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THE CORAL REEFS OF GOLFO DULCE, COSTA RICA: DISTRIBUTION AND COMMUNITY STRUCTURE

BY

JORGE CORTÉS

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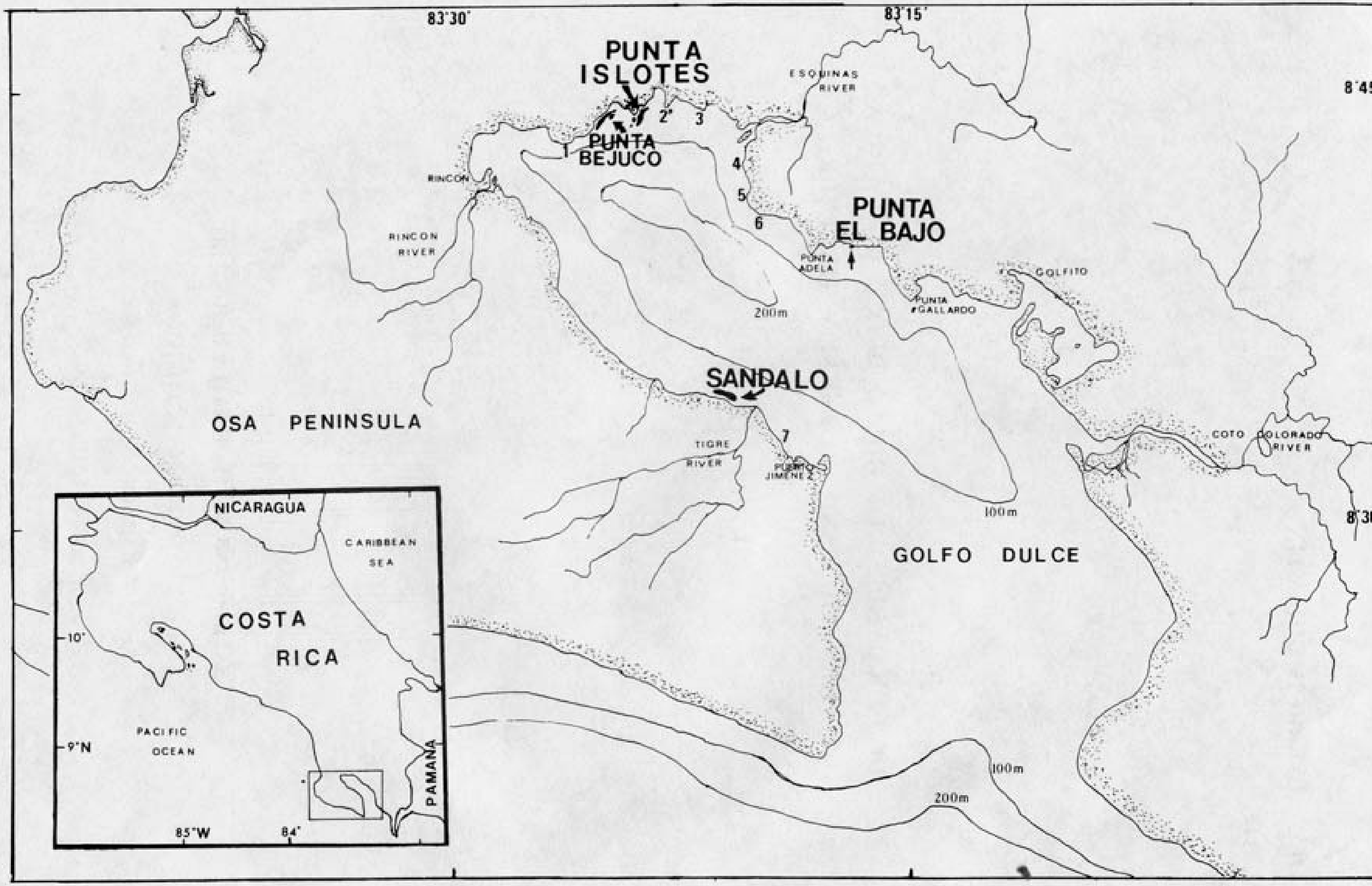
83°30'
83°15'
8°45'
8°30'
PUNTA ISLOTES
PUNTA BEJUCO
1
2'
3
4
5
6
7
ESQUINAS RIVER
RINCON
RINCON RIVER
PUNTA EL BAJO
PUNTA ADELA
PUNTA GALLARDO
GOLFITO
200m
100m
SANDALO
OSA PENINSULA
TIGRE RIVER
PUERTO JIMENEZ
COTO COLORADO RIVER
GOLFO DULCE
NICARAGUA
CARIBBEAN SEA
COSTA RICA
PACIFIC OCEAN
PAMANA
10°
9°N
85°W
84°

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Figure 1: Map of Golfo Dulce with indication of the reef areas. Dead reefs observed at: 1- Punta Estrella, 2- Mogos, 3- Playitas (aerial photograph, Fig. 16), 4- Punta Saladero (aerial photograph, Fig. 13), 5-Punta Esquinas, 6- Punta Cativo, 7- dead reef west of Puerto Jiménez. Map based on sheet CR2CM-9 (Golfito), scale 1:200,000, Instituto Geográfico Nacional, San José, Costa Rica.

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1 ABSTRACT

The fringing coral reefs of Golfo Dulce, Pacific coast of southern Costa Rica, can be divided into two types. (1) Inner Gulf reefs (Punta Islotes and Punta Bejuco) characterized by high coral coverage of live and dead *Porites lobata* on the periphery and dead *Pocillopora damicornis* and *Psammocora stellata* at the center, low coral diversity, and high topographic relief with a steep front and sides. These reefs are located on the north shore of the Gulf. (2) Outer Gulf reefs (Sándalo and Punta El Bajo), characterized by a relatively high live coral coverage, high species diversity and low relief. At Sándalo, a low profile *Pocillopora-Porites* reef is located on the south shore of Golfo Dulce, *Porites lobata* predominates on the shore-side with *Pocillopora damicornis* and three other species of corals covering most of the seaward side. The reef at Punta El Bajo is a low profile *Psammocora* reef located on the north shore of the Gulf, east of the Punta Islotes reef. This *Psammocora* reef is characterized by a central area approximately 50m^2 consisting of 100% live *Psammocora stellata* with live *Porites lobata* on the periphery. The community structure of the inner reefs of Golfo Dulce contrasts with other predominantly *Pocillopora* coral communities described from the eastern Pacific in that *Porites lobata* predominates at the reef-edge and slope and surrounds a *Pocillopora-Psammocora* reef-flat. The Punta El Bajo reef is also unique because no reef with 100% live *Psammocora* coverage has been described elsewhere in the eastern Pacific.

The difference between the inner and outer Gulf reefs may be related to two factors. (1) Tectonics – the north side of Golfo Dulce, where the inner Gulf reefs are located, is subsiding, which would explain their thicker accumulations. In contrast, the Sándalo and Punta El Bajo areas are not subsiding; in fact, they may be uplifting. (2) Siltation – the Sándalo and Punta El Bajo reefs are exposed to less terrigenous sediments than the inner Gulf reefs, which may explain the difference in live coral coverage and coral diversity.

Environmental conditions at Golfo Dulce were conducive to reef growth in the recent past but are now deteriorating. Siltation seems to be the main cause of coral reef demise at Golfo Dulce. Coastal areas around the inner Gulf reefs have been totally cleared of forest, exposing the red latosol soil to erosion. Deforestation, combined with poor agricultural practices, mining and the construction of roads have increased the sediment loads on the reefs, especially on the north shore.

2 INTRODUCTION

Coral reef development in the eastern Pacific was once considered meager to non-existant (e.g., Stoddart, 1969), but it has now been demonstrated that there are many reefs and coral communities in the area (for a summary see Glynn and Wellington, 1983). It has also been shown that some of these reefs have high accretion rates – 7.5m/1000yr (Glynn and Macintyre, 1977). The reefs in Costa Rica are found only in the southern part of the country (Glynn et al., 1983; Cortés and Murillo, 1985; Guzmán and Cortés, 1989a). Coral reef development on the northern Pacific coast of Costa Rica is restricted by upwelling (Glynn et al., 1983), but not on the southern nonupwelling section of the coast (Cortés and Murillo, 1985), including Isla del Caño (Guzmán, 1986; Guzmán and Cortés, 1989a) and Golfo Dulce.

Golfo Dulce is an enclosed embayment of tectonic origin located on the southern Pacific coast of Costa Rica (Fig. 1). It is located in one of the wettest regions of the country (Coen, 1983) and there are four major rivers flowing into it, two in the inner part and two near the Gulf mouth. These conditions would not appear to be conducive to coral reef development and the area was ignored by reef workers (e.g., Durham and Barnard, 1952) until the mid-1970's when almost by chance P. W. Glynn (pers. comm., 1985) overflew the Gulf and discovered extensive reef development. In 1978, he surveyed Golfo Dulce and found many coral reefs on the north and south shores of the Gulf, which he later described together with other reefs and coral communities of Costa Rica (Glynn et al., 1983). In order to assess the impact of the 1982-1983 El Niño disturbance, Golfo Dulce was surveyed again by Glynn and collaborators during February 1985. At that time it became apparent that (1) the reefs in the inner Gulf were different from the reefs of the outer Gulf, and (2) that the reefs in Golfo Dulce were in a state of decline possibly because of terrigenous sediments.

This paper describes and contrast the distribution of reefs and coral communities in Golfo Dulce in reference to their community structure and the associated sediments. Emphasis is given to a large coral reef (Punta Islotes) off the inner north Gulf shore (Fig. 1).

3 DESCRIPTION OF GOLFO DULCE

Golfo Dulce is located between $8^{0}27'$ and $8^{0}45'$N and $83^{0}07'$ and $83^{0}30'$W in the southern Pacific coast of Costa Rica (Fig. 1). It is oriented from NW to SE, is about 50km long and 10 to 15km wide, and covers an area of approximately $680km^2$. The inner part of Golfo Dulce has a maximum depth of slightly over 200m and there is a 60m deep sill at the opening to the Pacific Ocean (Fig. 1). It is similar to high latitude fjords both in bathymetry and the presence of anoxic deep waters (Richards et al., 1971).

3.1 GEOLOGY AND SOILS

The southern sector of Costa Rica is tectonically very active and it is uplifting (Morales, 1985; Obando, 1986; Gardner et al., 1987; Wells et al., 1988), however, Golfo Dulce is considered to be a modern pull-apart basin, where subsidence is active (Fischer, 1980; J. A. Obando, pers. comm., 1985; Berrangé, 1987a; Berrangé and Thorpe, 1988). Geologically, the western and northern sides of Golfo Dulce, known as the Fila Golfito, are formed by the Golfito Terrane, which is deeply weathered and covered by a thick, reddish-brown latosol (Obando, 1986; Baumgartner et al., 1989). The far eastern side of the Gulf consists of low lands of Quaternary alluvial origin, dominated by the Coto-Colorado River and the northern section of the Burica Peninsula, which is made up mainly of the Burica Terrane (Baumgartner et al., 1989). On the southern side, Golfo Dulce is bounded by the Osa Peninsula consisting of ophiolitic lavas of the Nicoya Complex (Santonian to Middle Eocene), the Osa Group conglomerates (Late Pliocene), and the Puerto Jimenez Group (Late Pliocene to Holocene), which contains alluvial sediments (Berrangé, 1987b; Berrangé and Thorpe, 1988).

