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COASTAL OCEANOGRAPHIC CONDITIONS AFFECTING CORAL REEFS ON BOTH SIDES OF THE ISTHMUS OF PANAMA

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ABSTRACT

While coral reefs are an important component of Caribbean coastal habitats, they make a trivial contribution to coastal habitats in the eastern Pacific. Those differences are thought to be related to differences in the physical environments in the two oceans. Coastal oceanographic conditions of Panamá have been well described for the Pacific coast, but not the Caribbean coast. Hence we measured various water-quality variables weekly for 3 years on both coasts. The Pacific is much more seasonal than the Caribbean. Nutrients, chlorophyll, phytoplankton, and zooplankton are more abundant in the Pacific, where seawater is more turbid, less saline, and slightly cooler. These differences are amplified during dry season upwelling on the Pacific coast, when conditions become eutrophic. There is no seasonal upwelling on the Caribbean coast and very little seasonal change in temperature, nutrients, phytoplankton, and zooplankton. These differences support the notion that coral reef development is favoured by warm, oligotrophic conditions, but not by eutrophic conditions.

INTRODUCTION

Coral reefs are restricted to the warm, relatively clear waters in the tropics (Wells 1957). Despite their geographical proximity and latitudinal similarity there are profound differences in the abundance of coral reefs between the tropical west Atlantic (TWA) and the tropical eastern Pacific (TEP): coral reefs represent an important component of habitats throughout the TWA, but make a trivial contribution to coastal communities in the TEP. The largest coral reef (3.7 Km^2) in the TEP is the offshore island of Clipperton (Glynn et al. 1996), while the largest reef close to the mainland, at Coiba Island in Panamá, covers only 1.6 Km^2 (Glynn and McCosker 1972; Glynn and Maté 1996; Guzmán and Cortés 1994).

The emergence of the Isthmus of Panamá some 3.5 m.a. (Coates et al. 1992), divided a single biota. The biotas of the TWA and TEP then diverged due to geographic isolation and extinction events, and in response to divergence in environmental conditions (Rosenblatt 1963; Glynn 1982; Knowlton et al. 1993). The marine environment experienced drastic changes in the two seas that had become separated by the isthmus, when the warm Equatorial Atlantic Current (EAC), which formerly flowed westward through the strait between North and South America, and had influenced the entire region, was blocked and deflected north by the emerged Isthmus of Panamá. The Caribbean Sea and the Gulf of Mexico continued to be influenced by the EAC, which currently flows in through the Lesser Antilles and other passages between the islands of the Caribbean arc (Wust 1964; Kinder et al. 1985). However, the TEP fell under the influence of colder currents flowing toward the equator from both North and South America, and of major, seasonal, wind-driven upwelling systems that developed at several sites along the coast of Central America (Wyrtki 1967; Legeckis 1985; McCreary et al. 1989). As a result, while the Caribbean Sea remained warm throughout the year, the TEP became more seasonal, and while coastal biological productivity is strongly related to benthic communities in the Caribbean, oceanic productivity and high availability of dissolved nutrients exerts an important influence in the coastal oceanography of the TEP. These differences in the physical environments of the two oceans are thought to have been responsible for the dramatic differences in the abundances of coral reefs in the TEP and TWA (Porter 1974; Dana 1975; Highsmith 1980; Birkeland 1987). However, currently there are very few data that actually define differences in coastal oceanographic conditions on the two sides of the isthmus. Simultaneous *in situ* measurements from both oceans do not exist. Previous studies have documented seasonal variation of dissolved nutrients and plankton production cycles in coastal areas of the TEP (Smayda 1966; Forsbergh 1969; Fiedler et al. 1991; and D'Croz et al. 1991). Here we present a 3 year time-series of data on various water quality variables from both the Pacific and the Caribbean coasts of Panamá. These data were collected to provide a better understanding of the similarities and differences in coastal water-quality in these two oceans, and the relationship between variation in the abundance of coral reefs and those differences.

CLIMATOLOGY AND OCEANOGRAPHY OF THE ISTHMUS OF PANAMA.

The climatology of Panamá is governed by the Inter-Tropical Convergence Zone (ITCZ), a zone of low atmospheric pressure. The position of the ITCZ defines the seasonal pattern of rainfall and wind in the area as follows: Between May and December, which is Panamá's rainy season, the ITCZ is located over or slightly to the North of Panamá. Winds are light and variable in direction during the wet season. Between January to March the ITCZ moves to a position slightly South of Panamá, which then experiences its dry season, a period when northeast tradewinds predominate (Forsbergh 1969).

