The location of the first sampling site at Gorgona (on the La Azufrada fringing reef) was selected blindly from the surface along the deep reef edge. Additional sites were measured at 8 m intervals toward the lee or shoreward side of the reef. The chain was laid out in a straight line, parallel with the isobath, so as to conform with the bottom irregularities, that is, with all links in contact with the substrate. Sampling in Panamá was carried out on a fringing reef (here named Secas-W) located on the south side of the largest, SW-most island in the Secas group, Gulf of Chiriquí (see GLYNN *et al.*, 1972, Fig. 1, p. 490 for exact location) on 16 January 1980. Here two transects were obtained at each of five sites, from near shore (3.7 m) to the deep reef edge (10.7 m). Sampling sites were spaced at 30 m intervals, beginning about 10 m seaward from the inshore edge of the reef frame. Coral species diversity (H') was calculated from the Shannon-Wiener measure of mean diversity per individual (PIELOU, 1969) with each chain link contact enumerated as a datum. The table of functions in Lloyd *et al.* (1968), with conversion to logarithms to base 2, was used for ease of calculation. Species evenness J′ or relative diversity was calculated from PIELOU's (1969) measure H′/H′ max. LOYA (1972) has offered empirical justification for use of the H′ diversity measure in coral communities.

Sections of iron pipe were driven into the reef frame (see GLYNN & MACINTYRE, 1977) in order to determine reef thickness.

Corallivorous fish were censused by swimming along measured transects running perpendicular to the reef face. The area and time period sampled were noted for each census. The abundances of invertebrate corallivores were sampled with 0.25 m^2 wire-frame quadrats. All coral inside each quadrat was inspected *in situ* and broken apart when necessary. The initial sampling site was selected blindly by dropping a quadrat from the surface above the deep reef base. Three zones, the reef base (5 quadrats), slope (7 quadrats) and reef flat (6 quadrats), were sampled. Subsequent quadrat sites within zones were selected by moving 2 m horizontally in the same direction along the reef. Sampling sites between zones were located by moving straight up the reef face from the last quadrat site in the deeper zone.

All coral species were collected (with the exception of *Porites lobata*) and voucher specimens deposited in the collections of the Departamento de Biología, Universidad de los Andes, Bogotá. The following are the scleractinian corals observed at Gorgona Island during this study. Detailed description of the species are presented by Von PRAHL & GUHL (1981).

Pocillopora damicornis (LINNAEUS), the variety often called *caespitosa,* i.e., *P. damicornis* var. *caespitosa* DANA, was also observed. *Pocillopora capitata* VERRILL; *P. danae* VERRILL; *P. elegans* DANA; *P. eydouxi* MILNE-EDWARDS & HAIME; *Psammocora (Stephanaria) stellata* VERRILL; *Porites panamensis* VERRILL; *P. lobata* DANA, large colonies were observed, but not collected, in the Banco del Horno area near Punta Coll. *Pavona varians* VERRILL; *P. clavus* DANA; *P. gigantea* VERRILL; *Gardineroseris planulata* (DANA); *Cycloseris elegans* (VERRILL); only a single, beath-worn specimen was found, and *Tubastraea coccinea* Lesson, an ahermatypic species.

OCEANOGRAPHY OF THE GORGONA AREA

Three oceanographic areas, Panamá Bight, equatorial front, and Perú Current, have been recognized in the coastal waters of the eastern

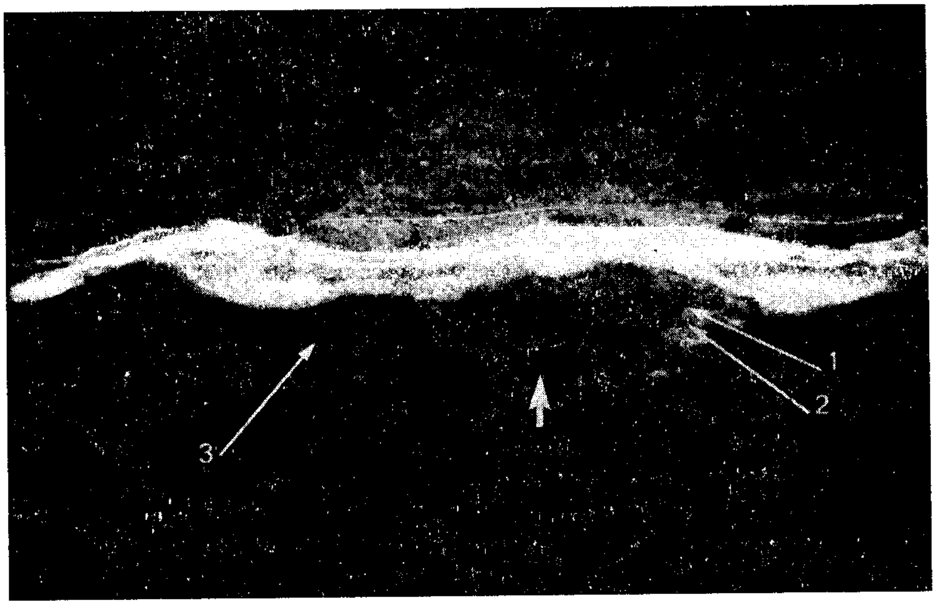

Figure 3. Aerial view of La Azufrada fringing reef (760 m, 28 March 1975). A small section of south end of reef is not shown. Note clearing in forest near center top of photograph. Arrows indicate locations of probe holes 1-3 and craterlike depression.

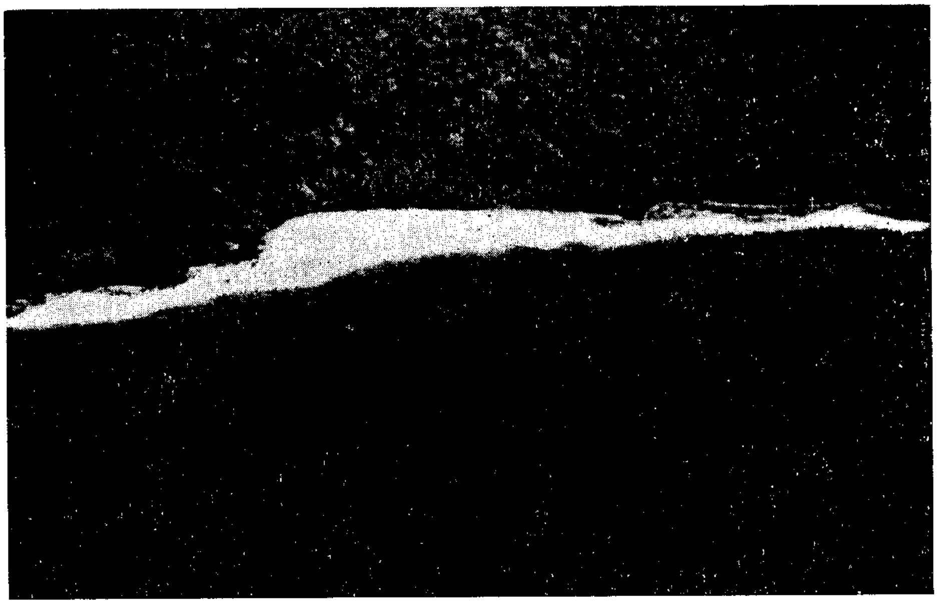

Figure 4. Aerial view of Playa Blanca fringing reef (760 m, 28 March 1975). A small section of south end of reef is not shown. The southern one-third of a smaller fringing reef is visible to the north of Playa Blanca. Note narrow zone of forest clearings above beach.

