

ATOLL RESEARCH BULLETIN

NO. 499

**CORAL COMMUNITY STRUCTURE OFF THE PACIFIC COAST OF
COLOMBIA: ONSHORE VS OFFSHORE CORAL REEFS**

BY

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**ISSUED BY
NATIONAL MUSEUM OF NATURAL HISTORY
SMITHSONIAN INSTITUTION
WASHINGTON, D.C., U.S.A.
AUGUST 2003**

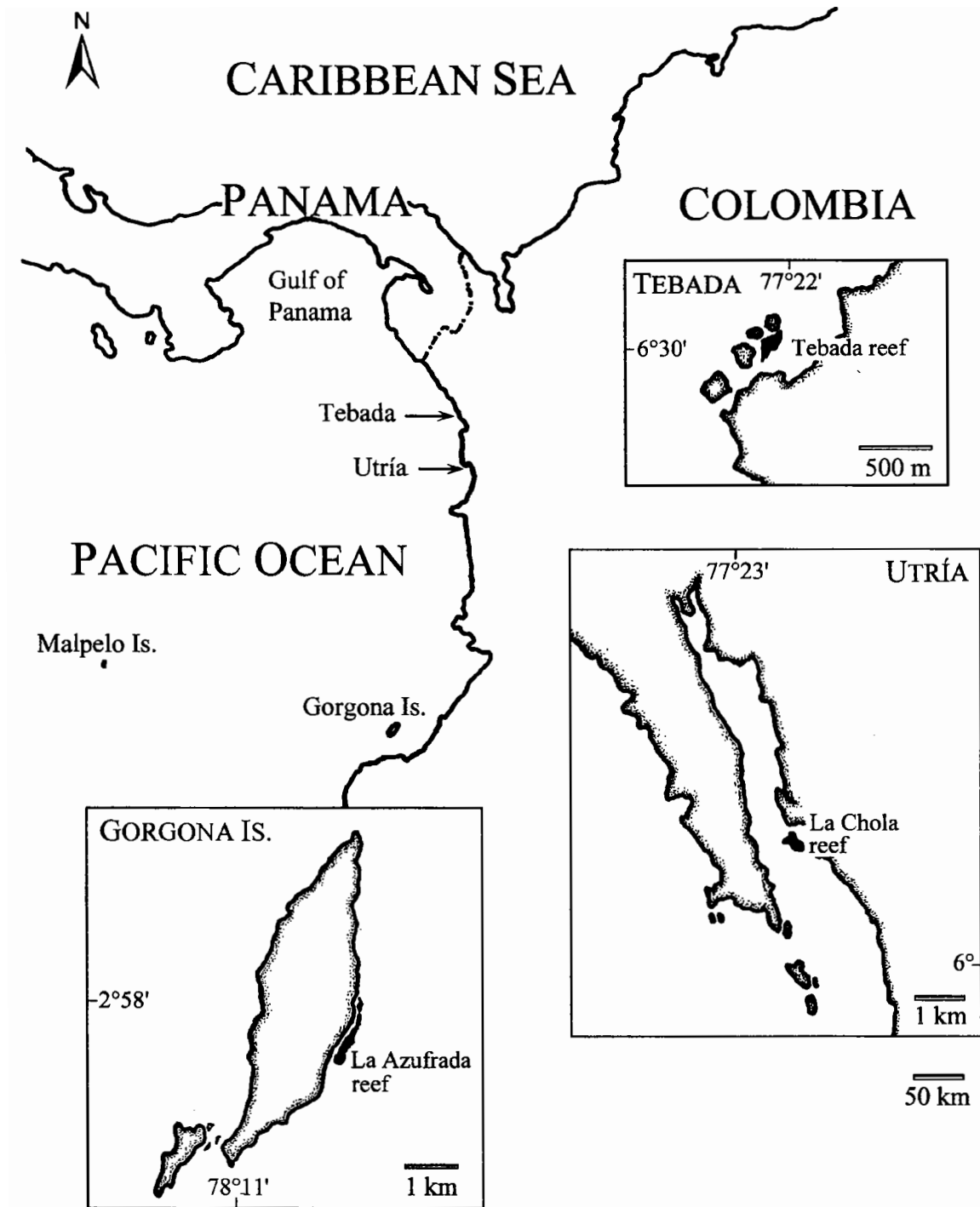


Figure 1. Location of study reefs surveyed on the Pacific coast of Colombia. In detail (inserts) Gorgona Island, Ensenada de Utría, and Tebada. Coral reefs are indicated in black (after Vargas-Ángel, 1996, 2001).

CORAL COMMUNITY STRUCTURE OFF THE PACIFIC COAST OF COLOMBIA: ONSHORE VS OFFSHORE CORAL REEFS

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BERNARDO VARGAS-ÁNGEL¹

ABSTRACT

Between 1996 and 1998 a quantitative assessment of coral community composition was conducted for three coral reefs off the Pacific coast of Colombia: La Azufrada reef (offshore); and La Chola and Tebada reefs (onshore). Several parameters were measured, including percent live and dead coral cover, algal cover, species richness, as well as the population densities of the corallivorous pufferfish *Arothron meleagris* and the sea urchin *Diadema mexicanum*. These parameters were contrasted within and among reefs in order to quantitatively describe and evaluate coral community structure in the region. All reefs exhibited paucispecificity. Zooxanthellate scleractinian species richness was high at La Azufrada reef (11 species), and lower at Tebada and La Chola reefs (six and five species respectively). Differences in generic composition were observed among reefs; *Pocillopora* was dominant at La Azufrada and La Chola, and *Psammocora* at Tebada. Mean percent coral cover also differed significantly among reefs; it was nearly 40% at the onshore localities and over 70% at the offshore site. Population densities of pufferfish and sea urchins were higher offshore than onshore. La Azufrada was the only reef to exhibit ecological differences among reef zones, namely 1) percent live coral cover; 2) coral species richness; and 3) turf algal cover. Differences among reef zones at the onshore sites were not statistically significant; the variability within reef zones was greater than among reef zones.

The results of this study were related with data for sea-surface temperature, insolation, sedimentation, freshwater discharge (rainfall and river discharge) and ocean-circulation patterns, as these measures of environmental variability may affect coral community composition. Coral cover and degree of community complexity (e.g., ecological differences among reef zones) were highest at the offshore locality where insolation was high and sedimentation low. Elevated freshwater discharge may limit coral larval dispersal and recruitment to the downstream onshore coral communities. Finally, extreme high- and low-water temperatures (El Niño-Southern Oscillation) and terrestrial runoff also appear to be important community-structuring determinants.