3.2 RAINFALL AND TEMPERATURES

The Golfo Dulce area receives 4,000–5,000mm of rain per year (Coen, 1983; Herrera, 1985). Data from two stations within the Gulf area, Playa Blanca ($8^{0}40'$N; $83^{0}25'$W) and Esquinas ($8^{0}44'$N; $83^{0}20'$W) and from two nearby stations, Palmar Sur ($8^{0}57'$N; $83^{0}28'$W) and Coto 47 ($8^{0}36'$N; $82^{0}59'$W), indicate that it rains every month of the year, with an average annual peak of 800mm in October. The driest months are December through March, with 100mm or less per month, except at Esquinas where the minimum was 160mm (Herrera, 1985; I.M.N., 1989). The air temperature at Palmar Sur in 1988 was $26.1\pm0.78^{0}C$ (mean and standard deviation), and at Coto 47, $26.8\pm0.57^{0}C$, with a range of 18 to $35^{0}C$, for both stations (I.M.N., 1988). Average hours of sunlight per day at Palmar Sur ranges from 3.4 to 10.4 (I.M.N., 1988). The lowest values occur between August and November, while the higher values occur between December and March. This corresponds with the wet and dry seasons, respectively, as noted above.

3.3 VEGETATION

The vegetation around the Golfo Dulce area corresponds to the Tropical Wet Forest type in the Holdridge Life Zone System (Allen, 1956; Holdridge et al., 1971). It is the only area with this type of forest still extant on the Pacific side of Central America (Hartshorn, 1983). Mangrove forests of different types and sizes are found around the Gulf. The most extensive are found at the mouths of the largest rivers, Coto-Colorado, Esquinas and Rincón (Allen, 1956; Jiménez and Soto, 1985). Since 1983 there has been a considerable increase in deforestation that corresponds with the opening of a road connecting the Osa Peninsula with the Interamerican Highway. In the past 50 years road construction in different parts of Costa Rica has resulted in extensive deforestation (Sader and Joyce, 1988).

3.4 TIDES AND CIRCULATION

Golfito (8^{0}39'N; 83^{0}11'W) is the only locality in the Golfo Dulce area where tidal data are available. It is a subordinate station to the reference station at Puntarenas, Costa Rica (9^{0}58'N; 84^{0}50'W). Tidal differences and other constants for Golfito, as well as tidal predictions for Puntarenas, can be found in the National Ocean Service Tide Tables (U.S. Department of Commerce, 1988). The tides are semidiurnal, with a mean range of 2.35m and a spring range of 2.89m (U. S. Department of Commerce, 1988). In this paper all depths cited are referenced to mean low water (MLW).

The currents of Golfo Dulce have not been studied, but field observations (*in situ*, from aerial photographs and river delta morphology) indicate that water circulation is similar during both ebbing and flooding tides. Apparently there is a counter-clockwise flow of water into the Gulf along the eastern and northern shores and out along the western and southern shores (Fig. 2). During the dry season (December to May), there are strong southeasterly winds during the afternoons that create a moderate chop in the inner part of the Gulf (pers. obs.).

4 PREVIOUS WORK

Oceanographic data for Golfo Dulce were collected during cruises by the University of Washington's R/V Thomas G. Thompson (Richards et al., 1971; Kuntz et al., 1975). Richards and colleagues visited the Golfo on two brief occasions (1-2 and 10 March, 1969) during cruise #35 of the R/V T. G. Thompson. Five stations were occupied during each of the two visits: one just outside Golfo Dulce, one on the sill and three inside the gulf. They measured salinity, temperature, dissolved oxygen, ammonium, nitrate, nitrite, phosphate, silicate, hydrogen sulfide, alkalinity and pH. The deep inner waters of the Gulf are anoxic and the data taken eight days apart indicated an influx of oceanic water into the basin. Salinity of the surface waters of the inner part of Golfo Dulce ranged from 30 to 32ppt, and the surface temperature between 28 and 31^{0}C. This contrasts with the deep anoxic waters that had salinities around 35ppt and temperatures around 16^{0}C. Similar values to cruise #35 were obtained during cruise #76 of the R/V T. G. Thompson in late January and early February, 1973 (Kuntz et al., 1975). Dr. James J. Anderson (University of Washington) provided another set of oceanographic data from Golfo Dulce, taken during cruise #46 of

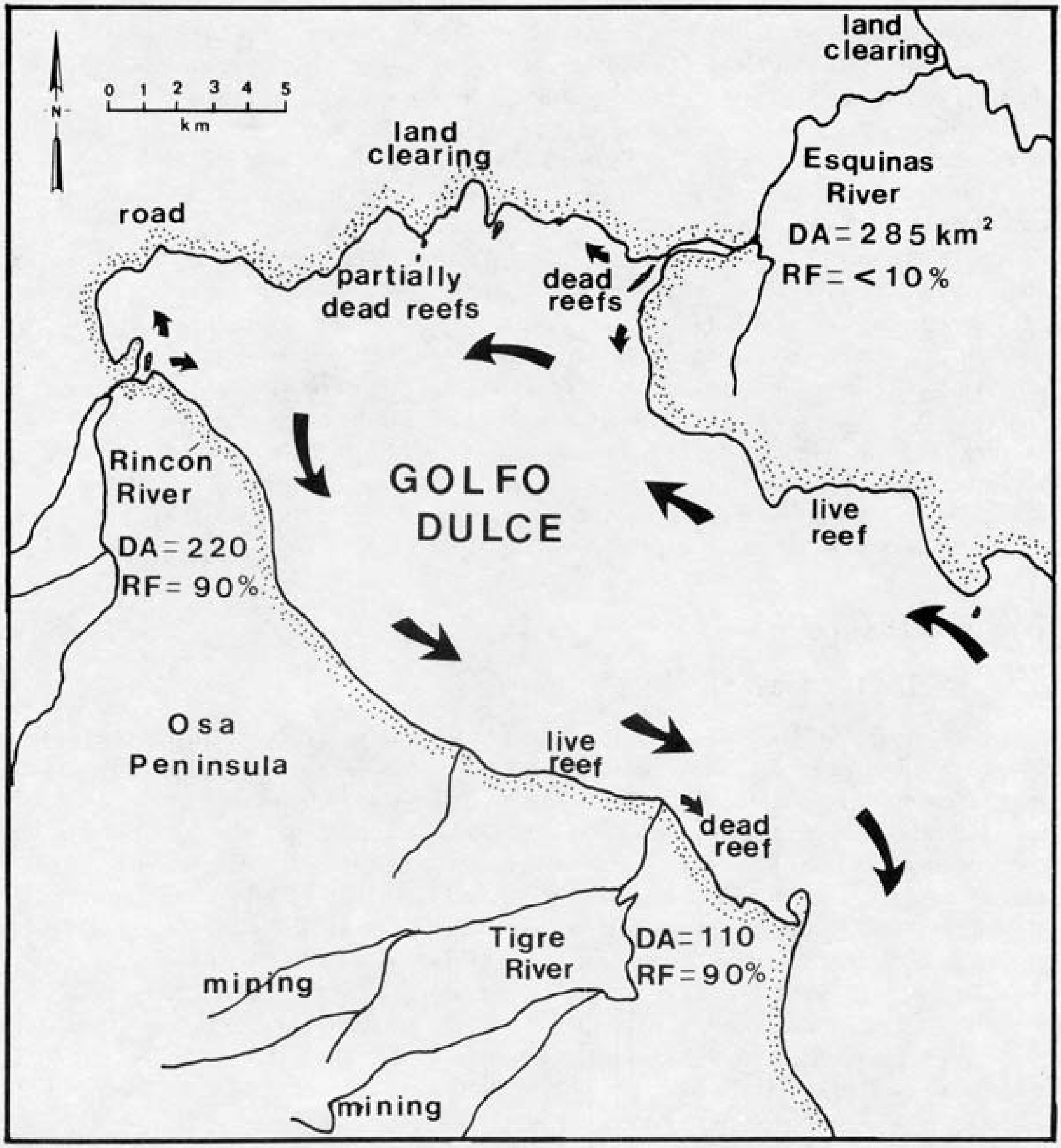


Figure 2: Putative water circulation at Golfo Dulce (large arrows). Direction of sediment movement indicated by small arrows. The main anthropogenic disturbances are indicated. D.A. = drainage area of the three main rivers in km^2. R.F. = remaining forest as of 1988 (D.G.F., 1989). Road refers to the area most affected by road construction.

the R/V T. G. Thompson in January, 1970. These data also indicate very low to no oxygen below 150m with an increase of hydrogen sulphide towards the bottom. The temperatures and salinities recorded during this cruise were similar to those reported previously.

Another paper, published by Nichols-Driscoll (1976), describes the deep, benthic, invertebrate communities of Golfo Dulce from samples collected during cruise #76 of the R/V T. G. Thompson. She found that the abundance and biomass of invertebrates were less than expected for a tropical environment. In addition, she reported that the deeper parts of the Gulf had very few species with low numbers of individuals.

Three main reef areas have been described in Golfo Dulce, two off the northern shore and the other off the southern shore. Most of the reefs in Golfo Dulce are paucispecific, dominated by *Porites lobata* Dana (Glynn et al., 1983). The largest reef off the northern shore at Punta Islotes covers several hectares, and has a well-developed reef-flat (0.5m deep, MLW) composed, for the most part, of dead *Pocillopora damicornis* Linnaeus, and small dead or live hemispherical colonies or large microatolls of *Porites lobata*. The edges, slope and base of these reefs are composed totally of large, live, partly dead or dead massive colonies of *Porites lobata*, with a few isolated colonies of *Pavona gigantea* Verrill and *Psammocora stellata* (Verrill). The reef slope is very steep, 45^0 or more, vertical in some places and extending to 10–13m depth (Glynn et al., 1983; Cortés and Murillo, 1985). Glynn and colleagues suggested that this *Porites* reef on the northern shore could have formed in 3,000–10,000 years (Glynn et al., 1983).

5 METHODS

5.1 CORAL COMMUNITY

The belt-quadrat method was used to quantitatively sample the Golfo Dulce reefs (Weinberg, 1981; Dodge et al., 1982). Areas around the reefs were chosen haphazardly and 10m long transects were sampled along the depth contours. A one square meter quadrat, divided into 100 cells of 10 x 10cm, was moved at each side of a 10m long chain (for a total of $20m^2$ per transect) and the area covered by live coral, dead coral and other substrate (rubble and/or sand) was recorded. Four reefs were studied in some detail: two inner Gulf reefs on the north shore (Punta Islotes and Punta Bejuco), and two outer Gulf reefs, a *Psammocora* reef (Punta El Bajo) also on the north shore, but east of the inner Gulf reefs, and a mixed *Pocillopora-Porites* reef (Sándalo) on the south shore (Fig. 1). Twenty two transects were sampled at the Punta Islotes reef and ten transects at Punta Bejuco in three reef zones: reef-flat (0–1m deep), reef-edge (1–2m) and reef-slope (>2m). At the other reef sites, transects were established along lines across the reefs. Five transects were sampled at Punta El Bajo in two zones: the periphery (shallow and deep) and the central *Psammocora* core. At Sándalo, ten transects were sampled in two zones: inshore (<3m depth) and offshore (>3m).