Pacific from Panamá south to Perú (STEVENSON *et al.,* 1970). The Panamá Bight area, characterized by warm surface water of low salinity, extends from the 81° W meridian east to the coast and from the entrance of the Gulf of Panamá (7.5° N) south to Punta Galera (1° N), Ecuador (Fig. 1). The strong upwelling system in the Gulf of Panamá, regarded here as an extension of the Panamá Bight, is centered between about 7.5° N and 9° N (SMAYDA, 1966). The equatorial front area, an abrupt transitional region between the tropical water of the bight and the cool saline water of the Perú Current system, lies between Punta Galera and Cabo Blanco (ca. 4° S), Perú. Thermal gradients of 5° C to 6° C per degree of latitude, and over short distances as much as 0.3° C per 1.6 km of latitude, have been observed in this area (STEVENSON *et al.,* 1970). The Perú Current area extends as far as 17° S. Gorgona Island (2° 58′ N; 78° 11′ W) is located in the southern half of the Panamá Bight area (Fig. 1). The Gorgona group is situated near the edge of the continental shelf and about 30 km off the mainland, a predominantly mangrove-fringed coast in this region (WEST, 1957). Gorgona Island, consisting chiefly of basic rock formations that are most likely late Upper Eocene in age (GANSSER, 1950), is a relic of the Coastal Cordillera which extends north-south from the mainland of Cabo Corrientes, Colombia to near Esmeraldas, Ecuador (GANSSER, 1950; OPPENHEIM, 1952).

Circulation of surface water within the bight is cyclonic, flowing counterclockwise (FORSBERGH, 1969; STEVENSON *et al.,* 1970). Water moving past Gorgona largely derives from the eastward branch of the bight circulation system and thus flows predominantly northward (NNE). Current velocities in the dry season (December to April) and also during mid to late wet season (August to November) are higher in this area (150 cm/sec. or 3 knots) than in the early wet season, from May to June (50 cm/sec. or 1 knot) (STEVENSON *et. al.,* 1970). At times currents also move toward the west (STEVENSON *et al.,* 1970) or the east (Wyrtki, 1965). [MURPHY (1939) noted that Antonio de Alcedo, a historian, asserted that Gorgona was named after the character of the currents surrounding the island. Evidently the occasionally strong easterly set of currents, and calm spells, rendered passage very tedious; this condition was described at the time by the term *engorgonarse,* meaning to be engulfed]. From about May through December, the Equatorial Countercurrent flows east between 4° N and 11° N, thereby entering to some extent the circulation system of the bight (WYRTKI, 1965). Also, the northerly flowing coastal current, the so-called Colombia Current (WOOSTER, 1959), eventually mixes with water in the Gulf of Panamá.

A thermal dome typically forms near the center of the Panamá Bight from January through March at the height of the dry season. Surface temperatures at this time are 25° C to 26° C, the lowest of the year. During the dry season in the Gulf of Panamá, however, surface temperatures are commonly 20° C to 24° C and occasionally drop to 16° C to 18° C locally (GLYNN & STEWARD, 1973; GLYNN, unpubblished observations). The cooler conditions associated with the upwelling system in the Gulf of Panamá do not appear to penetrate significantly into the Panamá Bight (WOOSTER, 1959).

Temperature observations over three dry seasons (1964 through 1966) showed 26° C, 27° C and 28° C surface isotherms surrounding Gorgona Island (STEVENSON *et al.*, 1970). Thus it does not appear that Gorgona experiences incursions of cool water from the north. It is possible that some water exchange occurs across the frontal boundary, but the amount involved and the extent of modification are presently unknown. Perhaps the 18.7° C temperature reported on the west coast of Gorgona (PRAHL *et al.*, 1979) was related to a narrow, northward-flowing coastal current that is sometimes observed in this area from April to June (STEVENSON *et al.*, 1970).

Salinities in the Panamá Bight often vary from 33.5‰ offshore to less than 20‰ near the Colombian coast (FORSBERGH, 1969). Dry season surfacing of water in the central bight increases surface salinities slightly, to 34‰. Low coastal salinities are due to the influence of the Intertropical Convergence Zone in this region resulting in high annual rainfall, ranging between 4000 mm to more than 7500 mm (FORSBERG, 1969), and a large runoff. Salinities slightly offshore near Gorgona ranged between 31‰ and 33‰ from February 1964 to March 1966, differing little between seasons (STEVENSON *et al.*, 1970). Apparently the strong NNE currents at Gorgona, originating to a large extent offshore, are responsible for the stable salinity and usually clear

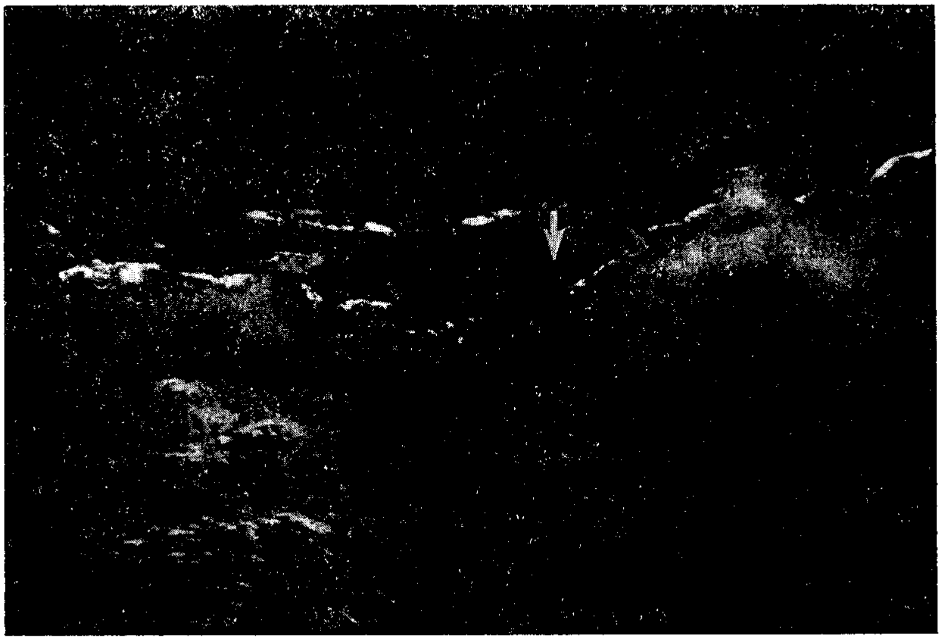

Figure 5. Aerial view of fringing reef (arrow) and linear ridges (lower left corner) immediately south of La Camaronera beach, west shore of Gorgona Island (760 m, 28 March 1975).

water close to the coast. Turbid water conditions resulting from runoff (producing suspended sediments and increased plankton productivity) seem to occur more frequently in the coral reef area of Chiriquí, Panamá (DANA, 1975) than at Gorgona.

Tides at Gorgona are of the semidaily type with the daily high and low waters varying little in height or duration of rise and fall (U.S. Dept. Comm., 1979). The maximum range is about 5 m. The extreme low water exposures (to - 0.64 m) occur during the dry season at midday, from January until about mid April. The average monthly rainfall in the dry season, falling mainly in the afternoon (PRAHL *et al.*, 1979), ranges between 0.3 and 0.5 m. A second and somewhat less extreme set of midday tidal exposures (to - 0.55 m) occurs from August through December. This is during the height of the wet season when average monthly precipitation ranges between 0.6 and 0.9 m. The range and seasonal diel patterns of the tides at Gorgona are remarkably similar to those in Panamá, especially in the Gulf of Chiriquí. The large tracts of dead coral (principally *Pocillopora*) on the emergent sections of the reef flat suggest that tide-related mortality occurs at Gorgona as in Panamá (GLYNN, 1976).