On the Pacific side of the isthmus, a large tidal range is one of the most distinctive features of the coastal environment (Glynn 1972). Tides are semi-diurnal and amplitudes may range up to 6 m. During most of the year, the surface water layer in the TEP is the Tropical Surface Water mass (TSW), the same water mass found over the center of the tropical Pacific Ocean at about 10° North (Wyrtki 1967). Two events regularly affect the coastal oceanography of the Bay of Panamá: (a) a wind-driven, seasonal upwelling, and (b) the episodic ocurrence (4-9 year interval) of sea warming due to the El Niño Southern Oscillation (Glynn 1984; Glynn et al. 1988). Upwelling develops during the dry season when northeast tradewinds cross to the Pacific over a low part in the Isthmian mountain range in central Panamá and displace nutrient-poor, coastal surface water offshore. This displaced surface water is replaced by upwelled cooler, more saline water (Smayda 1966; Forsbergh 1969).

On the Caribbean side of the isthmus, coastal oceanographic conditions are characterized by stability. The tidal range is small (< 0.5 m), with a complex seasonal pattern of change between diel and semi-diel tides of varying amplitudes. Also the effects of wind often overpower those of the tidal regime on shoreline sea level (Cubit et al. 1989). Annual rainfall is high and follows the same basic seasonal pattern as on the Pacific side of the isthmus. The surface water mass of the Caribbean has characteristics very similar to those in the adjacent Equatorial Atlantic, in which the upper 200 m layer is a mass of warm (heated by solar radiation), high salinity water (Wust 1964). This surface water flows into the Caribbean southeastern passages among the Lesser Antilles (Stalcup and Metcalf 1972) as the Caribbean current. The coast of the southwestern Caribbean, including Panamá, is affected by a cyclonic gyre that develops from this current (Gordon 1967; Kinder et al. 1985).

FIELD AND LABORATORY METHODS

Seawater samples were collected weekly at both sides of the Isthmus of Panamá (Fig. 1), from October 1993 to December 1996. On the Pacific side, the sampling site is located in the head of the Bay of Panamá, NE of Taboga Is. (Fig. 2a), where previous studies of hydrology and oceanography of Panamá Bay were conducted (Smayda 1966; D'Croz et al. 1991). Similarity in results of studies by Smayda (1966) and Forsbergh (1969) indicate that sampling site probably is fairly representative of this section of the head of the Bay of Panamá. On the Caribbean side, samples were collected at four sites at San Blas Point (Fig. 2b), an area with an extensive coral reef development (Glynn 1972; Porter 1974; Clifton et al. 1996).

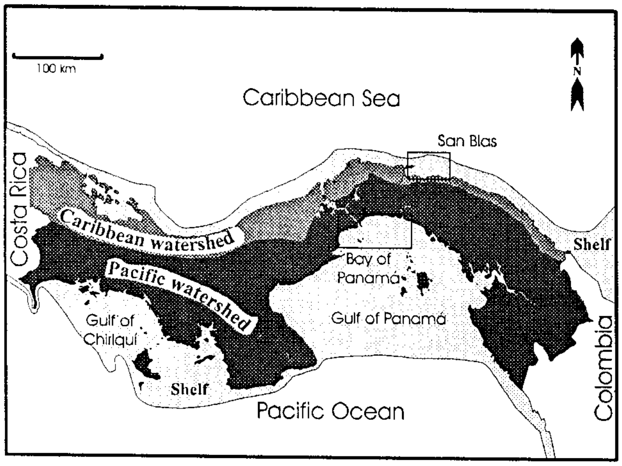


Fig. 1: Map of the Republic of Panamá. Study areas on the Pacific and Caribbean coasts are included in rectangles.

Water samples were collected using Niskin samplers at surface, 5 m, 10 m, and 20 m depth. Temperature of the seawater was measured during the collections using protected reversible thermometers installed in the Niskin samplers. Measurements of salinity of seawater were made for each sample in the laboratory using a salinometer. Secchi disk readings were used to estimate water visibility (to the nearest 0.1 m). After collection, each water sample was filtered through membrane filters (0.45 μm). The filtrate was frozen for subsequent analysis of nutrients. The concentration of chlorophyll was measured by spectrophotometry following the method of Parsons et al. (1984). Membrane-filtered water samples were analyzed for nitrite-nitrate, phosphate, and silicate following Parsons et al. (1984).