The percent data from the transect sampling were arcsine-transformed for one-way ANOVA analysis to test for differences between reef zones and inter-reef differences. To determine which mean differences were significant, the Student-Newman-Keuls (SNK) test was employed (Sokal and Rohlf, 1969). Species diversity of corals was calculated using the following indices: Shannon-Wiener (H') and species evenness (J'). Hutcheson's t-test was used to compare the Shannon-Wiener diversity indices (Poole, 1974).

Field observations were conducted mainly in February, 1985 (inner section of the Gulf: north shore east to Punta Islotes; south shore east to Puerto Jiménez) and June-October, 1988 (all of Gulf), and occasionally during other visits to the area in 1987 and 1989.

Depth profiles of the inner Gulf reefs were obtained using a portable echosounder (Raytheon DC 200 Z) during high tide. Depth profiles of the *Pocillopora-Porites* reef (Sándalo) and the *Psammocora* reef (Punta El Bajo) were constructed using measuring tape, compass and depth gauges while SCUBA diving.

5.2 SEDIMENTS

Sediment samples, two replicates per site, were collected from six different zones at the Punta Islotes reef: (a) shore, (b) beach, (c) back-reef, (d) reef-flat, (e) reef-edge and (f) reef-slope. Samples were also collected along transects across other reefs (Punta Bejuco, Sándalo and Playitas, location 3 in Fig. 1). The general appearance and consistency were recorded in the field. The sediment constituents were determined by visual inspection and the carbonate components identified. To determine the percentage of calcium carbonate, a titration method was used, similar to that described by Siesser and Rogers (1971) with modifications by J. Acuña (CIMAR, Universidad de Costa Rica). Size analyses were accomplished by standard sieve techniques with the following sieve sizes: 63, 125, 250, 500, 710, 1000, 2000 μm, USA Standard Testing Sieve (Folk, 1974; McManus, 1988). Size analyses and percent calcium carbonate were determined in triplicate for each sample.

5.3 ANTHROPOGENIC DISTURBANCES

The main human impacts on the Golfo Dulce watershed were determined from field observations, from interviews with people that live or have worked in the area and from the literature. The drainage area of the three main rivers flowing into Golfo Dulce was calculated using a Keuffel and Esser 620015 polar planimeter and 1:50,000 scale maps. The percentage of standing primary forest in the Golfo Dulce area was obtained from aerial photographs with subsequent ground confirmation. Maps depicting the forested areas in 1940 and later are available in Hartshorn et al. (1982), D.G.F. (1983) and Sader and Joyce (1988). The most recent survey was conducted in 1988 and this information is still in preliminary form (D.F.G., 1989), but was used in the present study because these results were confirmed by field observations.

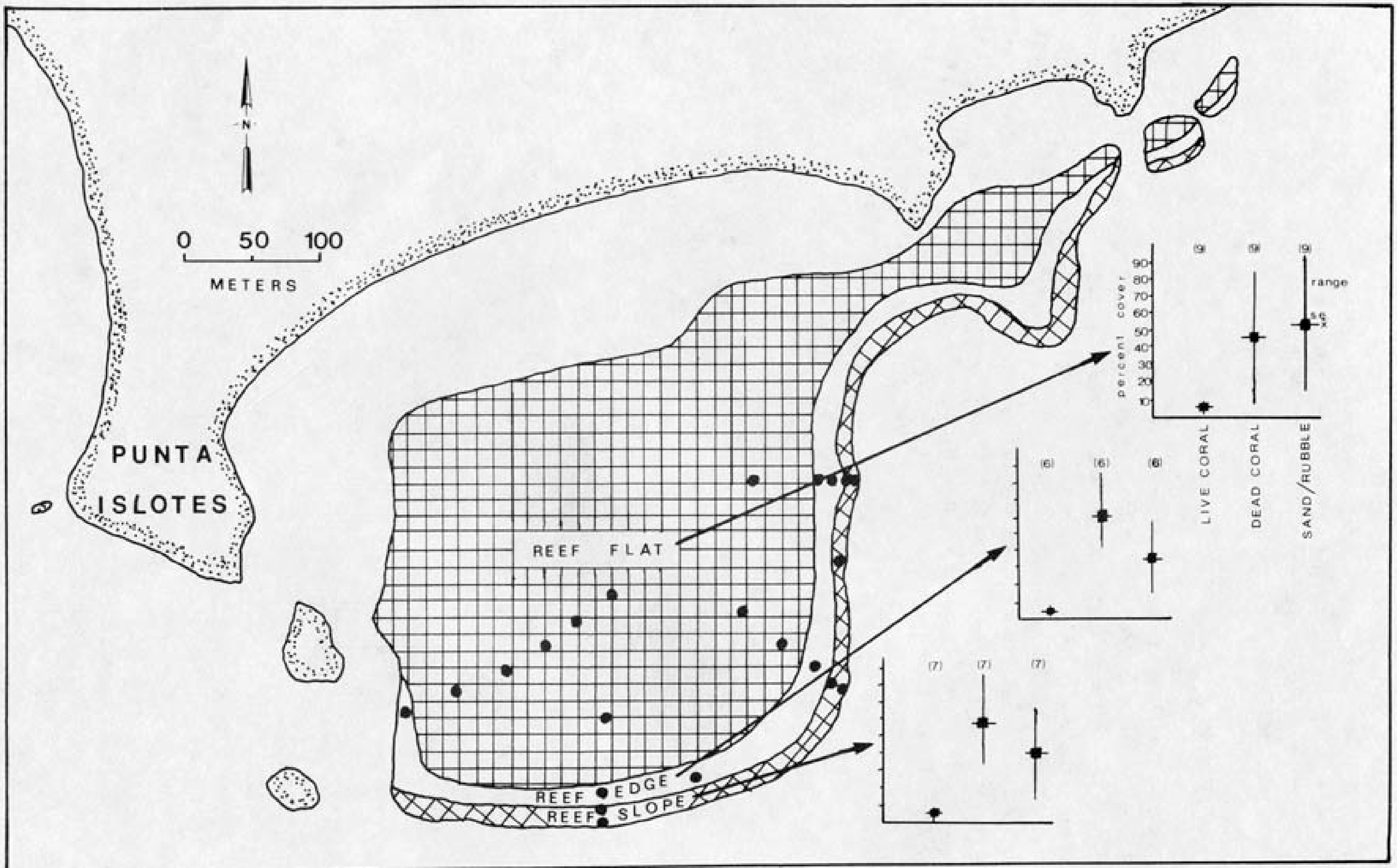
6 RESULTS

6.1 CORAL COMMUNITY

6.1.1 REEF DESCRIPTIONS –

PUNTA ISLOTES:

The coral reef at Punta Islotes (Figs. 3 and 4) can be divided into five zones: back-reef, reef-flat, reef-edge, reef-slope and fore-reef talus. Back-reef: 0–1m deep, is the area between the shore and the reef framework. It is covered by mud and sand. Reef-flat: 0–1m, consists of dead *Pocillopora damicornis* in growth position in some areas (Fig. 5) and as rubble with dead *Psammocora stellata* in others. Also, live and dead microatolls of *Porites lobata* are scattered over the reef flat. The reef-edge: 1–2m depth, marks the transition between the shallow, almost horizontal flat, and the deep and steep slope. The predominant coral species of the reef-edge and slope is *Porites lobata* (Fig. 6). The reef-front descends to a depth of 10–12m to a sand and mud bottom, i.e., the fore-reef talus (Figs. 7 and 8a).


N
0 50 100
METERS
PUNTA
ISLOTES
REEF FLAT
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percent cover
90
80
70
60
50
40
30
20
10
(9)
(9)
(9)
range
LIVE CORAL
DEAD CORAL
SAND/RUBBLE
(6)
(6)
(6)
(7)
(7)
(7)

Table 1: Relative abundances of live corals observed at the four study reefs and elsewhere in Golfo Dulce (see Fig. 1 for locations). Symbols: a = abundant; f = few; r = rare or unique; - = not observed. Species as in Wells (1983)

	LOCALITY					
SPECIES	Punta Islotes	Punta Bejuco	Punta El Bajo	Sándalo	Punta Adela	Punta Gallardo
Pocillopora eydouxi	-	-	-	r	-	-
Pocillopora damicornis	r	-	-	a	-	-
Pavona varians	r	r	-	a	-	-
Pavona gigantea	r	-	-	-	r	a
Psammocora stellata	r	r	a	a	-	-
Porites lobata	a	a	f	a	a	-
Tubastrea coccinea	-	-	-	-	-	f
Oulangia bradleyi	r	-	-	-	-	-
Astrangia browni	r	-	-	-	-	-

A summary of the transect data from Punta Islotes reef is given in Figure 3. The only live coral encountered in the transects was *Porites lobata*, but other live species were observed at the Punta Islotes reef: *Pavona varians* Verrill, *Pavona gigantea*, *Psammocora stellata*, *Oulangia bradleyi* Verrill and *Astrangia browni* Palmer (Table 1). A few small live colonies of *Pocillopora damicornis* were seen in 1985, but not in following surveys. A comparison of the percent cover of live coral, dead coral and sand/rubble in the three reef zones indicats that these are very similar (Fig. 3); statistical testing shows no significant differences (ANOVA, $p>0.05$, in all cases).

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Figure 3: Percent live coral (LC, only *Porites lobata*), dead coral (DC) and sand/rubble (S/R) at the three reef zones of the Punta Islotes reef: reef-flat (0–1m), reef-edge (1–2m) and reef-slope (>2m). Noted for each type of substrate are the mean percent, standard error of the mean, range, and number of transects. Dots indicate location of transects.

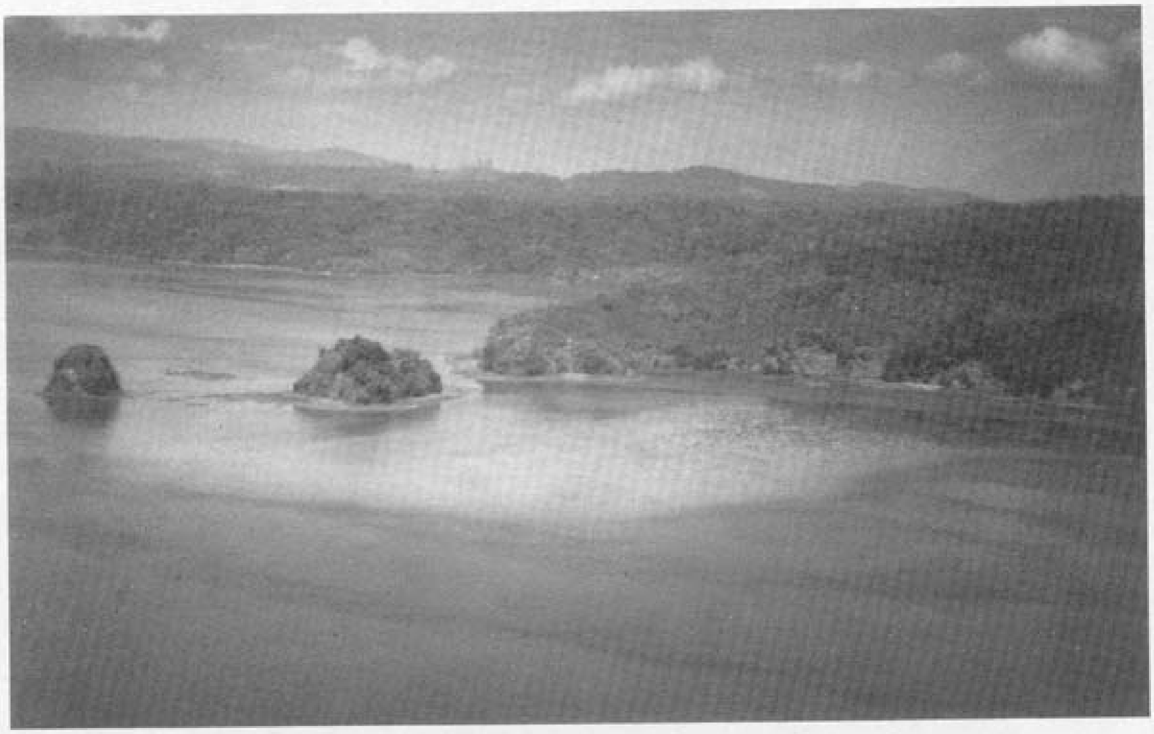

Figure 4: Oblique aerial photograph of the Punta Islotes reef during an extreme low tide, –0.3m (9.III.1989). Reef photographed at approximately 300m elevation.