DISTRIBUTION OF CORAL REEFS

Our findings generally confirm the pattern of coral reef distribution presented in PRAHL *et al.* (1979). Coral communities and pocilloporid reefs were present primarily along the east side of Gorgona and in the shallow channel between Gorgona and Gorgonilla (Fig. 2). The chief differences revealed by the aerial survey and *in situ* inspection involve three modifications to the earlier scheme. First, while coral communities were again observed from La Boca del Horno south to off the front of the prison, along the east side of Gorgona, no significant reef framework was found in this area. The Azufrada reef also proved to be slightly larger than the reef at Playa Blanca. The Azufrada reef was longer (ca. 1 km) and broader (ca. 150 m) than the Playa Blanca reef which measured approximately 0.8 km in length and 100 m in width (contrast Figs. 3 and 4). Finally, coral reefs and numerous incipient reef formations were observed on the rocky headland between the sand beach of La Camaronera and Puesto de Gorgonilla on the west coast of Gorgona. Reef development in this area was of two forms. The most coherent formations consisted of a closely packed intermeshing framework of *Pocillopora* spp., which appeared to rest on a basaltic base that abutted directly against the shore. According to GANSSER (1950) this section of the coast is a mountain slide lying adjacent to an inland and predominantly undifferentiated diabase-gabbro rock formation. These reefs were present at shallow depths (1 to 4 m) in the zone of strongest wave action (Fig. 5). Inspection of the fringing reefs at low water showed incipient reef-frame development in tide pools and basins receiving adequate circulation. Linear pocilloporid buildups or spurs and hillocks of various sizes were also present 100 to 200 m seaward of the fringing reefs (Fig. 5). The linear ridges were oriented parallel (or nearly so) to the prevail-

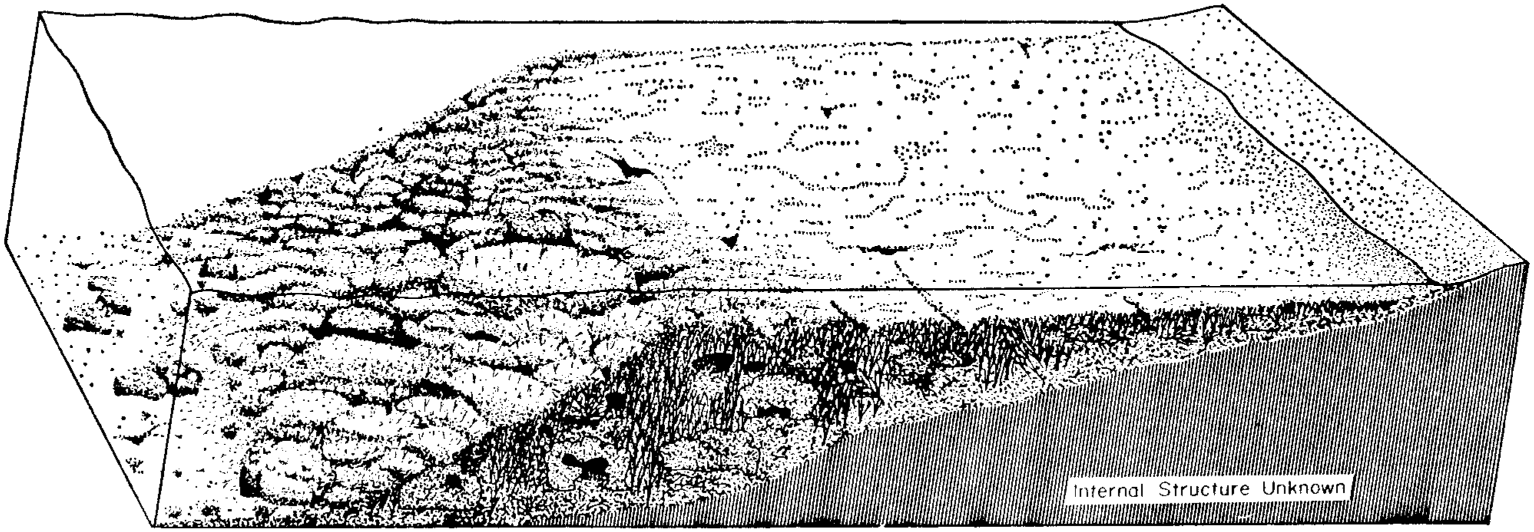

Figure 6. Stylized representation of a section of La Azufrada fringing reef. Water depth is approximately 15 m from surface to sand plain bordering the deep forereef slope. Horizontal distance from beach to sand plain is approximately 120 m. See Table I.

ing wave direction and reached a vertical buildup of at least 2 to 3 m. Shallow excavation (to 30 cm), at several sites along one ridge, failed to reveal any noncarbonate rock. Directly offshore at the south end of La Camaronera beach, the linear ridges gave way to numerous pocilloporid hillocks, some of which have apparently coalesced. Crustose coralline algae binding the reef frame were more in evidence on these windward reefs and ridges than on reefs present on the leeward (east) side of Gorgona. Additional information on the extent of framework development and species composition is noted in the next section. In summary, best reef development has occurred most frequently at protected or leeward island sites. Pocilloporid reefs, however, also formed on relatively exposed shores, a condition observed previously in Panamá (GLYNN *et al.*, 1972; GLYNN & STEWART, 1973).

REEF STRUCTURE AND ZONATION

Gorgona Island.

While massive corals contributed significantly to the reef frame (especially in deep forereef zones), all reefs observed were composed predominantly of ramose *Pocillopora* species. The reef framework was typical of other eastern Pacific pocilloporid reefs, consisting of closely spaced and interlocking branches of ramose *Pocillopora* corals having high vertical growth rates (GLYNN & MACINTYRE, 1977). All stages of fringing reef development were seen on reefs of varying maturity along the eastern shore of Gorgona. Surveys of reef morphology and coral community structure were carried out on the following reefs: Pier reef, La Azufrada reef, Playa Blanca reef, Paso de Tasca reefs and the reef buildups (onshore and offshore) south of La Camaronera (Fig. 2).

The Pier reef, roughly oval in outline, is only about 50 m in length. It is occupied almost entirely by pocilloporid corals from base to crest. The seaward face slopes steeply downward (at an angle of about 60° in places) to a coarse and largely bioclastic, carbonate sand plain. Inspection of the reef surface (i. e., extent of reef buildup in relation to the surrounding bottom topography) indicated that this reef frame may have a 6 m maximum thickness.

The La Azufrada reef is a broad, fringing reef with a reentrant (in conformity with the coastline) directly in front of the sand beach and the stream mouth of La Azufrada. A schematic cross section of this reef, based on a qualitative visual survey and transect sampling, is presented in Fig. 6. The coral species encountered, as well as live coral cover, diversity and evenness at seven sites from the reef flat across the face to the reef base, are presented in Table 1. At extreme low tides (about -0.3 m and lower) the reef flat is exposed. The principal corals populating this section of the reef were *Pocillopora damicornis, Psammocora stellata* and *Porites panamensis*. The outer drying reef flat, ca. 30 m

Figure 7. Large colony of *Pocillopora eydouxi,* about 1 m in diameter, growing above numerous smaller colonies of *Pocillopora damicornis, P. capitata,* and *P. elegans.* Mid forereef slope (5 m depth), Playa Blanca reef, 22 May 1979.