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Manuscript received 25 September 2002; revised 5 February 2003

INTRODUCTION

Quantitative descriptions of coral-reef community ecological characteristics are desirable for studies of reef dynamics across spatial scales. Detailed knowledge of coral community structure is also important to evaluate cause-effect relationships during/after environmental disturbances (Dustan and Halas, 1987). The need for such data has stimulated the study and documentation of local coral community composition and the possible causes of ecological differences within and across regions.

Eastern Pacific coral reef biota can offer an advantage in interpretative ecological studies due to the often marginal environmental conditions in which they occur (Glynn and Ault, 2000). Zonation and ecological partitioning in these marginal systems can be caused by recurrent and/or chronic disturbances which result in mass mortalities or the suppression of otherwise dominant species (see Riegl, 1999; Riegl and Riegl, 1996). Extensive research conducted in Panama, Costa Rica, and the Galapagos Islands has contributed substantially to our understanding of eastern Pacific coral-reef ecology and biogeography (Glynn, 1976; Glynn and Wellington, 1983; Cortés, 1990; Guzmán and Cortés, 1993; Glynn and Maté, 1996; Fong and Glynn, 1998; and Glynn and Ault, 2000). Coral reefs of the Pacific coast of Colombia so far have received little attention (Vargas-Ángel, 1996; Vargas-Ángel, 2001; and Zapata and Vargas-Ángel, in press), and a quantitative assessment of community status and variability across spatial and temporal scales is still needed.

The purpose of this study is to address coral community variability on the Pacific coast of Colombia as it relates to onshore and offshore localities. It provides information pertaining to: 1) coral cover, species richness and abundance; 2) community differentiation within reefs and among reefs; and 3) the possible role of local environmental conditions and disturbances as determinants of coral-reef community structure.

MATERIALS AND METHODS

Coral-Reef Community Structure

Coral reef community composition was studied at three sites: one offshore (La Azufrada reef, Gorgona Island); and two onshore (La Chola reef, Utría and Tebada reef, Cupica Fig. 1). Surveys were conducted between January 1996 and June 1998. Using haphazardly selected marks on the beach as a reference, 100-m long tape measures were extended under water perpendicular to the long-shore axis of the reefs from the shallowest areas of coral growth to the reef base where coral development ceased (hereafter referred as survey stations). Three survey stations were laid at each site. Sampling points along the survey stations were previously selected from a random number table. At each preselected point, a transect, consisting of a 10 m-long chain, was laid perpendicular to the tape measure following the bottom contour. Between 21 and 26 transects were surveyed at each station (total number of transects: La Azufrada reef, 78; La Chola reef, 61; and Tebada reef 67). Chain links were marked every 10 cm with flag

tape (see Rogers et al., 1994). Bottom type (i.e., dead coral, coral/rubble, live coral, and algae) was recorded only at labeled chain links. Scleractinian coral species were identified following Wells (1983). Depth was recorded using depth gauges (accuracy ~0.3 m) and values were adjusted to mean sea level. Data sets meeting parametric statistical requirements were analyzed using one-way Analyses of Variance (ANOVA). Transformations, including \ln and e^n , were applied to some data sets. When necessary, Kruskal-Wallis tests were used in lieu of single classification ANOVA.

Faunal Assemblages

Population densities of the corallivorous pufferfish *Arothron meleagris* (Bloch and Snieder) were estimated from man-hour counts by swimming along the reef flat. Individuals per man-hour (ind man-hr⁻¹) data were converted to individuals per hectare (ind ha⁻¹) according to Guzmán and Robertson (1989). In addition, the abundance of the sea urchin *Diadema mexicanum* Agassiz was determined by placing two 1 m² quadrats (one on each side of the tape measure) at each of the randomly selected points used in the bottom type surveys. The numbers of sea urchins were recorded and correlated with percent coral cover, percent dead coral/rubble, and macroalgae. Additionally, densities of pufferfish and sea urchins were compared among reefs using non-parametric Kruskal-Wallis tests and Mann-Whitney rank-sum tests respectively.

Environmental Data Sets

Sea surface temperature (SST) records between 1950 and 1992 were obtained from the ship-based Comprehensive Ocean-Atmosphere Data Set (COADS) on a 2×2° grid, centered at 5°N; 77°W for Utría-Tebada and 3°N; 77°W for Gorgona Island. SSTs between 1993 and 1998 were obtained from satellite-derived data series (Advanced Very High Resolution Radiometer, AVHRR) centered at 3°N; 78°W for Gorgona Island and 6°N; 77.5°W for Utría-Tebada.

Meteorological data sets were provided by the Colombian Meteorological Authority, based on instrumental measurements (Instituto de Hidrología, Meteorología y Estudios Ambientales, IDEAM 1999a,b). Rainfall, solar irradiance and cloud-cover data for Gorgona Island were derived from the Gorgona Island meteorological station (3°2'N; 78°09'W) for the period 1986–1999. Rainfall at Utría-Tebada was obtained from the Utría meteorological station (6°5'N; 77°23'W) for the period 1993–1997. Solar irradiance and cloud cover for Utría-Tebada were obtained from the Bahía Solano meteorological station (6°14'N; 78°25'W) between 1965–1998.

Average river discharge rates (m³ s⁻¹) on the Pacific watershed of Colombia were obtained from Lobo-Guerrero (1993). Snapshot measurements of sediment accumulation rates were obtained from Vargas-Ángel (2001), based on 1 L cylindrical traps (3:1 height to diameter ratio, ~7.5 cm diameter), placed on the reef edge at each site, approximately 5–10 cm above the substrate (see Gardner, 1980 a,b).

RESULTS

A schematic representation of coral species distributions and profiles of percent live coral cover and species richness are presented in Figure 2. All the coral reefs in this study can be classified as fringing reefs (see Kinzie and Buddemeier, 1996). They were separated from the shore by a shallow channel, considerably deeper than the reef itself, and generally covered with mud and/or fine sand. Reefs exhibited several topographical zones: back reef, reef flat, reef edge and reef slope (following Glynn, 1976; Cortés, 1990). The back reef was transitional between the sandy channel and the living reef flat. This zone was usually characterized by sparsely distributed corals intermingled with bioclastic sand and rubble. The reef flat was commonly the best-developed reef zone with the highest coral cover. Some reef flats were subject to periodic subaerial exposure during extreme low tides. The reef front marked the transition between the shallow reef flat and the reef slope. The reef slope descended gently to a fine sand and mud bottom at approximately 8–10 m depth.