Figure 5: Dead *Pocillopora damicornis* in growth position on the reef-flat of Punta Islotes. Depth 1m. Date: February, 1985. Distance across the middle of the photograph is 1.5m. Photograph by P. W. Glynn.

Figure 6: Live knobs of *Porites lobata* over large dead colonies of the same species from the reef-edge of Punta Islotes. Depth 2 m. February, 1989. Distance across the middle of the photograph is approximately 4m. Photograph by I. G. Macintyre.

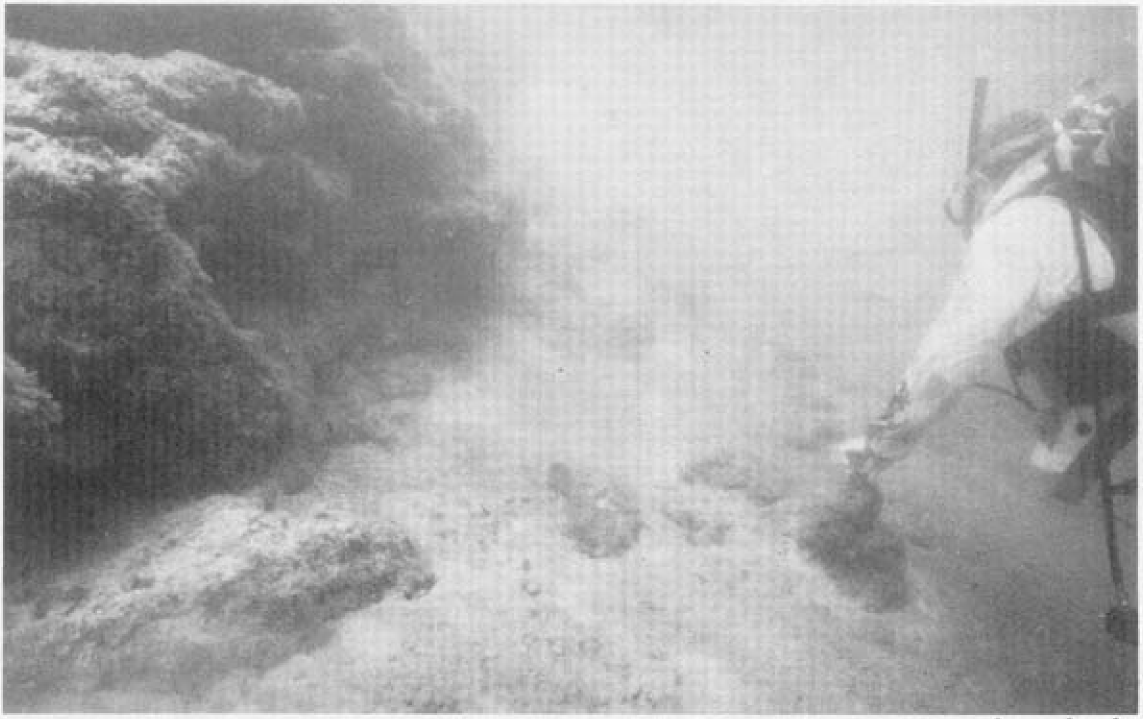

Figure 7: Base and fore-reef talus of the reef at Punta Islotes. The base is made up by dead colonies of *Porites lobata*. The fore-reef talus sediments consist of sand, mud and fragments of various sizes of *P. lobata*. Depth 10m. February, 1989. Photograph by I. G. Macintyre.

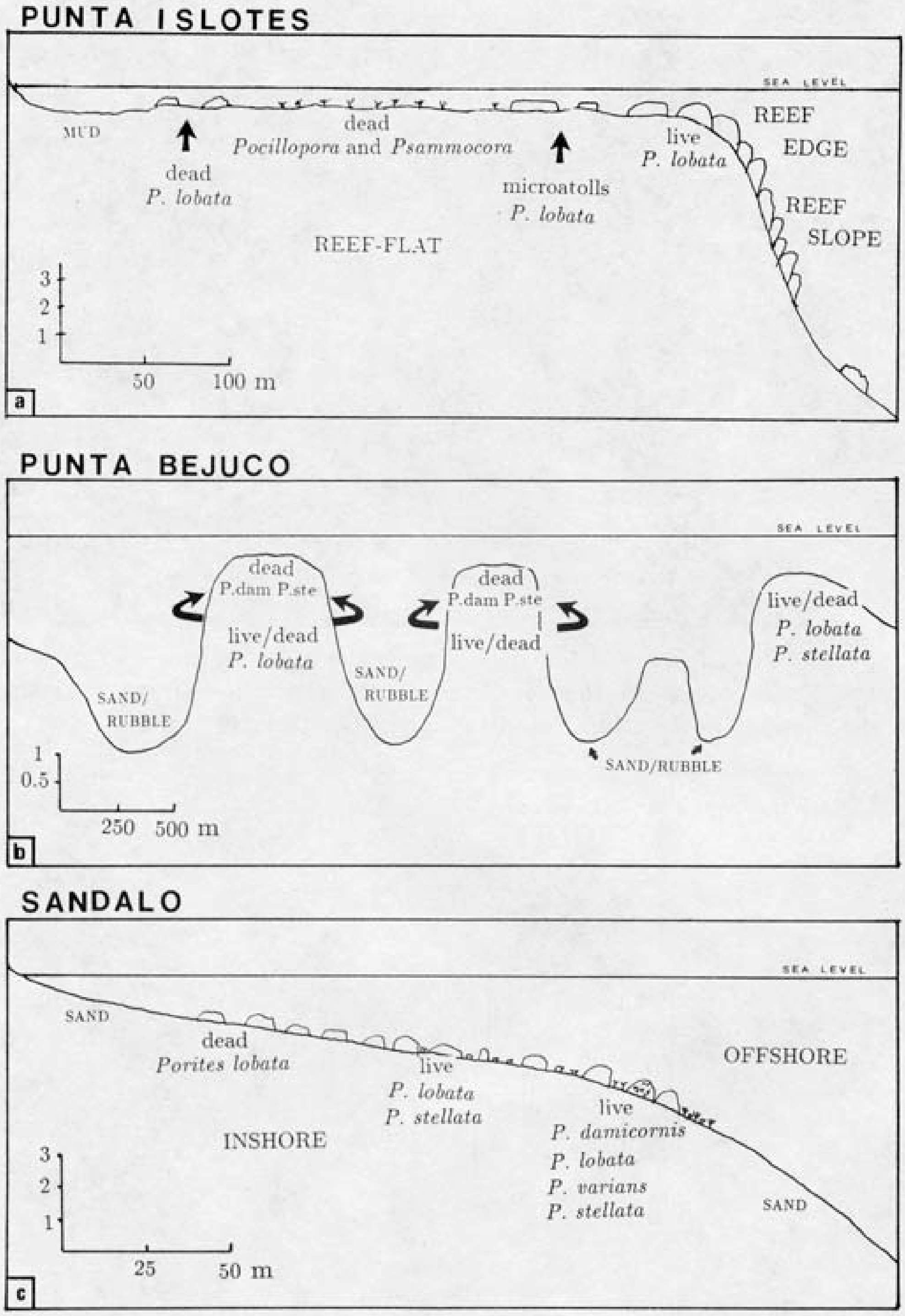

Figure 8: Schematic profiles based on echosound recording and field observations. a. Section perpendicular to shore through the middle of the Punta Islotes reef; b. Section parallel to shore, showing several reefs, Punta Bejuco reef complex. Species: P.dam = *Pocillopora damicornis*, P.ste = *Psammocora stellata*; c. Section perpendicular to the shore at the Sándalo reef.

PUNTA BEJUCO:

The Punta Bejuco reef complex (Fig. 1) includes several reefs separated by sand channels (Fig. 9). The reef fronts and flanks are steep and made up of live and/or dead colonies of *Porites lobata* (Fig. 8b). The central area of the reef consists of dead *Pocillopora* and *Psammocora* rubble. The predominant species in this reef complex is again *Porites lobata* with very low abundances of *Psammocora stellata* and *Pavona varians* (Tables 1 and 2). Live coral cover is low but not significantly different between reef zones. Dead coral cover and sand/rubble cover are high in the three reef zones (Table 2).

PUNTA EL BAJO:

The reef at Punta El Bajo is a small patch reef (Fig. 10) made up of only two species, *Psammocora stellata* and *Porites lobata* (Table 1). The central core of the patch consists of almost 100% live *Psammocora stellata* coverage of the bottom (Table 3). These colonies are tightly interlocked (Fig. 11). A rod was pushed into the *Psammocora* framework at several points, indicating a thickness of at least one meter. Toward the periphery, live *Porites lobata* is present, together with isolated unattached colonies of live *Psammocora stellata*. Live coral cover on the central *Psammocora* core is significantly higher than the shallow and deep periphery (1-way ANOVA, $F = 29.46$, $p<0.05$). Differences between the two zones in terms of dead coral cover and sand/rubble cover are not significant (Table 2-3). Many fragments of dead *Pocillopora damicornis* were observed.