Figure 8. Shorewardmost edge of eroded reef frame, composed dominantly of algal-coated blocks of pocilloporid corals, bordering a shallow sand basin that runs parallel to the beach (0.5 m depth), Playa Blanca reef, 22 May 1979.

wide, consisted of a dead pocilloporid frame in growth position. The inner reef flat, ca. 60 m wide, contained coral rubble and mixed carbonate and terrigenous sediments. Much of the dead coral comprising the shallow, back reef areas was probably killed by extreme, low water tidal exposures as documented for drying reefs in Panamá (GLYNN, 1976). The zones of greatest coral abundance and richness extended from the reef crest to the lower reef slope (Table 1, transects 2-5; Fig. 6). Here the number of coral species ranged from 4 to 5 species, diversity from 0.58 to 1.28 and live cover between 40% and 72%. Coral species observed here but not on the reef flat were *Pocillopora capitata*, *Pocillopora elegans*, *Pocillopora eydouxi*, *Pavona varians* and *Pavona clavus*. Some *P. eydouxi* colonies 2 m in diameter were the largest yet reported in the eastern Pacific. This coral, generally present on the upper and mid forereef slope, was locally abundant and contributed substantially to the reef frame in these areas (Fig. 7). Live coral cover decreased rapidly below about 11 m. At 15 m, for example, only 2.2% of the substrate was live coral. Massive corals commonly observed along the deep reef edge included *Gardineroseris planulata* and *Pavona gigantea*. Colonies of these species were usually a meter or less in diameter.

According to PRAHL *et al.* (1979), coral populations on the reef flat in front of the La Azufrada beach have suffered recently from increased sedimentation due to the construction of a small landing field. They observed a 240 m long strip of dead and stressed *Pocillopora* spp. which they claimed was caused by heavy rains and the massive transport of fine-grained lateritic soil. This suggestion is supported by the position of the sedimentary fan in relation to the air strip and forest clearing shown in figure 3.

The craterlike depression near the reef crest (Fig. 3) is a peculiar feature, the first observed on any eastern Pacific reef. It is largely sandfilled, about 50 m in diameter and 15 m in depth. This depressiòn is unlikely a result of a recent catastrophic event, such as a bomb blast or a meteoritic impact, because ejecta were not found nearby and because a large, live colony of *Gardineroseris planulata* (about 4 m in diameter) was present in the basin in its natural growth position. The maximum linear growth axis of this coral was about 2 m and, assuming an annual growth rate of 1 cm (GLYNN, unpublished data), the colony is probably near 200 years old. It seems more probable that the depressiòn was formed by coral growth around a small submarine valley (see location of valley in forest clearing in Fig. 3) or an erosional (storm ?) reentrant.

Reef probing, undertaken to determine the thickness and underlying composition of the coral framework, was completed at three sites only (Fig. 3). Holes 1 and 2 at the north end of the La Azufrada reef were drilled through a dead *Psammocora-Pocillopora* zone and a dead *Pocillopora* frame respectively. The coral stratum at hole 1 was 195 cm thick underlain by a stratum of compact calcareous sand and mud. Hole 2 revealed a 285 cm thick framework of *Pocillopora* spp. underlain by a compact stratum of calcareous sediment. Probing site 3, seaward of

La Azufrada beach, was located on the outer reef flat in the zone of compact dead *Pocillopora* frame. Here the drill string was driven to a depth of 827 cm. The drill-tip section was unfortunately lost during retrieval. The rate of entry of the probe suggested a framework buildup of around 8 m at this site.

The Playa Blanca reef was similar in form and zonation to the La Azufrada reef. Live coral cover was high along the seaward reef edge to 10 m depth. The sand plain, however, was somewhat shallower (ca. 12 m depth) than at La Azufrada (ca. 16 m depth). *Pavona clavus* colonies 1 to 2 m in diameter were abundant at the reef base, but pocilloporid corals were again the principal species making up the reef frame. Large colonies of *Pocillopora eydouxi* (Fig. 7), 1 to 2 m in diam-

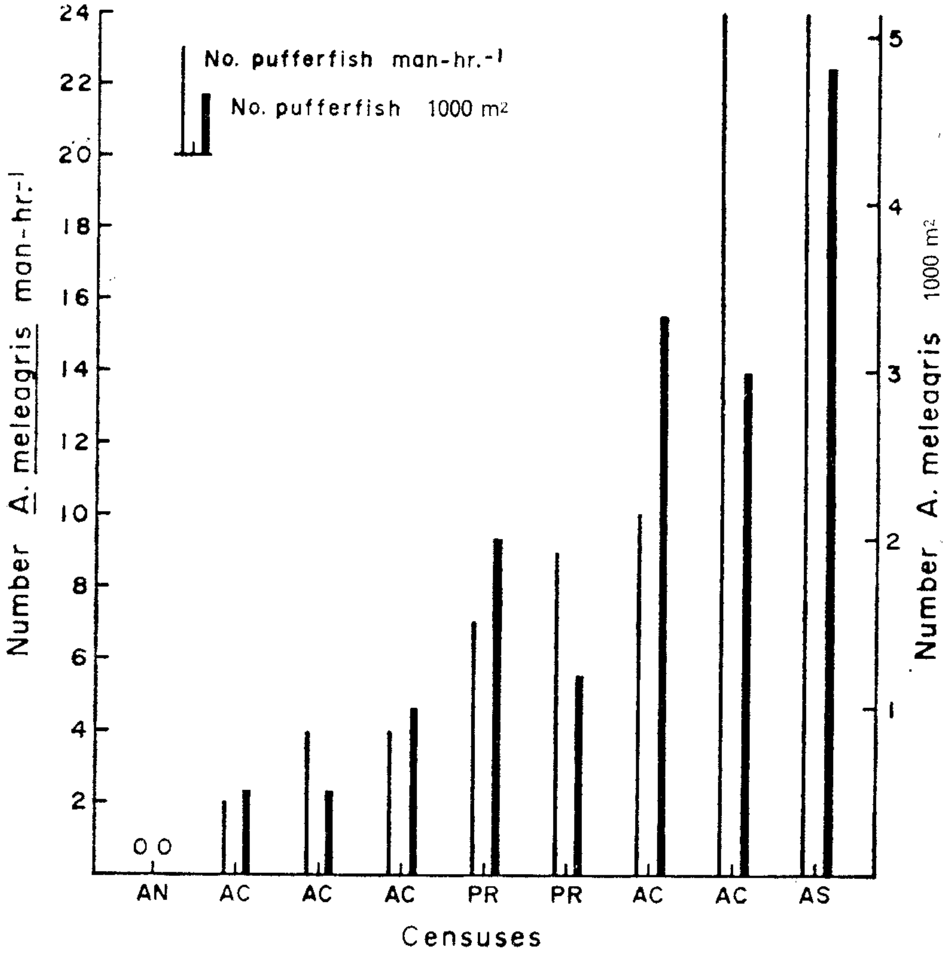

Figure 9. Numbers of the corallivorous pufferfish *Arothron meleagris* observed in 9 censuses on coral reefs at Gorgona Island. The censuses were conducted at the following sites: AN, AC, AS, the north, central and south sections respectively of the La Azufrada reef and PR, the Pier reef.

eter, were abundant on the seaward reef face and formed an important part of the reef framework in this zone. The dead leeward reef flat (Fig. 8), about 100 m wide, extended closer to shore than did this zone at La Azufrada. This is probably because the Playa Blanca reef has not been inundated recently by sediments which would bury this surface.

The linear ridges located off La Gómez (Fig. 2) were not surveyed directly, but appear to be pocilloporid buildups similar to those observed south of La Camaronera. Neither of these ridge systems appeared to follow rock alignments on the island (personal observations and see GANSSER, 1950), suggesting that the pocilloporid framework developed as a dynamic response to the prevailing set of sea and swell. Such buttress formations are a characteristic feature of numerous reefs throughout the Indo-Pacific and western Atlantic regions (STODDART, 1969). The shallow shelf (5-10 m) off shore of La Gómez and La Ventana supported dense stands of *Pocillopora* spp. which formed buildups approximately 1 m in thickness in some areas.

Near the north side entrance to Paso de Tasca are located one relatively large reef (ca. 250 m long) and a group of small patch reefs (Fig. 2). The larger reef was again similar to the fringing leeward reefs present at La Azufrada and Playa Blanca. The seaward reef base contained chiefly colonies of *Pavona clavus* growing in juxtaposition, the upper slope and crest were dominated by pocilloporid corals and the leeward drying reef flat was a long-dead, *in situ* pocilloporid frame that probably formed near shore during an early stage of reef growth. The small, disconnected reef patches present in the pass contained mostly pocilloporid corals.