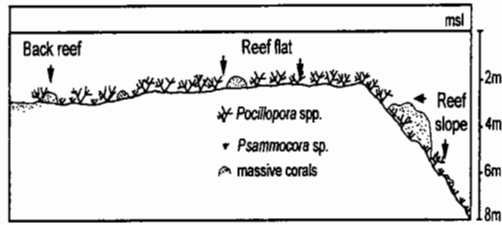
Inter-reef Comparisons

All reefs exhibited high levels of paucispecificity. *Pocillopora damicornis* represented 91% of all living corals at La Azufrada and La Chola reefs. At Tebada reef, *Psammocora stellata* and *Psammocora ?brighami* accounted for nearly 90% of the live cover. Live coral cover was highest at La Azufrada reef, with mean cover of over 72% (Table 1). Values as high as 100% cover were observed on the reef flat, mainly due to monospecific stands of *P. damicornis*. Mean live coral cover at La Chola reef was 41% and coral cover was patchy. At Tebada reef, live coral cover was slightly lower than at La Chola (39%), but differences in percent cover between these two reefs were not statistically significant (Table 1). During extreme low tides (~ -0.4 m or lower) large sections of the reef flat at La Azufrada and La Chola were subaerially exposed. Fleshy brown macroalgae and crustose coralline algae (CCA) were common growing on the dead coral surfaces. The reef flat at Tebada was substantially deeper (~0.5 m) than at La Chola and La Azufrada and was not subject to recurrent subaerial exposure during extreme low tides.

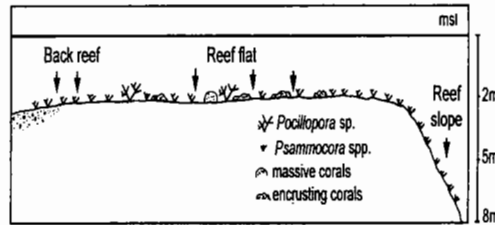
Dead coral cover and unoccupied substratum were nearly three times higher at Tebada reef than at La Azufrada and those differences were statistically significant ($P < 0.05$, Kruskal-Wallis test). By contrast, differences in dead coral cover between La Chola and Tebada reefs were not statistically significant (Table 1). Algal cover was higher at La Azufrada than at La Chola reef, but differences between reefs were also nonsignificant (Table 1). This occurred due to high variability in algal cover within reef zones at both sites.

The total number of scleractinian corals was higher at La Azufrada reef (11 species) than at La Chola and Tebada reefs (five and six species respectively). Branching *Pocillopora elegans* and *Pocillopora eydouxi* were common at La Azufrada reef but absent at La Chola and Tebada reefs. Similarly, the massive species *Pavona clavus* and *Pavona gigantea* were also common (but not abundant) at La Azufrada reef, but noticeably rare or absent at La Chola and Tebada reefs. Nearly 65% of the transects

La Azufrada reef



La Chola reef



Tebada reef

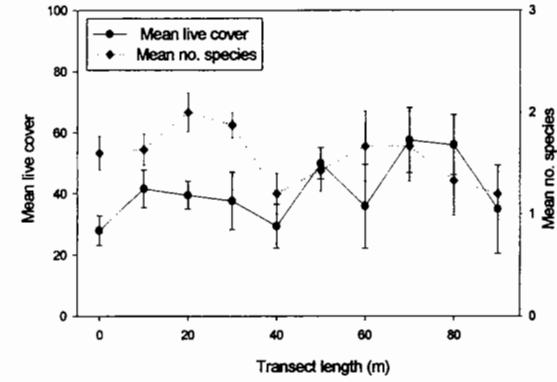
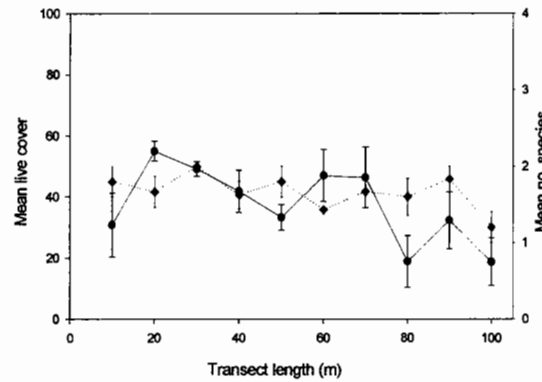
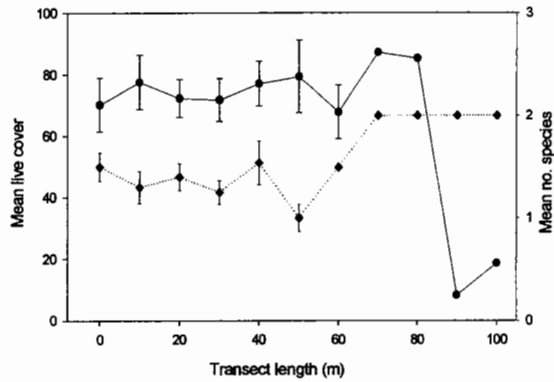
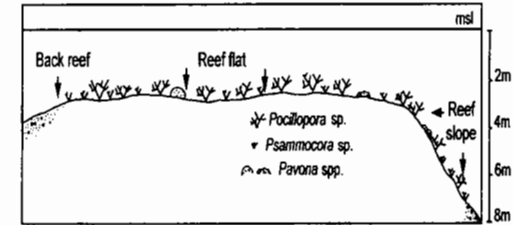


Figure 2. Profiles of coral-reef species distributions (upper panels), and percent live coral cover and species richness (lower panels) at La Azufrada reef (left), La Chola reef (center), and Tebada reef (right). Coral community surveys conducted on randomly selected, 10 m-long chain transects, laid parallel to the beach, along three 100 m-long survey stations at each site. Twenty-one to 26 chain transects were surveyed at each station (Total number of transects per site: La Azufrada reef, 78; La Chola reef, 61; and Tebada reef, 67; surveys conducted between January 1996 and June 1998; msl = mean sea level; vertical lines indicate standard error of means).

Table 1. Summary statistics (mean±SE) of coral-reef community composition at La Azufrada reef (Gorgona Island), La Chola reef (Ensenada de Utría) and Tebada reef (Tebada). A, *Pocillopora damicornis*; B, *Pocillopora capitata*; C, *Pocillopora elegans*; D, *Pocillopora eydouxi*; E, *Psammocora stellata*; F, *Psammocora ?brighami*; G, *Pavona clavus*; H, *Pavona gigantea*; I, *Pavona varians*; J, *Porites lobata*; K, *Porites panamensis*; L, *Gardineroseris planulata*. Statistical comparisons: Azf = La Azufrada reef; Cho = La Chola reef; Teb = Tebada reef.