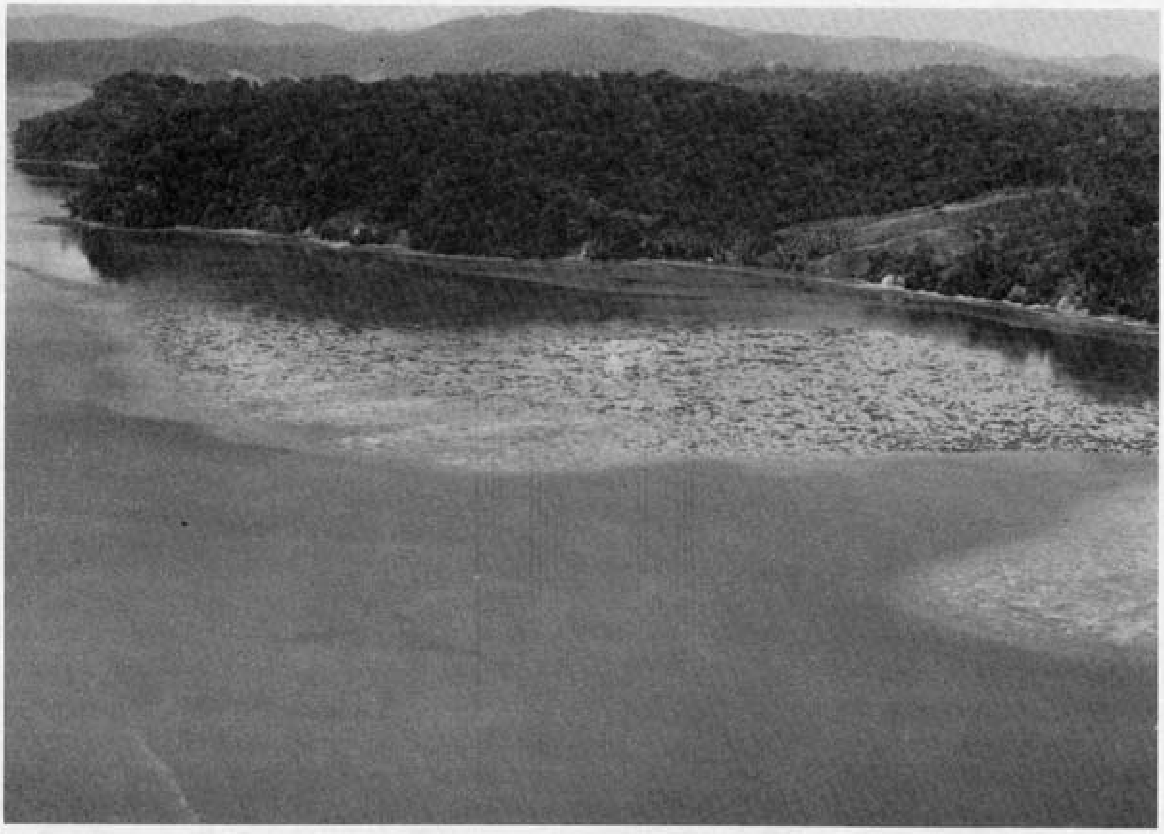

Figure 9: Oblique aerial photograph of the Punta Bejuco reef complex. Note the sediments moving onto the reef from the deforested shore. 9.III.1989. Tidal height -0.2m. Elevation, approximately 250m.

Table 2: Summary of the transect data from the Punta Bejuco reef complex, Golfo Dulce, divided into three reef zones. See Figure 1 for location of reef. The mean percent cover for each zone is given, with the standard error of the mean in parenthesis. Results of ANOVA given below, ns = not significant.

	ZONE		
	Reef-flat	Reef-edge	Reef-slope
depth (m)	0 – 1	1 – 2	2 – 8
number of transects	2	4	4
Pavona varians	0	0	0.1 (0.9)
Psammocora stellata	0	0	0.5 (0.04)
Porites lobata	0.3 (0.1)	0.9 (0.5)	1.2 (0.6)
dead coral (1)	61.1 (2.1)	41.1 (13.8)	55.6 (12.1)
sand/rubble	38.5 (1.9)	58.1 (13.6)	42.9 (11.9)

(1) mainly *Porites lobata* but also *Pocillopora* and *Psammocora* on the reef-flat

ANOVA: live coral $F = 0.34, p > 0.25$: ns
dead coral $F = 0.36, p > 0.25$: ns
sand/rubble $F = 0.37. p > 0.25$: ns

SANDALO:

The reef at Sándalo is over 500 meters long by 100 meters wide; it does not extend into deep water (Fig. 12). The inshore zone consists mainly of dead massive colonies of *Porites lobata*. The coverage by live *Porites lobata* and other species increases seaward (Table 4). Live coral cover is significantly higher offshore than inshore (ANOVA, $F = 14.65$, $p<0.01$). Species diversity also increases seaward, down to a depth of 5 m. Beyond the deepest corals, the sand bottom descends rapidly at a slope of around 20^0 (Fig. 8c). Dead coral cover and the area covered by sand/rubble are not significantly different at the two zones. This is the only reef in Golfo Dulce with a relatively large population of live *Pocillopora damicornis* and other coral species (Table 1). Also, a few live *Pocillopora eydouxi* Milne Edwards and Haime were found on this reef.

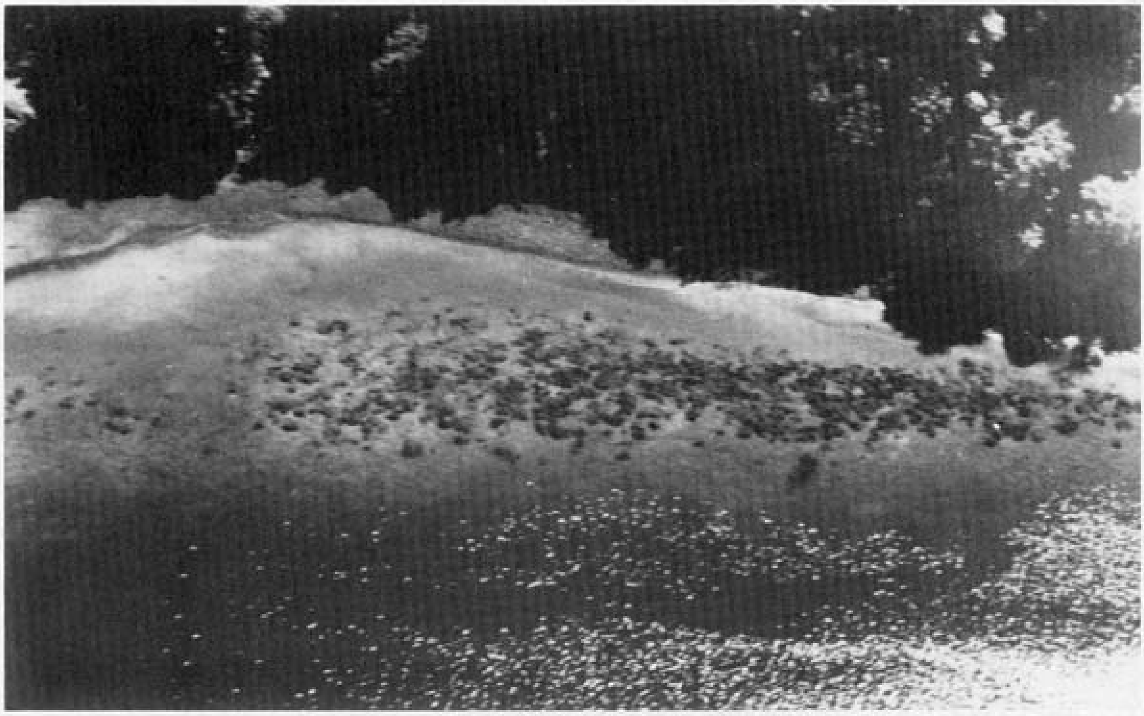

Figure 10: Oblique aerial photograph of the Punta El Bajo reef, 9.III.1989. Tidal height = –0.1m. Altitude = 300m.

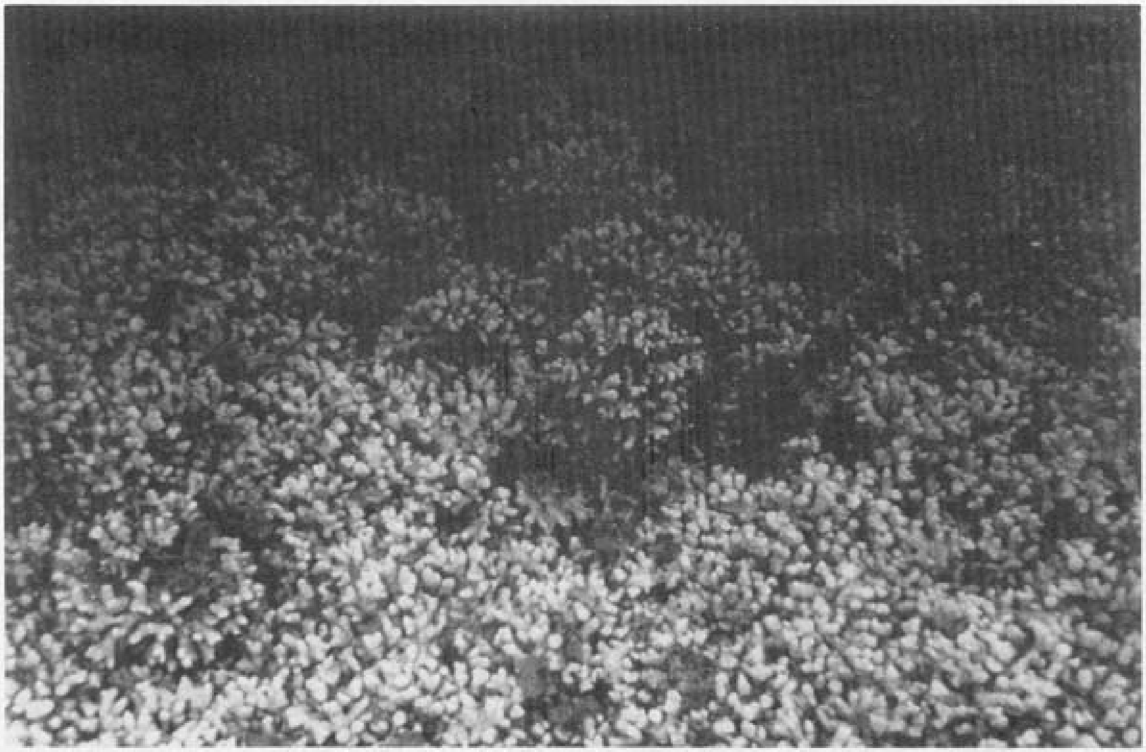

Figure 11: Monospecific stand of *Psammocora stellata* at the Punta El Bajo reef. Depth = 3m. Date = 11.III.1989. Distance across the middle of the photograph is approximately 1 m, branches are about 1cm in diameter.

Table 3: Summary of the transect data from the Punta El Bajo reef, divided into two zones: the periphery (shallow, 3 – 4 m and deep, 7m) and the central *Psammocora* core (5 – 6 m). * = significant at the 5% level, ns = not significant.

	ZONE	
	Periphery	Core
number of transects	3	2
Psammocora stellata	5.6 (3.3)	86.1 (2.2)
Porites lobata	11.6 (5.3)	2.6 (1.1)
dead coral (1)	28.2 (9.7)	10.9 (3.1)
sand/rubble	54.5 (14.9)	0.3 (0.2)

(1) *Porites lobata*, *Psammocora stellata* and some *Pocillopora damicornis*

ANOVA: live coral $F = 29.46$, $p < 0.05$ *
dead coral $F = 1.26$, $p > 0.25$: ns
sand/rubble $F = 9.62$, $p > 0.05$: ns

Figure 12: Oblique aerial photograph of Sándalo reef, looking seaward, 9.III.1989. Tidal height = –0.3m. Altitude = 200m.

Table 4: Summary of transect data from the Sándalo reef, divided into two zones. Mean percent cover for each zone and standard error of the mean in parenthesis are given. Results of ANOVA given below, ** = significant at the 1% level, ns = not significant.