Zonation was virtually nonexistent in the narrow, fringing pocilloporid reefs present south of La Camaronera. The reef flat consisted of a uniform and compact network of two species of *Pocillopora,* tentatively identified as *P. capitata* and *P. danae.* These reefs sloped abruptly to a sand bottom at ca. 4 m depth. The linear, spurlike buildups offshore also lacked any consistent pattern of zonation. The only reef-building corals observed in the linear ridges were *Pocillopora damicornis, P. capitata* and *P. elegans.* The ahermatype, *Tubastraea coccinea* Lesson was sometimes abundant in holes present in the reef frame.

Panamá.

This brief account on the structure and zonation of a fringing reef in the Secas Islands group, Gulf of Chiriquí, will serve as a basis for later comparisons (see Discussion) between Panamá and Gorgona Island. This reef, here called Secas-W, is located on the south or windward side of the largest, SW-most island in the Secas group (see GLYNN *et al.*, 1972, Fig. 7, for an underwater view of a shallow section of the reef).

At shallow depths (3 to 5 m) at Secas-W the most abundant coral was *Pocillopora damicornis* and it formed a typical reef frame of loosely interlocking, vertical branches. In some places the pocilloporid frame had grown upwards to the spring, low tide line, but did not form an extensive uninterrupted reef flat which is characteristic of Chiriquí

Figure 10. Two damselfish territories present on each side of a live ridge of *Pavona clavus* (foreground). The defending damselfish, their algal mats and live pocilloporid corals growing from the dead *Pavona* colony are all visible. Upper forereef sope (3 m depth), Playa Blanca reef, 22 May 1979.

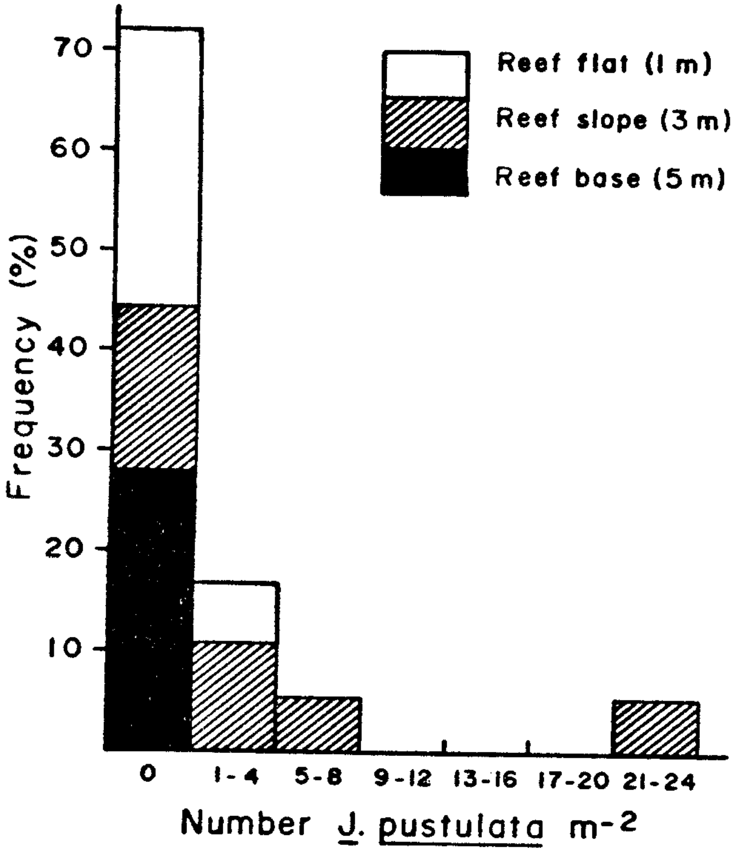

Figure 11. Numbers of the corallivorous gastropod *Jenneria pustulata* observed in 18 quadrats (0.25 m^2 each) in three reef zones at the south end of the La Azufrada reef.

reefs in more protected situations. Surface inspection and limited excavation along the sides of spurs revealed that the pocilloporid corals rested on large, massive colonies (usually *Pavona clavus*) up to 1 and 2 m in diameter. *Gardineroseris*, some colonies 2 m in diameter, was also present here but not sampled in the chain transects (Table 2). The reef appeared thickest at 3-4 m depth and probably did not exceed 4 to 5 m in maximum vertical buildup. At about 5 m depth, pocilloporid corals gave way almost entirely to large colonies of *P. clavus* which formed a continuous stand on the gently sloping bottom. Coral buildup had attained only about 2 m in thickness at greater depth. *Pavona clavus* predominated over a horizontal distance of about 100 m to a depth of 11 m. Beyond 11 m this coral occurred only as isolated colonies.

Live coral cover was high at all depths, ranging from 32% to 78% (Table 2). Species diversity was relatively high between 3 and 5 m depth and declined markedly between 7 and 11 m where *P. clavus* predominated (Table 2).

ABUNDANCE OF CORALLIVORES

Several species which feed on live reef-building corals have now been identified in the eastern Pacific. Because some of these corallivores are capable of consuming relatively large amounts of coral, and at times reach high population densities, it is useful to assess their potential impact on local coral communities.

Arothron meleagris (Lacépède), a specialist on the branch tips of *Pocillopora* spp., was the most abundant fish corallivore observed at Gorgona. Individuals were seen breaking off the tips of corals during daylight hours, especially in the morning and late afternoon. Figure 9 summarizes the abundances of *A. meleagris* in terms of individuals observed per man-hour and individuals present per 1000 m^2 of reef area. These pufferfish were present in every census except at the north end of the La Azufrada reef. As many as 24 individuals per man-hour and 3 to 5 individuals per 1000 m^2 were present in the central and southern sectors of La Azufrada. The median densities of *A. meleagris* at La Azufrada and the Pier reef were 6 individuals per man-hour (1.2 individuals per 1000 m^2). These densities appeared comparable with other reef areas at Gorgona.

Arothron hispidus (Linnaeus), a facultative corallivore was observed in only two of the nine censuses. Two and 6 individuals per man-hour, equivalent to 4.4 and 1.5 individuals per 1000 m^2 respectively, represented this pufferfish's abundance where present. Some individuals of *A. hispidus* had markedly sagging abdomens that has been shown to be a consequence of coral grazing in Panamá.

Recent data on the abundance of pufferfish corallivores in Panamá indicate comparable numbers in the two areas. *Arothron meleagris* was present in 5 of 11 censuses at Uva Island, Gulf of Chiriquí (10-14

January 1980). When present, it ranged in abundance from 2.8 to 33.3 individuals per 1000 m^2. The numbers encountered in the Gorgona and Panamá censuses did not differ significantly ($P > 0.05$, Mann-Whitney U test). The highest densities in both areas occurred on reef slopes where *Pocillopora* cover was high and shelter holes abundant. The population density of 4 individuals per 1000 m^2 in *A. meleagris* at Señora Islet in the Pearl Islands, Gulf of Panamá (GLYNN *et al.,* 1972) was also comparable to the nonupwelling sites at Gorgona and Chiriquí. As at Gorgona, *A. hispidus* was relatively uncommon on the Uva Reef with only 2 individuals per man-hour observed.