Community Parameter	La Azufrada reef	La Chola reef	Tebada reef	Statistical comparisons
Depth range (m)	0.5–8	0.5–7	1.0–8	no statistical comparison
Total reef extension (ha)	~15	~10.5	~4.5	no statistical comparison
Reef framework thickness (m)*	6–8	>4.5	~4.0	no statistical comparison
Coral species present**	ABCDEFGHIJKL	ABEHI	AEFHIL	no statistical comparison
% Live coral cover	72.89±3.02	41.15±2.59	39.03±2.47	Azf>Cho, Teb; P<0.05, Kruskal-Wallis ANOVA, Dunn's test
% Dead coral cover	20.08±2.64	52.28±2.81	60.9±2.46	Azf<Cho, Teb; P<0.05, Kruskal-Wallis ANOVA, Dunn's test
% Fleshy macroalgae	6.95±1.65	4.92±1.56	<2%	P>0.05, Mann-Whitney rank sum
% <i>Pocillopora</i> spp.	66.52±3.14	37.81±2.7	4.19±0.85	Azf>Cho>Teb, P<0.05, Kruskal-Wallis ANOVA, Dunn's test
% <i>Psammocora</i> spp.	4.52±1.08	3.19±0.54	34.20±2.47	Teb>Azf, Cho, P<0.05, Kruskal-Wallis ANOVA, Dunn's test
% Massive corals	0.01±0.01	0	0.47±1.24	Teb>Azf, Cho, P<0.05, Kruskal-Wallis ANOVA, Dunn's test
<i>Diadema mexicanum</i> (ind m ²)	2.27±0.38	0.492±0.27	0	Azf>Cho>Teb, Mann-Whitney rank sum
<i>Arothron meleagris</i> (ind ha ⁻¹)	6.58±0.88	5.65±1.15	1.94±0.06	Azf, Cho > Teb, Kruskal-Wallis ANOVA, Dunn's test

*obtained from Glynn et al. (1982) and Vargas-Ángel (2001)

**including observation outside the sampling transects

sampled at La Azufrada contained exclusively one coral species (i.e., *P. damicornis*) and only 2.5% contained more than two species. At La Chola reef, approximately 60% of the transects contained two coral species (i.e., *P. damicornis* and *P. stellata*) and at Tebada reef nearly 58% of the transects contained at least three species of scleractinian corals (i.e., *P. stellata*, *P. ?brighami* and *P. varians*).

La Azufrada was the only reef to exhibit structural differences among reef zones. These differences were due mainly to seaward changes in percent live coral cover and species composition (Table 2). The reef flat at La Azufrada was composed mainly of *P. damicornis*, while the reef slope exhibited higher cover of *P. stellata* and *P. varians*, as well as massive corals such as *P. clavus* and *Gardineroseris planulata*. Such ecological differences among reef zones were not observed at La Chola and Tebada reefs (Table 2). At these sites, the variation in coral cover and species composition was greater within reef zones than among reef zones.

Faunal Assemblages

The abundances of selected macroconsumers also differed among the study sites. Population density of the corallivorous pufferfish *A. meleagris* was higher on offshore than onshore reefs and these differences were statistically significant ($P < 0.05$, Kruskal-Wallis, Table 1). The mean population density of *D. mexicanum* was 2.27 ± 0.38 ind m^{-2} (mean \pm std error) at La Azufrada reef and 0.49 ± 0.27 ind m^{-2} at La Chola reef. Those differences between sites were also statistically significant ($P < 0.05$, Mann-Whitney rank sum, Table 1). At La Azufrada and La Chola reefs, highest densities of sea urchins ($6-12$ ind m^{-2}) were associated with dense monospecific stands of *Pocillopora* where coral cover was $>60\%$. Correlation analyses indicated that there was a statistical association between coral cover and density of sea urchins at La Azufrada reef ($r = 0.38$; $P < 0.05$, Pearson's product moment correlation) but not at La Chola ($r = 0.29$; $P > 0.05$, Pearson product moment correlation). The sea urchin *D. mexicanum* was absent at Tebada reef. Instead, other echinoids were observed, including *Centrostephanus coronatus* (Verrill) and the pencil sea urchin *Hesperocidaris asteriscus* Clark.

DISCUSSION

Coral-Reef Community Comparisons

Results showed that La Azufrada (offshore) was the largest, most diverse, and best developed coral reef. Ecological differences between the offshore (La Azufrada, Gorgona Island) and the onshore (Utría and Tebada) coral communities are based on the following criteria: 1) richness of the coral fauna; 2) coral species abundances; 3) percent of live coral cover; and 4) overall structural complexity (e.g., ecological differences among reef zones).

Coral species composition differed substantially between the onshore and offshore sites. Species richness and live cover were nearly twice as high at La Azufrada compared with the onshore reefs. Onshore reefs contained less than half (45%) of the

Table 2. Summary of coral-reef community structural statistics (mean±SE) based on 78 survey transects at La Azufrada reef, 61 at La Chola reef and 67 at Tebada reef. A, *Pocillopora damicornis*; B, *Pocillopora elegans*; C, *Psammocora stellata*; D, *Psammocora ?brighami*; E, *Pavona gigantea*; F, *Pavona varians*. Statistical comparisons: RF = reef flat, RS = reef slope, BR = back reef.

Reef/community parameter	Reef zone			Statistical comparison
	Back-reef	Reef-flat	Reef-slope	
La Azufrada reef				
No. of transects	12	58	8	no comparison
% live cover	56.87±13.7	76.12±2.9	44.48±16.4	RF>BR,RS; P<0.05, Kruskal-Wallis ANOVA, Dunn's test
species richness (No. coral species)	1.8±0.17 ABC	1.3±0.06 ABCE	1.7±0.15 ACF	RF<BR,RS; P<0.05, Kruskal-Wallis ANOVA, Dunn's test
La Chola reef				
No. of transects	12	36	13	no comparison
% live cover	44.2±5.01	43.7±3.60	34.0±5.11	P>0.05, Kruskal-Wallis ANOVA
# coral species	1.6±0.13 AC	1.6±0.09 AC	1.6±0.12 AC	P>0.05, Kruskal-Wallis ANOVA
Tebada reef				
No. of transects	20	39	8	no comparison
% live cover	33.79±4.31	39.75±3.09	51.14±8.81	P>0.05, Kruskal-Wallis ANOVA
# coral species	1.56±0.14 ACDF	1.62±0.09 ACDEF	1.60±0.24 ACDF	P>0.05, Kruskal-Wallis ANOVA

scleractinian species present at La Azufrada reef. Notable absences at La Chola and Tebada reefs were *P. clavus*, *P. elegans* and *P. eydouxi*, which were ubiquitous at La Azufrada reef. Similarly, no *Porites lobata* occurred at the onshore sites. *Pavona varians* was relatively abundant at La Azufrada and Tebada reefs but rare at La Chola. *Pocillopora damicornis* was common at all sites, but only dominant at La Azufrada and La Chola reefs. These results are surprising given the wide environmental tolerance, geographical distribution, and the rapid growth rate of this species (Glynn and Ault, 2000; Vargas-Ángel et al., 2001). Finally, *P. stellata* was common at all sites, but dominant only at Tebada. This situation may be related to the lower abundance of *P. damicornis* at this site. Like *Pocillopora*, *P. stellata* also exhibits a wide tolerance range

for temperature extremes (Maté, 1997). However, on shallow well-illuminated substrates, *Psammocora* is generally out-competed by fast-growing *P. damicornis*.