	ZONE	
	Inshore (2 - 3 m)	Offshore (3 - 5 m)
number of transects	5	5
Pocillopora damicornis	0	8.9 (7.1)
Pavona varians	0	6.8 (5.9)
Psammocora stellata	0.2 (0.1)	0.4 (0.2)
Porites lobata	12.0 (4.5)	29.8 (6.8)
dead coral (1)	64.8 (5.5)	44.8 (5.8)
sand/rubble	23.0 (6.3)	9.2 (3.6)

(1) mainly *Porites lobata* and *Pocillopora damicornis*, some *Psammocora stellata* and *Pavona varians*

ANOVA: live coral $F = 14.65$, $p < 0.01$ **
dead coral $F = 4.98$, $p > 0.05$: ns
sand/rubble $F = 3.48$, $p > 0.05$: ns

OTHER REEF SITES:

Totally dead reefs found at Punta Estrella, Isla Mogos, Playitas, Punta Saladero (Fig. 13), Punta Esquinas and Punta Cativo (for locations see Fig. 1) are made up of *Porites lobata* and some *Pocillopora damicornis* fragments. All of these reefs are located near the Esquinas River, and their surfaces are covered by terrigenous sediments. Colonies of *Porites lobata* are intensely bioeroded mainly by *Lithophaga* spp. and *Gastrochaena rugulosa* Sowerby.

At Punta Adela, there is a small coral community (Fig. 14) with a few live *Porites lobata* colonies, at least one live *Pavona gigantea* colony (Table 1) and many dead colonies of *Porites lobata*, *Pocillopora damicornis* and *Psammocora stellata*.

At Bajo La Viuda, off Punta Gallardo (Fig. 1) two species of corals, *Tubastrea coccinea* Lesson and *Pavona gigantea* (Table 1), absent or rarely found on other reefs of Golfo Dulce, were abundant. This area consists of a series of submerged rocky outcrops (only one is exposed) with tops at around 2m depth and the bases at 12–15m. These rocky outcrops are covered by a species of the octocoral *Telesto* sp., isolated live colonies of *Tubastrea coccinea* and some large (up to 40cm), live laminar colonies of *Pavona gigantea*. The bottom is composed of sand and rubble.

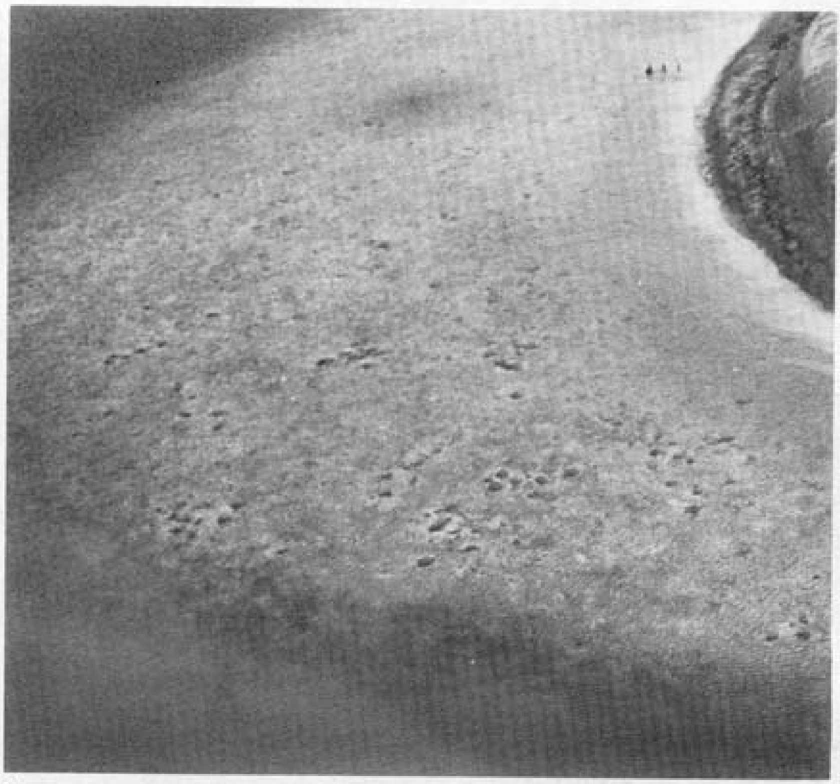

Figure 13: Oblique aerial photograph of the dead reef at Punta Saladero, 9.III.1989. Tidal height = -0.2m. Altitude = 300m.

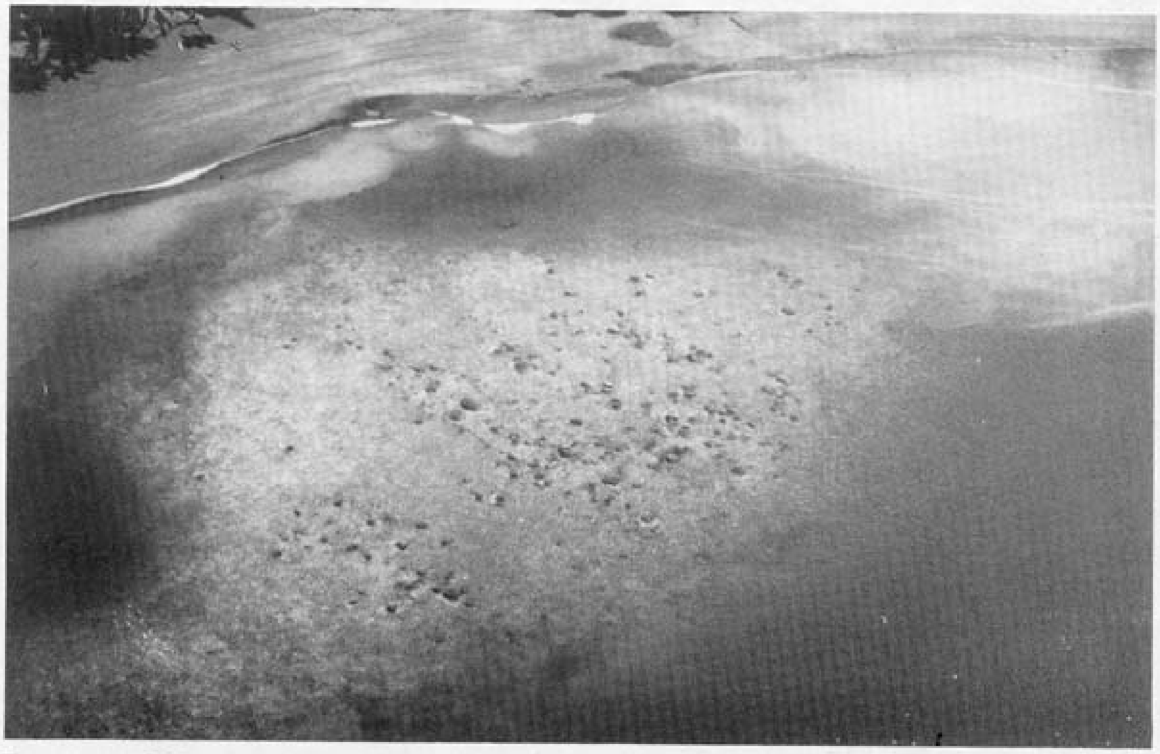

Figure 14: Oblique aerial photograph of the reef at Punta Adela, 9.III.1989. Tidal height = -0.2m. Altitude = 300m.

6.1.2 INTER-REEF COMPARISONS –

Live coral cover is highest at Punta El Bajo, with a mean of 45.9% (Table 5), but with values as high as 93.4% (Table 3), due to the presence of *Psammocora stellata*. The area with the next highest live coral cover is Sándalo with an average of 29.1% (Table 5) and values as high as 49.1% (Table 4). Both at Punta Bejuco and Punta Islotes, live coral cover is low (highest value was 8.4%), while dead coral cover makes up 50% or more of the substrate (Table 5). There were significant differences in live coral cover between reefs (1-way ANOVA, $F = 21.21$, $p<0.05$), dead coral cover ($F = 3.09$, $p<0.05$) and area covered by sand/rubble ($F = 4.00$, $p <0.05$) (Table 6). Results of the SNK test of the above ANOVA (Table 7) indicate that there is no difference between the live coral cover of Punta Islotes and Punta Bejuco, and that they are lower than Sándalo. Live coral cover on Sándalo is lower than and significantly different from Punta El Bajo. In the case of dead coral cover, there is no significant difference between Punta Bejuco, Punta Islotes and Sándalo. At Punta El Bajo, the mean dead coral cover is significantly lower than at the other three reefs because of the high percentage of live *Psammocora stellata*. The area cover by sand/rubble is very similar at Punta El Bajo, Punta Islotes and Punta Bejuco (Table 7). The percentage of sand/rubble at Sándalo is significantly lower than at the other reefs because most of the substrate is covered by live and dead coral.

The inner Gulf reefs on the north side of Golfo Dulce (Punta Islotes and Punta Bejuco) are similar: live and dead *Porites lobata* form the flanks of the reefs and dead *Pocillopora damicornis* in growth position and/or fragments of dead *Pocillopora* and *Psammocora* are found on the reef-flat. Also, most of the reefs have almost vertical fronts and sides, with a topographic relief of up to 12m. The number of abundant coral species (Table 1) and diversity (Table 8) are low. All the diversity indices at Punta Islotes are zero because only one species was encountered (Table 8).

On the south shore of Golfo Dulce, the living reef at Sándalo consists of mostly dead *Porites lobata* in the near-shore, while live *Pocillopora damicornis* and *Porites lobata* are abundant on the seaward side. The highest value of live species diversity of the four reefs studied corresponded to this reef, where evenness was also high (Table 8). The reef at Punta El Bajo has *Porites lobata* on the periphery and live *Psammocora stellata* at the center and exhibits low values of species diversity but high values of species evenness ($J' = 0.669$) because the only two species found were present in similar proportions (Table 8). Coral diversity (Shannon-Wiener index) is significantly higher ($t = 5.749$, $p<0.001$) at Sándalo ($H' = 0.822$), than at Punta El Bajo and Punta Bejuco. Diversity in these last two reefs is not significantly different.

6.2 SEDIMENTS

The sediments from the shore, beach and back-reef of Punta Islotes (Fig. 15a) are mainly brick red and are composed of very fine terrigenous latosol – a soil that has been observed inland in forest clearings and road cuts. The size distribution of the reef-flat sediments was bimodal – consisting of coral (*Pocillopora damicornis* and *Psammocora stellata*) and molluscan fragments with finer sediments including unidentifiable carbonate skeletal fragments, sponge spicules and terrigenous mud. The reef-edge sediments contained a high percentage of fine carbonate material in contrast to the reef-slope sediments that had a high percentage of coarse carbonate grains – mainly molluscs and coralline algae (e.g., *Amphiroa*).

Table 5: Summary of transect data for the four reefs studied. Average percentage coverage of each species, dead coral and sand/rubble are given, with the standard error of the mean in parenthesis.

	REEF			
	Punta Islotes	Punta El Bajo	Punta Bejuco	Sándalo
number of transects	22	5	10	10
Pocillopora damicornis	0	0	0	4.44 (3.82)
Pavona varians	0	0	0.045 (0.004)	3.41 (3.17)
Psammocora stellata	0	37.83 (17.78)	0.025 (0.02)	0.31 (0.01)
Porites lobata	1.71 (0.49)	8.04 (3.78)	0.91 (0.33)	20.92 (4.95)
dead coral	54.34 (5.25)	21.32 (7.06)	50.90 (7.80)	54.79 (5.08)
sand/rubble	43.95 (5.27)	32.81 (14.87)	48.12 (7.71)	16.13 (4.23)

Similarly, the percentage of calcium carbonate in the Sándalo reef sediments increased seaward (Fig. 15b). The coarse sediment fraction consisted mainly of dead coral fragments (*Pocillopora damicornis* and *Psammocora stellata*) and whole and fragmented molluscs. The fine sediment fraction consisted of carbonate silt and sponge spicules.