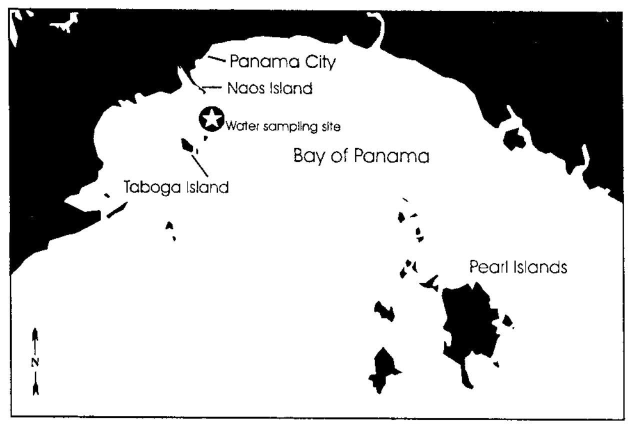
Phytoplankton (diatoms and dinoflagellates) from the water samples was counted in Sedwig-Rafter cells following the APHA method (1991). When necessary phytoplankton contained in water samples was concentrated by sedimentation before analysis. Duplicate oblique plankton tows of 30 minutes duration were carried out during the sampling at each site, using standard plankton nets (0.5 m mouth diameter, 300 μm mesh). A Folson plankton splitter was used to obtain two aliquots from each sample of zooplankton, and the organisms present in each aliquot were counted using a binocular stereomicroscope. The abundance of zooplankton was then calculated following Omori and Ikeda (1984).

RESULTS

THE PACIFIC COAST

Rainfall followed the usual seasonal pattern during our study period - low during the first 1/4 of the year and increasing in intensity towards the end of the wet season (Fig. 3a). Our water quality data (Table 1), corroborated the strong seasonal pattern of variability previously recorded in the coastal environment in this area of the TEP (Smayda 1966; Forsbergh 1969; Fiedler et al. 1991; D'Croz et al. 1991). This is due largely to the effects of upwelling in the Gulf of Panamá. When the upwelled water surges to the surface of the sea, sea surface temperatures may decline to as low as 15° C (Glynn and Maté 1996), although we recorded a minimum of only 18.7° C during our study period. Sea temperature in the upper 20 m of the water column ranged 10° C between the rainy and the dry season, although the seasonal means were only about 3° C different (due largely to weak upwelling in 1996). Inter-annual differences in the intensity of dry season upwelling are indicated from our data (Fig. $4a_1$, 1995 vs 1996, and see also D'Croz et al. 1991). Water salinity was inversely related to sea temperature, ranging from the "full strength" salinity (34‰) during upwelling episodes, to dilutions below 30‰ during the rainy season (Fig. $4b_1$). Secchi disk readings did not show a strong seasonal pattern of change - the lowest secchi disk readings occurred during both the dry season, and the peak of wet season (Fig. $4c_1$). Light penetration is decreased both by the abundance of plankton during the upwelling, and by sediments released with freshwater discharge from rivers during wet season.

a



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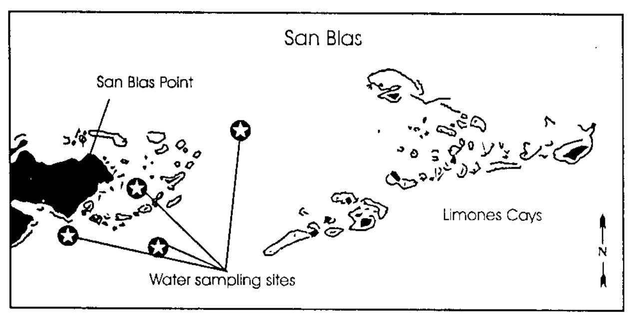

Fig. 2: Study sites in the Bay of Panamá, Pacific coast (a), and San Blas Point, Caribbean coast (b).

The concentration of dissolved nutrients was much higher during dry season than wet season. During dry season upwelling phosphate and nitrate concentrations (Table 1, Fig. $5a_1$) reached as much as 50 and 35 times higher, respectively, than during wet season (Table 1, Fig. $5a_1$, b_1). Seasonal change in the concentration of dissolved silicate followed the reverse of this pattern (Fig. $5c_1$, Table 1), because silicate derives from wet season terrestrial input. The renewal of nutrient in the upper

Table 1: Mean values of water variables measured weekly in the Bay of Panama (Pacific), and San Blas Point (Caribbean). Dry season: from January to April; Rainy season: from May to December; sampling period: from October 1993 to December 1996. SE: standard error; Min: minimum value; Max: maximum value; n: number of measurements.