The ecological zonation of the reef community along environmental gradients was relatively clear at La Azufrada. For example, the shallow reef flat exhibited higher cover of *P. damicornis* and reduced species richness. This shallowest area of the reef experienced warmer temperatures and higher light levels than other reef zones. Conversely, lower coral cover and greater abundance of non-pocilloporids were evident on the back reef and the slope. These areas experienced lower light levels. At La Chola and Tebada, community differentiation along gradients of depth and light was not clear. The variation of coral cover and species richness was greater within reef zones than among reef zones. This lack of zonation is probably an indicator of “instability”. Environmental stress and disturbances can offset competitive interactions and biological processes among species, resulting in phase shifts in community structure (see Karlson 1999).

Possible Factors Determining Ecological Differences Between Reefs

Regional differences in coral community composition have been explained in terms of shallow-water habitat availability (Bellwood and Hughes, 2001). In low diversity regions, such as the eastern Pacific, patterns of coral species richness can also be influenced by local environmental differences as well as human impacts. For example, Carriquiri and Reyes-Bonilla (1997) found that the scleractinian coral fauna at Nayarit was 30% more diverse at insular localities as compared to mainland Mexico. They suggested that lower water transparency, higher river discharge and upwelling events may be the principal factors determining among-site coral community differences (Carriquiri and Reyes-Bonilla, 1997; Reyes-Bonilla, pers. comm). It is proposed that the ecological differences between the onshore and offshore coral communities observed in this study exist due to a gradient of environmental conditions in combination with natural and human perturbations. Some of these limiting factors are identified and discussed below.

Temperature. Sea-surface temperatures (SSTs) on the Colombian Pacific are relatively warm, ranging between 20–28°C, depending on location and season (Wyrski, 1965). At Gorgona Island, sea surface isotherms range between 25–28°C year round. At Utría and Tebada, SSTs vary between 25–28°C during the rainy season (May–Dec) and between 24–26°C during the dry season (Jan–April). Recurrent anomalously high and low SSTs occur in the Colombian Pacific. During severe El Niño sea warming events, thermal anomalies can be as high as +2–3°C (i.e., 30–32°C) (in situ hand-held temperature measurements, as well as long-term temperature records derived from COADS and remotely-sensed data; see Prah, 1985; Vargas-Ángel et al., 2001). Coincidentally, negative temperature excursions, as low as 16°C can occur during La Niña (sensu Philander, 1990) conditions (see Vargas-Ángel, 1996, 2001).

El Niño-Southern Oscillation (ENSO) disturbances during 1982–83, and more recently (1997–98), have demonstrated that prolonged warm sea conditions can have devastating and profound effects on coral reefs in the region. The 1982–83 ENSO