Samples from two other areas (Table 9) indicated a pattern similar to that described for Punta Islotes with near-shore sediments containing higher percentages of fine terrigenous sediments.

Clay mineral analysis of sediments from north shore reefs revealed two sources of terrigenous input (Cortés and Brass, in prep.). One source is inland with sediment transport to the sea via the Esquinas River. The other source is from nearby hills adjacent to the reefs with sediments supplied by land slides.

Table 6: ANOVA results of the comparisons of mean live coral, dead coral and sand/rubble at the four reefs studied in Golfo Dulce.

LIVE CORAL

LEVEL	SS	DF	MS	Fs
1	8850.25	3	2950.085	21.206 ***
0	5981.92	43	139.114	

VARIANCE COMPONENTS

LEVEL	PERCENT
1	65.51
0	34.49

DEAD CORAL

LEVEL	SS	DF	MS	Fs
1	1995.57	3	665.191	3.0903 *
0	9255.82	43	215.251	

VARIANCE COMPONENTS

LEVEL	PERCENT
1	16.42
0	83.58

SAND/RUBBLE

LEVEL	SS	DF	MS	Fs
1	3408.30	3	1136.101	4.0040 *
0	12200.76	43	283.738	

VARIANCE COMPONENTS

LEVEL	PERCENT
1	22.02
0	77.98

SIGNIFICANCE LEVEL:

* = $p < 0.05$

*** = $p < 0.001$

Table 7: Student-Newman-Keuls (SNK) test of Table 2-6 ANOVA results. Sites: PB = Punta Bejuco, PI = Punta Islotes, S = Sándalo, PEB = Punta El Bajo. Statistically similar mean values are joined by a horizontal line.

LIVE CORAL

Locality rank	1	2	3	4
Site	PB	PI	S	PEB
Means	0.96	1.71	29.08	45.87

DEAD CORAL

Locality rank	1	2	3	4
Site	PEB	PB	PI	S
Means	21.32	50.90	54.34	54.79

SAND/RUBBLE

Locality rank	1	2	3	4
Site	S	PEB	PI	PB
Means	16.13	32.81	43.95	48.12

Table 8: Shannon-Wiener diversity index (H') and species evenness (J') for the four reefs studied.

REEF	no. of species	H'	J'
Punta Islotes	1	0	0
Punta Bejuco	3	0.273	0.248
Punta El Bajo	2	0.464	0.669
Sándalo	4	0.822	0.593

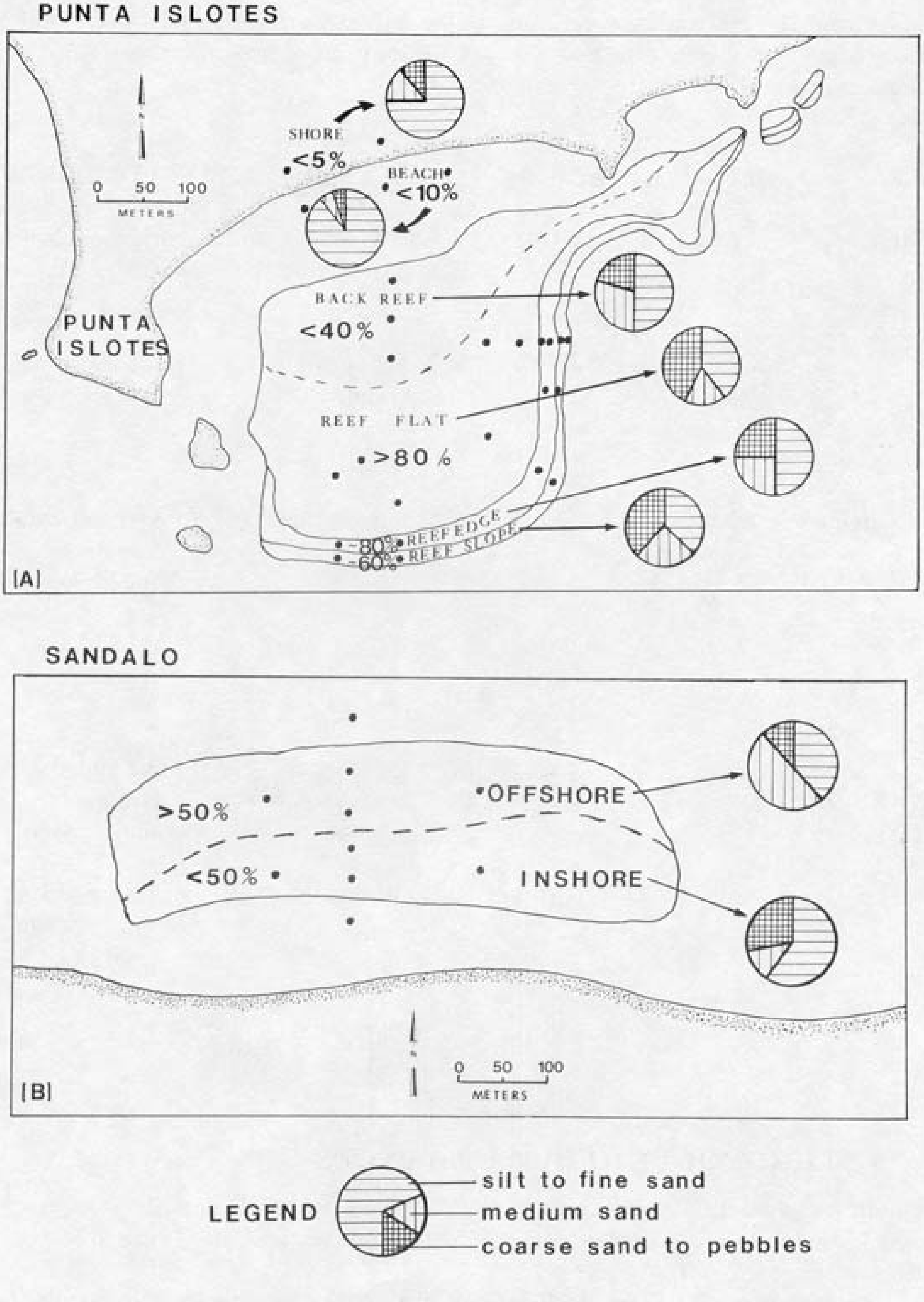

Figure 15: Percent calcium carbonate at the different reef and shore zones. Grain size distribution of the bottom sediments (percent) in the different zones is denoted by the pie diagrams. Dashed line separate the back-reef from the reef-flat at Punta Islotes (A); and the inshore from the offshore zone at Sándalo (B). Dots indicate sampling sites.

Table 9: Analysis of sediment samples from two reefs in Golfo Dulce. Average percent calcium carbonate and standard deviation in parenthesis; principal grain size(s) and main sediment components are given. See Figure 1 for location of reefs, Playitas is site number 3 on map. n = number of samples.

REEF	DEPTH	n	%$CaCO_3$	GRAIN SIZE	MAIN COMPONENTS
Playitas	1.5 m	2	54.8 (0.3)	41 % silt 26 % coarse sand-pebbles	coral and shell fragments
	2 m	2	63.8 (0.3)	70 % fine-medium sand	coral and shell fragments
Punta Bejuco	1.5 m	2	40.0 (0.5)	45 % fine-medium sand	forams and coral fragments, echinoid spines
	2 m	2	54.0 (0.5)	54 % silt-fine sand 22 % coarse sand-pebbles	coral and shell fragments
	2.5 m	2	57.7 (0.5)	67 % silt-fine sand 20 % coarse sand-pebbles	coral and shell fragments, echinoid spines
	3 m	2	77.4 (0.5)	83 % silt-fine sand	shell fragments, forams, sponge spicules

6.3 ANTHROPOGENIC DISTURBANCES

The main human activities around the Golfo Dulce area are indicated in Figure 2, and changes in the percent cover of standing primary forest in the Golfo Dulce area from 1940 – 1988 are presented in Table 10.

The watershed of the Esquinas River was the first to be altered (mid 1940's) for the cultivation of bananas. Today less than 10% of the forest is standing in the Esquinas drainage basin. The sediment-loaded waters of the Esquinas River flow south along the coast – over the area of dead coral reefs – until they merge with the main northwest circulation (Fig. 2 and 16). This pattern of circulation produces an eddy at the river's mouth and over the reefs to the west (Fig. 17).

Table 10: Percentage of standing primary forest in the Golfo Dulce area. North shore refers to the coastal area between the Esquinas River and Rincón. Punta el Bajo and Sándalo refers to the shore area adjacent to the reefs (see Figure 1 for locations). Years refers to the year the aerial photographs used for the analysis were taken.

AREA	YEAR					
	1940	1950	1961	1977	1983	1988
NORTH SHORE	100 a	100 a	100 a	100 a	30–60 b	0 d
ESQUINAS RIVER	100 a	50 a	20 a	20 a	30 b	<10 d
RINCON RIVER	100 a	100 a	100 a	100 a	90–100 b,c	90 d
TIGRE RIVER	100 a	100 a	90 a	90 a	80–90 b,c	90 d
PUNTA EL BAJO	100 a	100 a	100 a	100 a	60–90 b	90 d
SANDALO	100 a	100 a	100 a	100 a	90–100 b	90 d

REFERENCES:

a- Hartshorn et al., 1982
b- D.G.F., 1983
c- Sader and Joyce, 1988
d- D.G.F., 1989

The north shore of the inner Gulf, adjacent to the Punta Islotes and Punta Bejuco reefs, has been completely cleared in the last 10 years. As a consequence, soil erosion has increased considerably with an increase in sediment input to the marine environment (Fig. 9).

A dirt road was opened in 1983 along the north shore of Golfo Dulce. This has resulted in significant erosion in the inner sector of the Gulf' because of the road cut (Fig. 18). And has opened the area to loggers which have started to cut down the forest.

The Tigre River is an important source of terrigenous sediments to the outer Gulf area, even though 90% of the forest is still present (Table 10). The reason for this significant sedimentary input is the type of activity taking place along the course of the river. This area has been impacted recently by gold mining with river dredging, which has a limited impact on the forest canopy, but devastating effects on drainage systems (Berrangé, 1987b).

The forests of the Rincón River watershed, as well as those bordering the Sándalo and Punta El Bajo reefs, are still in fairly good condition, with 90% of the forest standing (Table 10), and are not affected by mining or other anthropogenic activities.

Figure 16: Aerial photograph of the Esquinas river near its mouth. Note the sediment plume as it encounters the main northwest current of the inner Gulf. Dead reefs are found along the shore. 9.III.1989, altitude = 300m.

Figure 17: Eddy of sediment laden waters from the Esquinas river over a coral reef (Playitas) about 2km west of the river's mouth, 9.III.1989. Altitude = 300m.

Figure 18: Road construction near Rincón. Note the erosion of the road cut exposing the red latosol soil. Photographed in February, 1985.

7 DISCUSSION

7.1 POSSIBLE REASONS FOR INTER-REEF DIFFERENCES

7.1.1 TECTONICS

The differences in reef structure and development between the inner Gulf reefs, Punta Islotes and Punta Bejuco – thick, high topographic relief – and the outer Gulf reefs, Punta El Bajo and Sándalo – low topographic relief – may be related to differences in the tectonic regimes at the opposite ends of Golfo Dulce. Differences in the recent tectonic history of these areas have been documented from evidence of relative subsidence in several areas of Golfo Dulce, especially of the basin on the north shore (Fischer, 1980; Obando, 1986; Berrangé and Thorpe, 1988), and of uplift of the Osa Peninsula and the south Gulf shore (Berrangé and Thorpe, 1988; Bullard et al., 1988; Wells et al., 1988). The Punta El Bajo area has been identified as a zone of intense uplifting (Gardner et al., 1987). This difference in tectonic regimes may explain the thicker reef accumulations in the north Gulf, which has experienced more subsidence, than the south Gulf region.