Other fishes that feed less frequently on live coral and were present in the Gorgona censuses were the parrotfish *Scarus ghobban* FORSSKA°L and the triggerfish *Sufflamen verres* (GILBERT and STARKS). Two small schools of the parrotfish (4 and 6 individuals each) and two individuals of *S. verres* were observed. PRAHL *et al.,* (1979) noted that parrotfishes grazed most intensively on massive colonies of *Porites* (probably *P. lobata*) at the northeast end of Gorgona (Punta Coll) near La Boca del Horno. Only two individuals of a second triggerfish known to break apart (but not ingest) live corals, *Pseudobalistes naufragium* JORDAN and STARKS), were observed during the entire survey. This large triggerfish (up to 60 cm total length) is uncommon on reefs in the Gulf of Chiriquí, Panamá, but common to abundant on incipient reefs and in coral communities in upwelling environmens where molluscan prey species are plentiful (G. M. WELLINGTON, pers. comm.).

It is now well substantiated that damselfish are capable of killing relatively large areas of live coral during the enlargement of their algal mats (KAUFMAN, 1977; WELLINGTON, in press). Damselfish normally feed on fleshy and filamentous algae. Since it is not known to what extent they ingest and utilize live coral, these fishes may not be true corallivores. WELLINGTON (in press), working in the Pearl Islands, Panamá, has demonstrated that *Eupomacentrus acapulcoensis* (FOWLER) kills a higher proportion of massive corals *(Pavona)* than of ramose pocilloporid species. This damselfish was very abundant at Gorgona and was often associated with *Pavona gigantea* and *P. clavus.* The colony of *P. clavus* in Figure 10 contained two damselfish territories, one on each side of the ridge of live coral. It is highly likely that these damselfish, or earlier occupants of the sites, were responsible for killing the *Pavona* coral up to the border of their territories. Also visible on the dead *Pavona* base and within the damselfish territories were live colonies of *Pocillopora damicornis* (of several sizes) and *Pocillopora elegans.*

Like *A. meleagris,* the cypraeacean gastropod *Jenneria pustulata* (LIGHTFOOT), preys almost exclusively on pocilloporid corals. *Jenneria* was found in 5 of 18 quadrats taken on the south end of the La Azufrada reef (Fig. 11). As many as 6 individuals (24 individuals per m^2) were found in a single quadrat. A chi-square test of the goodness-of-fit to the Poisson distribution indicates that *Jenneria* was distributed randomly over the reef area sampled ($X^2 = 2.43$, $P > 0.10$). While *Jenneria* was more prevalent in samples from the reef slope zone, the

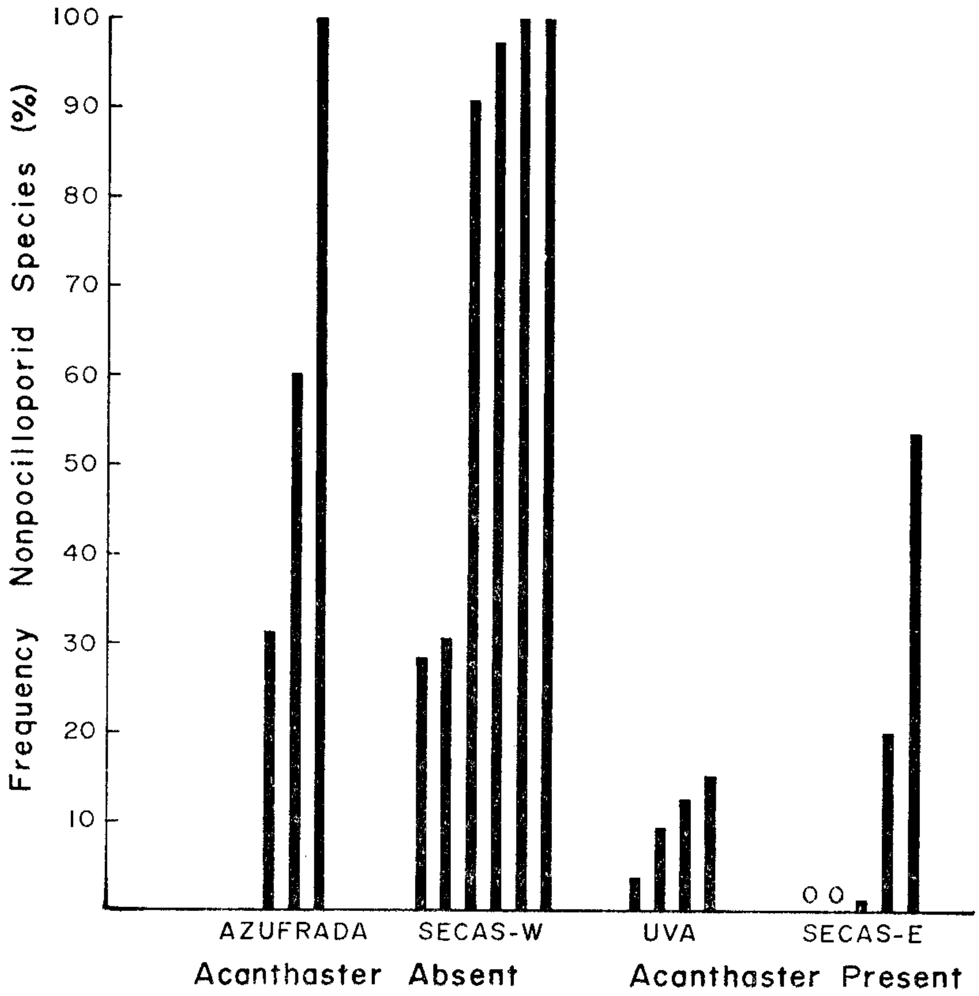

Figure 12. Relative frequency of pocilloporid and nonpocilloporid coral species present in the lower forereef slope and reef base zones (5.2 - 15 m depth) in reefs with and without *Acanthaster*.

differences in abundance between zones were not statistically significant ($0.10 > p > 0.05$, Kruskal-Wallis anova).

The numbers of *Jenneria* found on reefs in Panamá also usually demonstrated a strong, positively skewed frequency distribution similar to that shown in Figure 11. *Jenneria* was absent from approximately one-half or more of the quadrat samples taken in the Taboga Island group, Gulf of Panamá [4 collections with n (number of quadrats in each collection) = 10, 11, 14, and 15] and in the Contreras and Secas Islands groups, Gulf of Chiriquí (2 collections, n = 9, 13). Pooling of three samples from Taboga Island (same site with n = 35) reveals a clustered distribution. The observed distribution deviated markedly from the Poisson distribution ($X^2 = 207.51$, $P << 0.001$). Occasionally several individuals were found together on a single coral colony, suggesting a tendency to aggregate while feeding. The abundances of *Jenneria* in these six collections and the single collection from Gorgona were not dissimilar ($0.70 > P > 0.50$, Kruskal-Wallis anova), indicating that the population densities of this corallivore are comparable in the two regions.

A single individual of the trochid gastropod *Calliostoma mcleani* SHASKY and CAMPBELL was found in the quadrat sampling. Observations in the Gulf of Chiriquí suggest that this species feeds preferentially on pocilloporid corals. It is, however, apparently uncommon at both localities.

Hermit crabs that occasionally rasp pocilloporid corals (e.g., species of *Trizopagurus* and *Aniculus*) were not present in the quadrat sampling. Additional inspection of several *Pocillopora* colonies, and the earlier observations of PRAHL *et al.* (1979), indicate that these hermit crabs are probably not so abundant at Gorgona as at Panamá.

Eight quadrats contained the cidarid echinoid *Eucidaris thouarsii* (Valenciennes). When present, it was small (with maximum test diameter usually <20 mm) and ranged in abundance from 4 to 20 individuals per m^2. Unlike *E. thouarsii* in the Galápagos, which grazes heavily on pocilloporid corals (GLYNN *et al.*, 1979), the Gorgona cidarids were secretive and appeared to feed primarily on crustose coralline algae and other encrusting species present on the dead basal branches of *Pocillopora*.