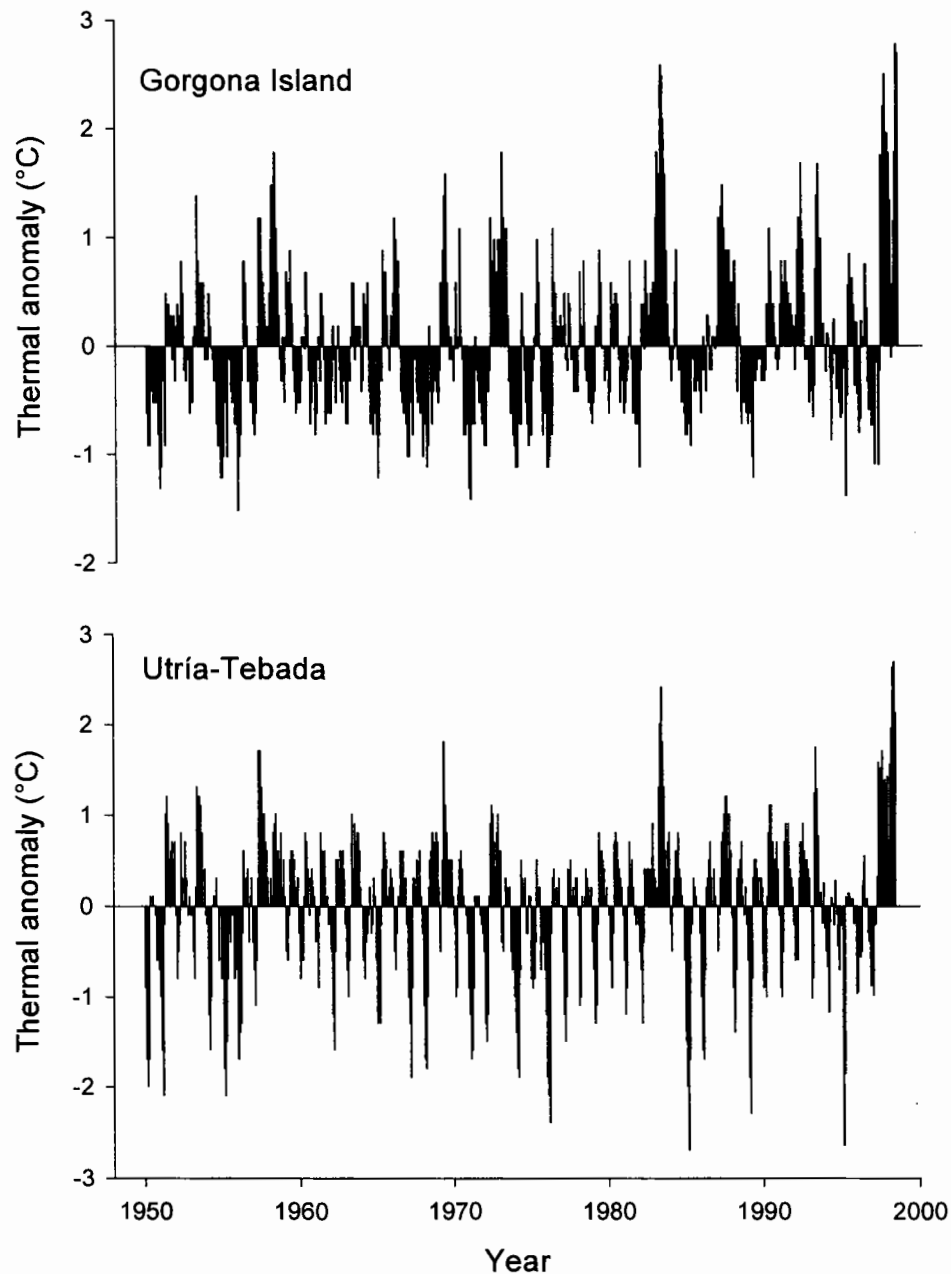


Figure 3. Time series of sea-surface temperature (SST) anomalies for two regions of the Pacific coast of Colombia; Gorgona Island, and Utría-Tebada. SSTs between 1950–1992 were obtained from the Comprehensive Ocean and Atmosphere Data Set (COADS) on a $2 \times 2^\circ$ grid, centered at 3°N ; 77°W for Gorgona Island, and 5°N ; 77°W for Utría-Tebada. SSTs between 1993–1998 were extracted from satellite data series centered at 3°N ; 78°W for Gorgona Island, and 6°N ; 77.5°W for Utría-Tebada.

resulted in catastrophic coral mortality and loss of diversity at La Azufrada reef. Live cover was reduced by ca. 85% (from surveys conducted in 1979; see Glynn et al., 1982),

and massive species including *G. planulata*, *P. lobata* and *Porites panamensis* were nearly eliminated (see Prah, 1985). By contrast, during the 1997–98 El Niño event, coral bleaching and mortality at La Azufrada did not reach the catastrophic proportions of the 1982–83 event. Despite the fact that thermal anomalies in 1997–98 were comparable to those of the 1982–83 event, only 24% of corals bleached and ~1–2% died in 1998 (Vargas-Ángel et al., 2001). One common aspect to both disturbances was that massive corals were the least resilient and thus exhibited the highest mortality rates. In light of these findings, Vargas-Ángel et al. (2001) proposed that preferential bleaching and mortality of massive corals during severe El Niño conditions may control the relative abundances and richness of these species at La Azufrada. Conversely, resilient species such as *P. damicornis* may promote rapid community regeneration and prevent framework erosion after El Niño disturbances. Thus, it is possible that under recurrent and severe El Niño conditions, thermally sensitive corals at La Azufrada reef may become eliminated, leaving behind more resilient species and resulting in loss of coral richness at this site.

The short-term and long-term effects of El Niño events on onshore reefs have been less studied. Based on the pre- and post-disturbance research by Prah and Erhardt (1985) and Vargas-Ángel (1996) respectively, it can be inferred that the 1982–83 El Niño did not have catastrophic consequences on the onshore reef localities. Added evidence in support of this notion was obtained during the 1997–98 disturbance. Coral bleaching at La Chola and Tebada reefs during 1998 was minimal (<1%), and no coral mortality was observed. Additionally, in situ and remotely sensed data showed that positive thermal anomalies at La Chola and Tebada reefs were lower (~1°C) and extended for a shorter period of time than at Gorgona Island (Vargas-Ángel et al., 2001).

Long-term temperature records indicate that El Niño-related positive thermal anomalies have been consistently lower at La Chola and Tebada reefs than farther south (Fig. 3). This probably occurs because the effects of ENSO sea warmings are attenuated by normal seasonal oceanographic processes in the region, such as the mixing of water masses and the upwelling system in the Panama Bight.

By contrast, negative thermal excursions are greater at northern coastal localities than farther south at Gorgona Island. These occur due to persistent and intense wind-driven upwelling in the neighboring Gulf of Panama. For example, in February 1989 unusually cold water (16–18°C) in association with blooms of *Gymnodinium* sp. resulted in widespread coral bleaching at La Chola reef. Underwater temperatures as low as 18–20°C were reported at Gorgona Island at this time. However, no coral bleaching was observed in association with this event.

During periods of intense upwelling, low sea-water temperature, eutrophication, algal overgrowth, and bioerosion acting alone or together can reduce coral cover and even cause local extinctions (Glynn and Ault, 2000). Thus, it is suggested that corals at La Chola and Tebada reefs may be more vulnerable to stress due to cold-water spells and intense upwelling than by sea-warming events. In contrast, corals at La Azufrada reef, located outside the influence of upwelling conditions, experience more bleaching and mortality from anomalous and recurrent high SST events.

Light. Light quality and quantity can be important determinants of coral community composition and structure at the study sites. Instrumental data sets indicate that solar irradiance is on average 10% higher at Gorgona Island than at Utría-Tebada and, during the dry season, differences between sites are twofold. Cloud cover also differs between onshore and offshore localities (Table 3) and it is nearly 10% higher at Utría-Tebada than at Gorgona Island. Decreased light quality and quantity conditions at La Chola and Tebada reefs may be unfavorable for coral metabolism and photosynthesis-driven calcification. Phototrophic species such as pocilloporids and agariciids largely depend on higher light levels to balance their energetic needs (Wellington, 1982). This condition may explain the lowered coral extension rates, species absences and reduced coral cover at the onshore sites compared to Gorgona Island (see Vargas-Ángel, 2001).

Table 3. Summary statistics (mean±SE) of selected environmental parameters at Gorgona Island and Utría-Tebada. Environmental parameters of rainfall, solar irradiance and cloud cover were obtained from instrumental records provided by the Colombian Meteorological Authority (Instituto de Hidrología, Meteorología y Estudios Ambientales, IDEAM 1999a,b), see materials and methods for details. Sediment accumulation rates were obtained from Vargas-Ángel (2001) based on 1 L tubular traps (3:1 height to diameter ratio, ~7.5 cm diameter) placed approximately 5–10 cm above the substrate.