7.1.2 SILTATION

The distribution of terrigenous sediments may explain the difference in percent live coral cover between the inner reefs and the other reefs of Golfo Dulce. The live reefs of the outer Gulf (Sándalo and Punta El Bajo) have been exposed to limited sedimentation stress. This situation contrasts with the dead reefs and the live *Porites* reefs of the inner Gulf that have all been subjected to heavy terrigenous sediment concentrations associated with the outflow of the Esquinas River (Fig. 2) and landslides on the coastal area adjacent to the reefs (Fig. 9). The Esquinas River, which drains deforested mountains and agricultural and cattle land (Table 10), carries heavy sediment loads during the long rainy season (Fig. 16). In addition, flooding has increased in recent years, probably due to deforestation as demonstrated for others areas by Clark (1987). More recently, the construction of a road through the Osa Forest Reserve on the north shore (Fig. 18), together with accelerated deforestation of the steep shore areas (Table 10), have contributed significantly to the siltation problem. It has been demonstrated that trees near the shore regulate the input of sediments and nutrients to near-shore environments (Kühlmann, 1985). In this context, it is worth noting that the coastal forests adjacent to the Punta El Bajo and Sándalo live reefs are still relatively undisturbed (Table 10).

A similar distribution of living reefs in relation to sedimentation patterns was found by Roberts and Murray (1983) on the Caribbean shelf of Nicaragua. No reefs were found in near-shore turbid environments and most coral reef development was restricted to clear waters at the shelf edge. On the Nicaraguan shelf edge, the percentage of carbonate sediments was 80% or more (Roberts and Murray, 1983) – this contrasts with the low values of calcium carbonate for Golfo Dulce sediments. These Gulf values were in the lower range of high-carbonate facies of the Great Barrier Reef (Maxwell, 1973) and were similar to the values obtained from near-shore terrigenous environments on the Miskito Bank, Nicaragua (Roberts and Murray, 1983). Acevedo et al. (1989) observed that in southern Puerto Rico live coral cover and species diversity increased away from a terrigenous sediment source.

Water circulation within the Gulf appears to be counter-clockwise, i.e., there is a general flow into the Gulf along the eastern and northern shore and an outward flow along the western and southern shore (Fig. 2). This pattern of water movement will transport sediments from the Esquinas River into the area of the inner Gulf reefs and away from Punta El Bajo reef, which is not influenced by any other large river. The waters of the Rincón River, which drain pristine forests, north-west of the Sándalo reef, generally have low sediment loads. As a result, no significant amount of sediment is transported to the Sándalo area. Also, sediments from the Tigre River, to the east of the Sándalo reef, are transported away from the reef by the counter-clockwise currents (Fig. 2). This pattern is probably the reason why a *Pocillopora* reef, east of Sándalo, observed alive in 1978 (P. W. Glynn, per. comm., 1985) was found covered with mud – only the tallest colonies could be seen – in February 1985. This reef was probably killed by the severe floods of 1984 (Cortés and Murillo, 1985) in the mining area of the Osa Peninsula (Berrangé, 1987b).

Siltation may be the main cause of coral reef demise worldwide (Johannes, 1975; Rogers, 1985, 1990; Wells, 1986; Kühlmann, 1988; UNEP/IUCN, 1988). It has been demonstrated that high sediment loads around coral reefs can cause a reduction in coral species diversity and live coral coverage, and alterations in coral species composition and distribution (Loya, 1976; Cortés and Risk, 1985; Hubbard, 1986; Rogers, 1990) and, ultimately, coral death (Bak, 1978; Rogers, 1979; 1983; Thompson et al., 1980). The coral reefs of Golfo Dulce show all the signs of siltation stress – low live coral cover and species diversity, and high dead coral cover and concentrations of terrigenous sediments – especially the reefs in the inner Gulf area. Coral reefs near the Esquinas River are all dead and those farther away are in a state of decline.

7.2 OTHER CAUSES OF CORAL DEMISE

In addition to the stress caused by high sediment loads, other factors may have played a role in the demise of corals in Golfo Dulce reefs: coral collecting, low salinity, high sea surface temperature and phytoplankton blooms. These factors are discussed below and their impacts on Golfo Dulce corals are evaluated.

Several people interviewed around Golfo Dulce stated that there has been extensive collecting of coral colonies in the recent past, especially *Pocillopora damicornis.* But this does not seem to be a significant factor because many fragments of dead *Pocillopora* were found at all reefs, and at Punta Islotes large areas of the reef were covered with dead *Pocillopora* in growth position.

Golfo Dulce is located in one of the wettest regions of Costa Rica and four large rivers flow into it. During the rainy season a fresh water lens forms and it is very persistent, salinity may drop to 25ppt (M. L. Fournier, pers. comm., 1990). Moreover, the Spanish name of the Gulf implies the presence of fresh water (Golfo Dulce = Fresh Water Gulf). Two lines of evidence indicate that salinity may not be an important factor in the demise of the Golfo Dulce coral reefs. First, the surface salinity of Golfo Dulce during the dry season ranged from 30 to 32ppt (Richards et al., 1971; Kuntz et al., 1973), and may drop to 25ppt during the rainy season (M. L. Fournier, pers. comm., 1990). These values above or close to the generally accepted low salinity tolerance limit (<27ppt) for corals (Wells, 1956). Second, experimental evidence and laboratory observations indicate that some species of corals are tolerant to pronounced salinity changes. Muthiga and Szmant (1987) demonstrated a high tolerance of salinity change by *Siderastrea siderea.* Glynn (1974) indicated that eastern Pacific corals remained healthy in aquaria during the wet season in Panama, when salinities dropped below 25ppt and even reached 19ppt on two occasions.

In recent years there have been reports of extensive coral mortality in the eastern Pacific: in 1983 due to high and prolonged sea surface temperatures that accompanied a severe El Niño event (Glynn, 1984; 1988a; 1990; Glynn et al., 1988), and in 1985 in association with dinoflagellate blooms (Guzmán et al., 1990). Unfortunately, there are no quantitative data from Golfo Dulce before the 1982-1983 El Niño to evaluate the impact of the warm water as a possible factor in the demise of Golfo Dulce reefs. However, in Golfo Dulce coral mortality does not seem to have been as intense as in other eastern Pacific reefs (Glynn, 1990). One reason for this may be that most of the Golfo Dulce corals were dead prior to 1982, especially *Pocillopora damicornis* that was the most affected in the eastern Pacific (Glynn et al., 1988).

In 1985, intense dinoflagellate blooms caused coral mortality in several eastern Pacific reefs (Guzmán et al., 1990). At Golfo Dulce, during that same period, intense blooms were observed, but their effects may not be significant since the main genera affected elsewhere, *Pocillopora*, was dead prior to 1985.

7.3 COMPARISON WITH OTHER EASTERN PACIFIC REEFS

The coral species associated with the Golfo Dulce reefs (Table 2-1) are characteristic of eastern Pacific reefs (Wells, 1983). The Golfo Dulce reefs, however, lack some common eastern Pacific corals including *Pocillopora elegans* Dana, *Pavona clavus* Dana and *Gardineroseris planulata* (Dana).

In contrast to most eastern Pacific coral reefs (e.g., Panamá: Glynn et al., 1972; Gorgona Island, Colombia: Glynn et al., 1982; Prahl and Erhardt, 1985; Los Frailes Bay, Baja

California: Glynn and Wellington, 1983; and some reefs in the Galápagos Islands: Glynn and Wellington, 1983), with large portions composed of pocilloporid framework, the Golfo Dulce reefs are constructed chiefly by poritid coral frameworks. Other coral communities, for example, in the Sea of Cortés (Squire, 1959; Brusca and Thomson, 1975), off some islands in the Galápagos (Glynn and Wellington, 1983) and off the Costa Rican mainland coast (Glynn et al., 1983; Cortés and Murillo, 1985) are composed of sparse populations of both pocilloporid and massive corals. At Caño Island, Costa Rica, *Porites lobata* is the main reef building coral (Guzmán, 1986; Guzmán and Cortés, 1989a), as well as in some areas at Malpelo Island, Colombia (Birkeland et al., 1975) and Cocos Island (Bakus, 1975; Guzmán and Cortés, in review). On the inner reefs of Golfo Dulce, *Porites lobata* is also the predominant species, but there it forms extensive monospecific stands on the reef-edge and slope with a pocilloporid reef-flat located behind the reef-front.

Porites lobata is sometimes the only species alive at some reef sites in Golfo Dulce, suggesting that it is the most tolerant coral to physical disturbances. Massive *Porites* species have been reported to be the dominant corals on the inner shelf reefs of the Great Barrier Reef (Done, 1982). Indeed, *Porites lobata* is the predominant species at Pandora reef, an inner shelf reef of the Great Barrier Reef, in terms of physical mass, amount of living tissue and colony number (Potts et al., 1985). The inner shelf of the Great Barrier Reef is characterized by low water transparency, low wave action and the presence of terrigenous silicates and silts (Done, 1982) – similar to conditions associated with Golfo Dulce reefs. *Porites lobata* is a very hardy species, and at Caño Island its predominance was attributed to its resistance to environmental fluctuations, frequent asexual reproduction by fragmentation, as well as sexual reproduction, high rate of wound recovery, and low levels of predation (Guzmán, 1988; Guzmán and Cortés, 1989a,b). As at Caño Island, *Porites lobata* in Golfo Dulce reproduces by fragmentation caused by the feeding of the triggerfish *Pseudobalistid naufragium* on the boring bivalve *Lithophaga* spp. (H. M. Guzmán, pers. comm., 1989), and probably also by sexual means. It is exposed to low levels of predation since *Acanthaster planci* (Linnaeus) and *Phestilla* sp., two predators of *P. lobata* (Glynn, 1974, 1976; Hadfield, 1976; R. C. Highsmith, pers. comm. in Glynn, 1982; Guzmán, 1988) have not been found in Golfo Dulce.

There is little echinoid bioerosion taking place on the Golfo Dulce reefs. Spines of the sea urchin *Eucidaris* sp., an important carbonate bioeroder in the Galápagos Islands (Glynn et al., 1979; Glynn, 1988b), are found in the sediments, but live animals have not been seen in Golfo Dulce. In addition, very few *Diadema mexicanum* A. Agassiz, another important bioeroder in the eastern Pacific (Glynn, 1988b; Guzmán and Cortés, in review), have been observed in Golfo Dulce. By contrast, internal bioerosion appears to be important (Cortés, in prep.), especially by the boring bivalves *Lithophaga* spp. and *Gastrochaena rugulosa*, a boring sponge *Cliona ensifera* and a coral boring shrimp *Upogebia rugosa*.

8 CONCLUSION

Environmental conditions for coral growth in the Golfo Dulce area have been deteriorating since the 1940's, coinciding with the initiation of extensive deforestation. The size of the reefs and the abundances of dead corals indicate that environmental conditions were more conducive to reef growth in the recent past. The increase in sediment loads, caused by deforestation, deleterious agricultural practices, road construction and mining activity, may be the main sources of stress on the Golfo Dulce reefs.

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