Bay of Panama (Pacific)	Dry Season				Rainy Season				Sampling period			
	Mean (SE)	Min	Max	n	Mean (SE)	Min	Max	n	Mean (SE)	Min	Max	n
Temperature (°C)	25.5(0.2)	18.7	28.8	102	28.1(0.1)	24.9	30.2	264	27.4(0.1)	18.7	30.2	366
Salinity (o/oo)	32.2(0.2)	27.1	34.9	102	29.2(0.1)	21.5	33.9	264	30.1(0.1)	21.5	34.9	366
Secchi disk (m)	9.3(0.4)	3.5	15.8	36	9.3(0.2)	4.8	14.3	94	9.5(0.2)	3.5	15.8	130
Nitrate-nitrite (μM)	1.03(0.05)	0.11	2.23	100	0.27(0.01)	0.06	0.70	272	0.47(0.02)	0.06	2.23	372
Phosphate (μM)	0.37(0.03)	0.04	0.99	102	0.12(0.01)	0.02	0.33	270	0.19(0.01)	0.02	0.99	372
Silicate (μM)	3.95(0.24)	1.62	9.10	96	8.24(0.33)	2.75	18.75	273	7.13(0.28)	1.62	18.75	369
Chlorophyll a (mg m^{-3})	1.48(0.07)	0.44	2.87	96	0.59(0.01)	0.10	0.87	283	0.95(0.03)	0.10	2.87	379
Phytoplankton (cells ml^{-1})	663.3(47.3)	79.7	2301.1	107	166.4(8.3)	10.5	953.3	279	304.1(18.3)	10.5	2301.1	386
Zooplankton (10^3 per sample)	8.76(1.00)	0.64	29.70	36	7.02(0.50)	1.36	30.76	92	7.51(0.50)	0.64	30.76	128

San Blas Point (Caribbean)	Dry Season				Rainy Season				Sampling period			
	Mean (SE)	Min	Max	n	Mean (SE)	Min	Max	n	Mean (SE)	Min	Max	n
Temperature (°C)	27.9(0.0)	27.1	30.0	369	28.7(0.0)	26.6	30.0	791	28.5(0.0)	26.6	30.0	1160
Salinity (o/oo)	34.8(0.0)	31.0	36.3	369	34.2(0.0)	30.5	37.2	791	34.4(0.0)	30.5	37.2	1160
Secchi disk (m)	16.6(0.4)	4.5	23.4	170	16.4(0.3)	4.0	27.7	400	16.4(0.2)	4.0	27.7	570
Nitrate-nitrite (μM)	0.23(0.01)	0.05	0.48	332	0.29(0.01)	0.09	0.75	622	0.27(0.01)	0.05	0.75	954
Phosphate (μM)	0.04(0.01)	0.01	0.14	303	0.04(0.01)	0.01	0.22	695	0.03(0.01)	0.01	0.22	998
Silicate (μM)	3.06(0.05)	1.52	7.64	334	6.42(0.08)	2.23	15.82	717	5.70(0.08)	1.52	14.50	1051
Chlorophyll a (mg m^{-3})	0.36(0.01)	0.06	1.00	368	0.41(0.02)	0.11	0.99	841	0.40(0.01)	0.11	1.00	1209
Phytoplankton (cells ml^{-1})	60.3(2.3)	19.9	152.3	119	99.9(6.0)	17.1	579.6	220	85.9(4.1)	17.1	579.6	339
Zooplankton (10^3 per sample)	0.80(0.03)	0.17	2.97	197	1.15(0.04)	0.19	5.70	445	1.04(0.03)	0.17	5.67	642

water column clearly is related to the upwelling rather than runoff, as there was no relationship between fluctuations in dissolved nitrogen/phosphorus and silicate (Correlation of silicate versus nitrate-nitrite $r=0.03$, $p=0.67$ and silicate versus phosphate $r=0.03$, $p=0.64$). This suggests that terrestrial runoff may not be an important source of nutrients in the Bay of Panamá.