Asteroids that sometimes prey on reef corals, notably *Pharia pyramidata* (GRAY), reported by DANA & WOLFSON (1970) to feed on *Pocillopora* in the Gulf of California, and *Nidorellia armata* (GRAY), observed by GLYNN & WELLINGTON (in preparation), to feed on *Pavona clavus* in the Galápagos Islands, were uncommon at Gorgona and were not observed feeding on coral.

Acanthaster planci was not observed at Gorgona during this study or on previous occasions (PRAHL *et al.*, 1979). Indeed, its absence from the Galápagos Islands, Malpelo Island (BIRKELAND *et al.*, 1975), a coral reef off the mainland of Ecuador, and the Gulf of Panamá indicate that the crown-of-thorns sea star probably does not occur as a persistent population anywhere south of the nonupwelling region of the Gulf of Chiriquí (GLYNN, 1974). Since the larval stages of *Acanthaster* are adversely affected by low temperatures (≦24°C to 25°C) and low salinities (≦22‰) (HENDERSON & LUCAS, 1971; LUCAS, 1973; YAMAGUCHI, 1973), it is likely that *Acanthaster* has been prevented from spreading further south along the mainland by strong upwelling in the Gulf of Panamá and low salinities characteristic of the Colombian Chocó coast. Because temperatures and salinities at some offshore islands in this region (e.g., Malpelo Island and parts of the Galápagos Islands) are less extreme than along the eastern Pacific mainland, it is not known if the absence of *Acanthaster* in such areas is due to local or distant adverse conditions, chance colonization events or other factors.

DISCUSSION

Coral Community Structure and the Role of Acanthaster.

Gorgona Island bears a strong resemblance to the Contreras-Secas island groups in the Gulf of Chiriquí, Panamá. Both are located offshore on the continental shelf, they are present in nonupwelling areas, and their reef-building coral faunas contain very nearly the same species. The only obvious difference is that hydrocorals *(Millepora)*, present in Chiriquí, are absent from Gorgona. With respect to corallivores, *Acanthaster* is common on many reefs in Chiriquí (2 to 25 individuals per hectare; GLYNN, 1974), but is not present at Gorgona, probably because of the temperature-salinity conditions referred to earlier. Considering the impact of *Acanthaster* on coral communities in Panamá (see PORTER, 1972; GLYNN, 1976), it is instructive to compare reefs at Gorgona and Chiriquí with respect to differences in their structure that could be attributed to *Acanthaster.*

The La Azufrada reef and a coral reef in the Secas Islands, Secas-W, that has not been subject to *Acanthaster* predation for probably a very long time, will be compared first. No *Acanthaster* were observed on the Secas-W reef when first surveyed in March 1970 nor since during sporadic surveys to the present (January 1980). Judging from the large size (1-2 m diameter) and uniform morphology of the predominant coral, *Pavona clavus,* it is not likely that Secas-W has suffered serious damage by *Acanthaster* for decades and perhaps over the past century. *Pavona clavus* is extensively preyed upon by *Acanthaster* on Panamanian reefs where they occur together. In such areas, e.g., Uva and Secas study reefs (GLYNN, 1976), this coral is not abundant, only a few large colonies (about 1 m diameter) are present, and extensive surface areas of colonies are dead (due largely to heavy *Acanthaster* feeding in 1970) and commonly invaded by other coral species. It was first reasoned that *Acanthaster* was absent from Secas-W due to the exposed location of this reef. In the Gulf of California (DANA & WOLFSON, 1970) and in the Indo-West Pacific generally (CHESHER, 1969; GOREAU *et al.*, 1972), *Acanthaster* is not abundant on highly exposed shores. Since

Acanthaster occurs commonly on exposed shores elsewhere in Chiriquí (personal observations), an explanation for its absence at Secas-W will probably involve other factors (perhaps chance recruitment events).

A direct comparison of the La Azufrada and Secas-W reefs (Tables 1 and 2, all transects) fails to reveal any significant differences with respect to a) number of coral species present, b) species diversity (H′), c) species evenness (J′), or d) live coral cover ($P > 0.05$ in every case, Mann-Whitney U test).

Since the reefs examined above without *Acanthaster* were similar, the samples from each were pooled and then compared with reefs in Chiriquí (Table 3) where *Acanthaster* has a significant impact on corals (GLYNN, 1976). The numbers of coral species and the three attributes of community structure compared for La Azufrada and Secas-W reefs were also pooled for the Uva and Secas-E reefs since these were tested among themselves and also found not to differ. For pooled data, only species evenness, J′, was statistically different (Table 3; $P < 0.025$, Mann- Whitney U test). This indicates the relative abundances of coral species were more nearly uniform on reefs free from *Acanthaster* predation.

Table 1. Coral species richness, diversity, evenness and live cover across the La Azufrada fringing reef (Fig. 6), Gorgona Island. Coral species sampled in chain transects are listed in rank abundance; coral species present but not sampled in transects (in parentheses) are listed in alphabetical order. A, *Porites panamensis;* B, *Pocillopora damicornis;* C, *Pocillopora capitata;* D, *Pocillopora elegans;* E, *Psammocora stellata;* F. *Pavona varians;* G, *Pocillopora eydouxi;* H, *Pavona clavus;* I, *Pavona gigantea;* J, *Gardineroseris planulata.*

Transect number	Depth below MLWS (m)	Number coral species[a]		Species diversity H'	Species evenness J'	Live coral cover (%)
1	0.3	0	(ABE)	—	—	0
2	0.4	3	BCD(AE)	1.13	0.72	47.3
3	2	4	CBEF(G)	0.58	0.29	72.3
4	5	5	CDBEF(GH)	0.87	0.38	70.5
5	8	4	ECFB(H)	1.28	0.64	40.0
6	11	2	BE(FI)	0.90	0.90	23.4
7	15	1	E(FIJ)	0	0	2.2

Considering that *Acanthaster* forages primarily in the deep, forereef slope and reef base zones (GLYNN, 1976), it is more valid to compare coral communities in these particular habitat. Moreover, since *Acanthaster* feeds preferentially on all nonpocilloporid corals (GLYNN, 1974, 1976), it is reasonable to contrast the relative abundances of these corals in reef areas with and without *Acanthaster.* Hydrocorals (two species of

Millepora) were excluded from this analysis because of their absence from Gorgona. Overall, they made up only 1.7% and 2.1% respectively of the total live coral cover at Uva and Secas-E. This more restricted comparison disclosed a marked difference in the relative abundances of nonpreferred pocilloporid and preferred nonpocilloporid corals on the two sets of reefs ($0.02 > P > 0.01$, Kruskal-Wallis anova). The median frequencies of nonpocilloporid corals on reefs without *Acanthaster* were high (namely, 60.3%, La Azufrada, and 94.3%, Secas-W). The nonpocilloporid species sampled in the deep La Azufrada coral communities were, in order of increasing abundance, *Psammocora stellata* and *Pavona varians*. On the Secas-W reef, *Pavona clavus* was the only nonpocilloporid coral sampled in the deep zones. The Uva and Secas-E reefs, where *Acanthaster* was always present, contained only 10.4% and 1.3% nonpocilloporid corals respectively (Fig. 12). The predominant nonpocilloporid corals on these reefs were *Gardineroseris planulata* and *Pavona varians*. A multiple-comparison test (with $\alpha = 0.20$) showed that all pairwise combinations differed significantly except where *Acanthaster* was absent on both reefs or present on both reefs.