Environmental variable	Location		Statistical comparisons
	Gorgona Is.	Utría-Tebada	
Rainfall (mm yr ⁻¹)	6725.62±178.87	7367±263.64	no comparison (low sample size)
Irradiance (hr d ⁻¹)	79.87±8.75	70.64±1.77	P<0.05, t-test
Cloud Cover (%)	72.60±0.58	79.92±1.53	P< 0.05 t-test
Sedimentation (mg cm ⁻² d ⁻¹)	4.07±0.35	6.46±1.13 ^a 3.54±0.59 ^b	Ch>Teb,Az; P<0.05, one-way Anova, Tukey Test

a = La Chola reef

b = Tebada reef

Sedimentation and Water Turbidity. High-water turbidity due to excessive runoff is notable at all the study areas. Increased terrigenous siltation and sediment loading due to forest clearing, indiscriminate land use and destructive subsistence farming have caused damage to reef corals at La Azufrada and La Chola (see Prahl et al., 1979; Vargas-Ángel, 1996, 2001). At La Chola reef, it is not uncommon for underwater visibility to be reduced to 1.0 m or lower during excessive rainfall and heavy runoff. Sediment accumulation rates at this site range between 3.1–7.9 mg cm⁻² d⁻¹ (Table 3; Vargas-Ángel, 2001, unpubl.data). These values are comparable to

accumulation rates obtained by Rogers (1990) and Chansang et al. (1992) on chronically sediment-stressed reefs in the Caribbean and Thailand, respectively. Secondary evidence in support of siltation stress at La Chola reef is presented by Prahla and Estupiñán (1990), who suggest that the thin-branched ecomorph of *P. damicornis* prevalent at La Chola reef is a clear indication of stress due to increased sedimentation and turbidity. Thus, it is proposed that increased turbidity and sediment loading, together with reduced solar irradiance at La Chola reef, may result in lower coral extension and calcification rates as well as lowered coral cover and decreased reef-building potential at this site (Prahla and Vargas-Ángel, 1990; Vargas-Ángel, 1996, 2001).

Freshwater Input. Freshwater input on the Pacific coast of Colombia is high; rainfall is in the order of 5000–7500 mm yr⁻¹ and total river discharge amounts to nearly 9200 m³ s⁻¹. Both totals rank among the highest for the tropical eastern Pacific (Fig. 4). As a result, seawater surface salinity (SSS) can range between 30 and 35‰ offshore to less than 20‰ in coastal areas and near river mouths (Cantera, 1993). This low range of salinities can limit the occurrence of zooxanthellate corals in onshore localities. Waters reaching La Chola and Tebada originate from the south (Fig. 4), thus, freshwater dilution due to elevated river discharge may restrict coral larval dispersal from La Azufrada to farther north. Additionally, due to the presence of long stretches of mangrove forests, potential stepping stone habitats that could facilitate the interchange of coral species from the south to the north are scarce. Thereby, coral recruitment on onshore reefs may be highly dependent on local larval supply. Additionally, since most eastern tropical Pacific scleractinian corals spawn during the rainy season (see Glynn et al., 1991, 1994, 1996), rapid dilution of reef waters due to increased rainfall can also negatively affect coral larval viability, hence larval settlement and survival (see Coles and Jokiel, 1992). Thus, recurrent SSS reductions of reef waters at the onshore sites may further exacerbate the effects of limited allochthonous larval supply.

Species Interactions. Species interactions in concert with local environmental conditions have been central in explaining community regulation (Cornell and Karlson, 2000). For example, lower coral cover and reduced species abundances in coral-reef ecosystems have been attributed, among other factors, to competitive exclusion and predation. In the absence of the crown-of-thorns starfish *Acanthaster planci*, the pufferfish *A. meleagris* is an important coral predator on Colombian Pacific reefs (Glynn et al., 1982; see Glynn et al., 1972; Guzmán, 1988). In this study, densities of pufferfish differed among sites. However, there was no apparent relationship between puffer density and coral cover or puffer density and reef location (offshore vs onshore). Previous studies on other eastern Pacific coral reefs suggest that abundance of puffers may not be related to resource abundance but to juvenile recruitment (Guzmán and Robertson, 1989). In this study, densities of puffers were lowest at Tebada reef coincident with low abundance of *Pocillopora* spp. It is possible that low recruitment rates may determine the abundance of puffers at Tebada. However, even when uncommon, puffers at Tebada reef may impact the population of *Pocillopora* by selectively feeding on these species (see Guzmán and Robertson 1989). Further research is needed in this matter.

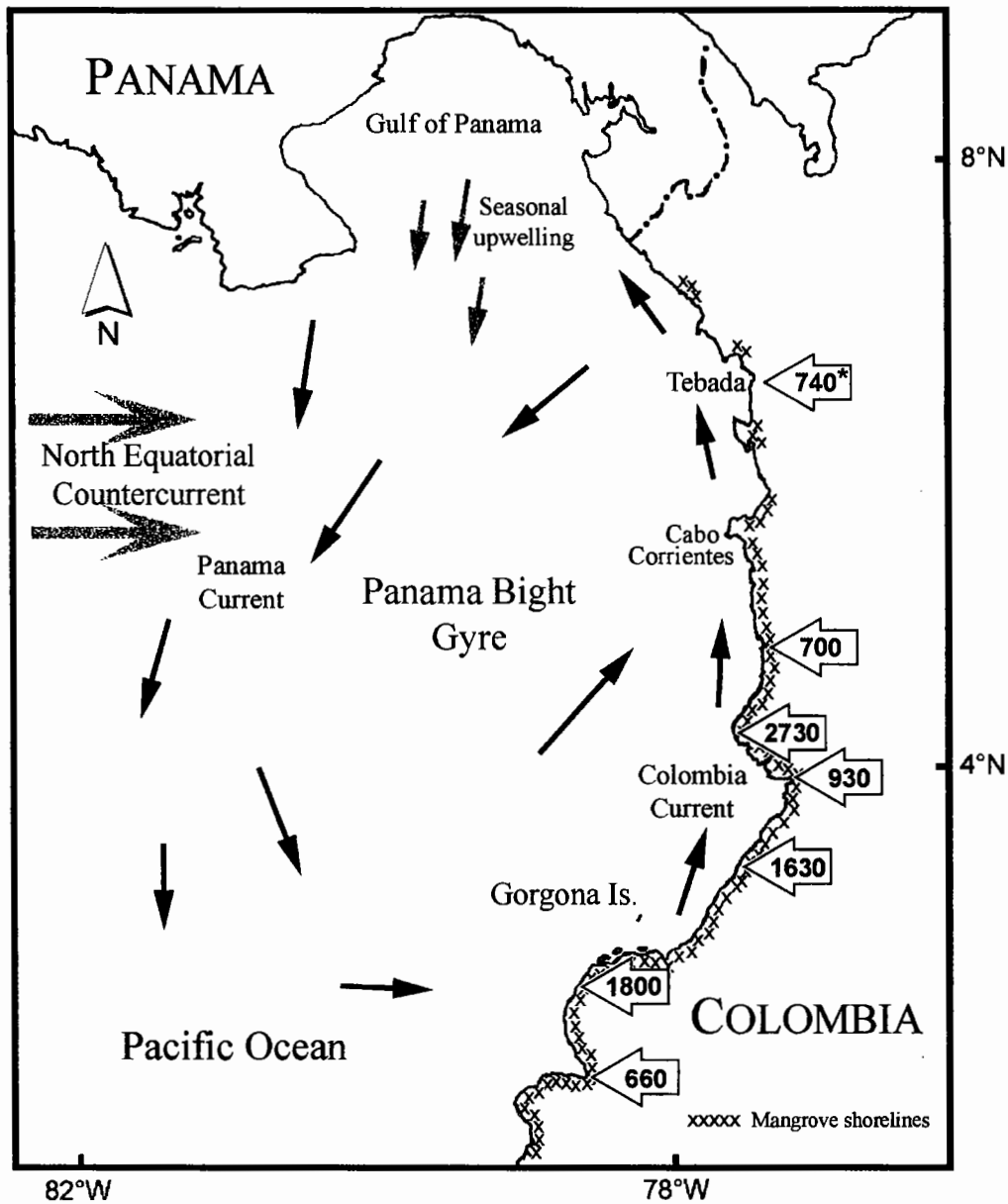


Figure 4. Schematized surface-water circulation in the Panama Bight (after Cromwell and Bennett, 1959; Wooster, 1959; Wyrki, 1965; Fieldler, 1992) and freshwater discharge on the Pacific watershed of Colombia. Location and average freshwater discharge rate ($\text{m}^3 \text{s}^{-1}$) of major rivers is indicated by horizontal white arrows. Average river discharge for the region between Cabo Corrientes and the Panamanian border is indicated with an asterisk. River discharge data obtained from Lobo-Guerrero (1993). Distribution of mangrove shorelines (x); obtained from Sánchez-Páez and Álvarez-León (1997); Vargas-Ángel (pers. observ.).

Sea urchins have been recognized as important grazing bioeroders in coral-reef habitats (Glynn, 1988). Researchers have found that sea urchins may be responsible for extensive coral-reef framework erosion and reef destruction, especially after severe disturbances. Their grazing activity can alter the spatial differences in bioerosion thus

influencing coral-reef morphology and development (Glynn, 1997). In this study, echinoid densities at La Azufrada reef were higher than at La Chola and Tebada reefs. Sea urchin abundances at La Azufrada were comparable to those reported at Caño Island, Costa Rica (Guzmán, 1988) but lower than those observed by Guzmán and Cortés (1993) and Glynn (1988) at Cocos Islands and Panama, respectively, where *Diadema* caused severe framework destruction after the 1982-83 El Niño event. At La Azufrada reef, high coral cover in concert with moderately high densities of urchins, probably maintain a balanced carbonate budget conducive to net reef accretion. At La Azufrada reef, *Pocillopora* is essential to the development of the surface bottom topography, which in turn provides habitat and shelter for numerous associated fauna and commensal symbionts (see Rios, 1986; Vargas-Ángel, 1989). Field observations indicated that there was a positive association between substratum complexity and the abundance of *Diadema* at La Azufrada reef. The highest densities of sea urchins (7–12 ind m⁻²) were found at localities with high live pocilloporid cover (mean cover >60%) (see also Glynn, 1988). It is possible that the absence of *D. mexicanum* at Tebada reef may be controlled in part by the limited abundance of suitable habitat (i.e., *Pocillopora*). In addition, low water salinities and sharp haloclines due to increased freshwater input may also affect *Diadema* larvae dispersal, survival and recruitment at Tebada (see Roller and Stickle, 1993; Metaxas and Young, 1998).

Finally, macroalgal proliferation can be another factor contributing to decreased coral cover, diminished scleractinian larval recruitment and reef development (Potts, 1977; Hughes, 1989; Tanner, 1995; Miller and Hay, 1998). In many cases, increased macroalgal cover has been preceded by drastic changes in the physical or biotic environment (Carpenter, 1990, 1997; Glynn and Colgan, 1992; Hughes, 1994). In this study, macroalgal cover was relatively high and patchy, particularly on shallow substrata at La Azufrada and La Chola reefs. Algal cover in excess of 50% was observed in areas where corals experienced partial mortality due to recurrent subaerial exposure during extreme low tides. These algal patches were guarded by territorial damselfish. In contrast, in deeper areas where corals do not become subaerially exposed, algal cover was low (0–5%). The combined effects of subaerial exposure and territorial damselfish algal lawn expansion seem to be an important control of algal cover along shallow reef areas at the study sites. By contrast, in deeper reef habitats, algal cover may be determined by factors such as light penetration and herbivore grazing.

CONCLUSIONS

Based on their location and ecological structure, coral reefs of the Pacific coast of Colombia can be grouped into two types; offshore reefs at Gorgona Island are the largest and best developed. La Azufrada reef is characterized by high coral cover of *P. damicornis* along the shallow substrates and *P. stellata* on the periphery of the reef. Scattered colonies of encrusting and massive corals are present in all reef zones but these colonies only attain larger sizes on the deeper substrates of the reef slope. La Azufrada reef exhibits the highest number of zooxanthellate coral species and lowest percentage of dead coral cover.

By contrast, onshore fringing reefs at La Chola and Tebada are smaller in size and exhibit lower coral cover, reduced coral species richness, and ill-defined zonation patterns. They lack some of the aspects of the structural complexity present at La Azufrada. *Pocillopora damicornis* and *Psammocora* spp. are ubiquitous at la Chola and Tebada reefs, respectively, and massive corals are scarce.

It is proposed that these differences exist due to a gradient of environmental conditions in concert with natural and human impacts including: 1) recurrent thermal stress during El Niño and La Niña episodes; 2) increased sedimentation and elevated water turbidity; 3) increased terrestrial runoff and coastal erosion; 4) seasonal upwelling; and 5) increased freshwater inputs and low coastal salinities (Vargas-Ángel, 2001; Zapata and Vargas-Ángel, in press). These gradients and disturbances operate on a wide range of spatial and temporal scales and can selectively eliminate coral species, especially when impacts are chronic, act synergistically with other disturbances, or when they significantly alter the physical environment (see Karlson, 1999).

ACKNOWLEDGMENTS

I am especially grateful to P.W. Glynn for his inspiration, guidance and support. Fieldwork assistance was offered by F. Estupiñán, C.J. Moreno, F. Ortega and H. Hernández. The Colombian Administrative Unit for National Parks granted permission to conduct studies at Gorgona Island and Utría National Parks. Thanks are due M. Cano, C. Acevedo, H. Arboleda, G. Mayor, L. Moya, and R. Pardo. Financial support for this study was provided by the Government of Colombia (Colciencias, Grant 3253-09-204-97), the National Science Foundation (Grant OCE971529 to Peter W. Glynn) and by the University of Miami, Rosenstiel School of Marine and Atmospheric Science (Reitmeister Fellowship). Fundación Natura provided logistical and financial support. Thanks are also extended to E.M. Escobar, X. Franco, C. Vieira. Comments by B. Riegl, P.W. Glynn, M. Hoke, H. Halter and an anonymous reviewer greatly enhanced this manuscript.

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