The prominence of massive *Pavona clavus* and *P. gigantea* colonies in coral communities in the Galápagos Islands and at Malpelo Island could be due, in part, to the absence of *Acanthaster* from these areas. In the Galápagos, the bulk of the reef framework was composed of

Table 2. Coral species richness diversity, evenness and live cover across the Secas-W reef, Gulf of Chiriquí, Panamá. Coral species sampled in chain transects are listed in rank abundance; coral species present but not sampled in transects (in parentheses) are listed in alphabetical order. Coral species C, F, G, and I listed in Table 1 were present in Chiriquí but not sampled at Secas-W. A, *Porites panamensis;* B. *Pocillopora damicornis;* D, *Pocillopora elegans;* E, *Psammocora stellata;* H, *Pavona clavus;* J, *Gardineroseris planulata.*

Transect number	Depth below MLWS (m)	Number coral species[a]		Species diversity H'	Species evenness J'	Live coral cover (%)
1	3.7	2	BH(AJ)	0.85	0.85	32.3
1a	3.7	3	BDH(AJ)	1.09	0.69	54.0
2	3.0	1	B(ADHJ)	0	—	51.4
2a	3.0	2	BH(ADJ)	0.60	0.60	61.4
3	5.2	3	BHD	1.29	0.81	69.0
3a	5.2	3	DHB	1.37	0.86	50.9
4	7.6	2	HD(E)	0.19	0.19	72.5
4a	7.6	1	H(E)	0	—	77.8
5	10.7	2	HD(E)	0.42	0.42	46.1
5a	10.7	1	H(E)	0	—	68.9

Table 3. Coral reefs with and without *Acanthaster* contrasted with respect to four community attributes. The paired reefs within each test condition, i.e., *Acanthaster* absent or present, do not differ significantly among themselves. Confidence limits in parentheses: 0.95 confidence limits of median, calculated from $K = 50/100\ (n + 1) - \sqrt{n}$ with n = number of observations; confidence limits located by counting K units toward the median from ends of ranked observations.

Attribute	*Acanthaster* absent Gorgona/Secas-W	N	*Acanthaster* present Uva/Secas-E	N	P
Number of coral species	2 (1–3)	17	2 (2–3)	18	>0.05
Live coral cover	51.4 (32.3–70.5)	17	35.9 (13.1–66.9)	18	>0.05
Species diversity (H')	0.72 (0–1.13)	16	0.40 (0.16–1.00)	18	>0.05
Species evenness (J')	0.64 (0.29–0.85)	13	0.28 (0.16–0.52)	14	<0.025

massive pavonid corals which often contributed 90% or more to the live coral cover from depths of 8-10 m to 20-25 m (GLYNN & WELLINGTON, in preparation). Pocilloporid buildups were present, but small in area and almost always confined to shallow depths ($\leq$10 m). At Malpelo Island, *Porites lobata* was the predominant coral species, but *Pavona clavus* and *Gardineroseris planulata* were also abundant (BIRKELAND *et al.*, 1975). Old colonies of *Porites lobata* are also abundant in some areas with *Acanthaster* (see below), probably because this coral is a nonpreferred prey and is attacked by the crown-of-thorns only when most other species have been eaten. *Acanthaster* is present at Cocos Island (5° 33′N; 86° 59′W), where the predominant coral, *Porites lobata* (erroneously identified in Bakus, 1975, as *P. californica;* J. W. WELLS (personal communication), extends from just below the extreme low tide level to at least 31 m depth (BAKUS, 1975). *Pocillopora* is also present at Cocos but has not been reported to form buildups. The steeply sloping island shores at Cocos, as at Malpelo and in the northern Galápagos Islands, probably prevent the buildup and stabilization of a pocilloporid frame at these localities. This possibility indicates that other factors besides *Acanthaster* must also play an important role in determining the structure of coral communities.

The Role of other Corallivores.

Corallivores consuming the greatest amount of live coral at Gorgona were apparently *Arothron meleagris* and *Jenneria pustulata,* both specialists on *Pocillopora* spp. The abundances of these corallivores at Gorgona were comaparable with reef sites in Panamá and their role as the most important corallivores at Gorgona is largely inferred from a study of their abundances and feeding rates in Panamá (GLYNN *et al.,* 1972). In the coral community at Señora Islet, Gulf of Panamá. *A. meleagris* and *J. pustulata* together consumed 5.6 metric tons of coral (tissues plus skeleton) per ha per year (GLYNN *et al.,* 1972). While this amounted to about 27% of the annual coral growth (plus 6% due to hermit crabs) the coral community still showed vigorous growth with significant framework production.

Corallivores observed to have an important effect on reefs elsewhere in the eastern Pacific, such as hermit crabs in Panamá and *Eucidaris* in the Galápagos, were either uncommon at Gorgona or did not prey on live coral there.

It is conceivable that *Eupomacentrus acapulcoensis,* by selectively killing pavonid corals while enlarging its algal mat (WELLINGTON, in press), exercises a considerable effect on the relative abundances of corals at Gorgona. The greatest coral damage caused by this damselfish was inflicted on *Pavona clavus* and this appeared to be most pronounced on colonies present in the mid and upper forereef slope. Numerous massive species *(Pavona clavus, P. gigantea* and *Gardineroseris)* present in the lower foreref slope and on the sand plain seemed to harbor fewer damselfish and suffered less damage than colonies at shallow depth. WELLINGTON (in press) has shown that the differential effect of damselfish on massive corals between reef zones is due primarily to depth-related differences in substrate complexity a necessary requisite for the establishment of damselfish territories. The increased cover available in the pocilloporid framework at shallow depths provides high substrate complexity supportive of high damselfish densities. Present observations suggest that massive colonies grow to a large size, with little interference, in deep forereef habitat but are damaged extensively by damselfish in shallow areas with high substrate complexity and are subsequently colonized and/or overtopped there by branching (pocilloporid) colonies. The dead massive species are then incorporated into the reef foundation as the pocilloporid reef front expands seaward. It is worth noting that the two damselfish species that form and maintain algal mats in coral communities in the Galápagos do not kill live coral (GLYNN & WELLINGTON, in preparation). Thus the prevalence of pavonid corals in the Galápagos could be due to the absence of both damselfish damage and *Acanthaster.*

Two remarks are in order regarding reef associates that do not feed on coral directly. The blunthead triggerfish, *Pseudobalistes naufragium,* which incidently destroys large areas of live *Pocillopora* in the Pearl Islands, Panamá (WELLINGTON, in preparation), while searching for prey that live among the basal branches of coral, was uncommon at Gorgona. *Toxopneutes roseus* (AGASSIZ), a sea urchin that, by its daily feeding movements through the sediment, adversely affects the survival of young corals on certain reef areas in Panamá (GLYNN, unpublished observations) was also uncommon on the reefs we examined.

Concluding Remarks.

In the light of a) the rapid growth of *Pocillopora* and its overtopping, growth habit (PORTER, 1974), b) its ability to colonize new surfaces (HARRIGAN, 1972) and to propagate asexually from broken branches (GLYNN, unpublished observations), c) its capacity to produce sweeper tentacles which are effective in killing adjacent massive corals (WELLINGTON, 1980), d) *Acanthaster's* avoidance of intact colonies (with their protective crustacean symbionts) (GLYNN, 1976), and e) the selective grazing (predation) by damselfish on nonpocilloporid corals, it is not surprising that so many eastern Pacific reefs are composed primarily of pocilloporid species. The following sequence of events in the development of an eastern Pacific fringing reef is thus proposed.

During the earliest stages of reef formation, when the incipient coral framework is located at shallow depth near shore, pocilloporid corals and small nonpocilloporid species are predominant. As the reef grows horizontally in a seaward direction, massive corals which initially had a refuge in the forereef zones are surrounded, and eventually overwhelmed (overgrown) by the prograding front of pocilloporid corals. The death and eventual overgrowth of massive colonies present at upper and mid forereef levels are hastened on many reefs by damselfish. Massive corals and small nonpocilloporid species are preferentially eliminated in mid and lower forereef zones by *Acanthaster* when present. The last situation, especially evident on many reefs in Panamá, results in low diversity reefs with a high relative abundance of pocilloporid corals.

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