Fluctuations in the concentrations of chlorophyll and the abundance of phytoplankton (Figs. $6a_1$, b_1) paralleled changes in the concentration of dissolved nutrients, with peaks during the upwelling episodes. Average chlorophyll levels during upwelling were three times as high as during the rainy season (Table 1). Unlike the situation with phytoplankton, there was no pronounced seasonal change in the abundance of zooplankton, although there were suggestion that the highest abundance occurred shortly after the dry season bloom of phytoplankton, and that a decrease in abundance occurred in late rainy season (Fig. $6c_1$, Table 1).

THE CARIBBEAN COAST

Rainfall followed the same general seasonal pattern as on the Pacific coast, although there were differences between the patterns on the two coasts within each year (Fig. 3a, b). In general, most of the measured water quality variables show only small seasonal fluctuations (Table 1). Sea surface temperature (Fig. $4a_2$) ranged only 3° C during the study period, with a small drop (1-2° C) evident during the dry season (i.e. the northern winter). Salinity (Fig. $4a_2$) remained relatively high throughout the year, and showed only a suggestion of a peak in late dry season. Water visibility in San Blas (Fig. $4c_2$), which was about double that on the Pacific side (Fig. $4c_1$), showed a weak tendency to peak in late wet season.

Concentrations of dissolved nitrate and phosphate (Figs. $5a_2$, b_2) were lower in the Caribbean than in the Pacific.

The concentration of nitrogen in the Caribbean during the dry season was 1/5 that on the Pacific, but was about the same in the two oceans during the rainy season. Phosphate concentration in the Caribbean was 1/10 that in the Pacific during the dry season, and 1/4 that in the Pacific during the wet season. Silicate levels in the Caribbean were similar to those in the Pacific, and increased in both oceans as the wet season progressed (Fig. $5c_2$), although differences in the relative abundance of silicate in the Pacific and Caribbean during the two wet seasons did not parallel differences in the relative intensity of rainfall on those two coasts in those two years (Figs. 3 and 5). The mean concentration of silicate in the Caribbean during the rainy season was about twice higher than during the dry season (means were 6.42 μM and 3.06 μM, respectively; t test $p<0.001$). The existence of a weak positive correlation between concentrations of nitrate and silicate (Fig. 5; $r=0.39$, $p<0.001$) indicates that freshwater runoff is the main source of dissolved inorganic nitrogen in this area. However, there was no such relationship between phosphate and silicate (Fig. 5; $r=0.09$, $p=0.13$). Unlike the situation in the Pacific there were no differences in the mean concentrations of nitrate or phosphate in the dry and wet season (Fig. 5, Table 1).

The average level of chlorophyll in San Blas was half that on the Pacific side (Table 1), and there was very little variation with no obvious seasonal pattern (Fig. $6a_2$). The abundance of zooplankton in the Caribbean was about 1/10 of that in the Pacific side during both seasons (Fig. $6c_{1,2}$), again with little variation and no obvious seasonal pattern in the Caribbean.

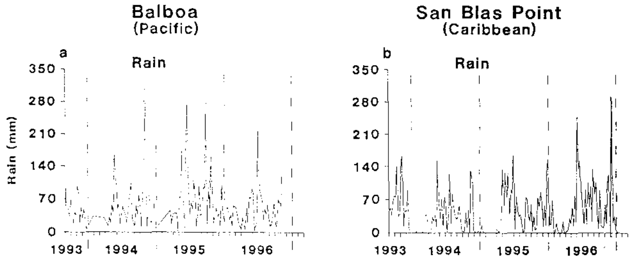

Fig. 3: Patterns of weekly rainfall at Balboa (Pacific, data from the Panamá Canal Comission), and San Blas Point (Caribbean, data from the STRI San Blas Field Station), from October 1993 to December 1996.

DISCUSSION

Our measurements indicate an oligotrophic Caribbean coastal area in which nitrate-nitrite and silicate are replenished through terrestial input by freshwater runoff. However, there is no evidence of notable phosphorus input through such runoff. The low terrestrial input of nitrate/phosphate in San Blas might be due to a combination of (a) the reduced size of the coastal watershed (Fig. 1), and (b) low human impact on that watershed, which is lightly populated and has experienced little agricultural clearing or use of artificial fertilizers. Phosphorus limitation has been reported for other carbonate-rich environments in the Caribbean and Florida (D'Elia et al. 1981; Fourqurean et al. 1992). Absorption of phosphorus by abundant biogenic (i.e. coral reef) calcium carbonate deposits (cf Suess 1973) might be contributing to low phosphate levels in San Blas. However, the levels we recorded there are similar to those recorded by Kwiecinski and Chial (1983)

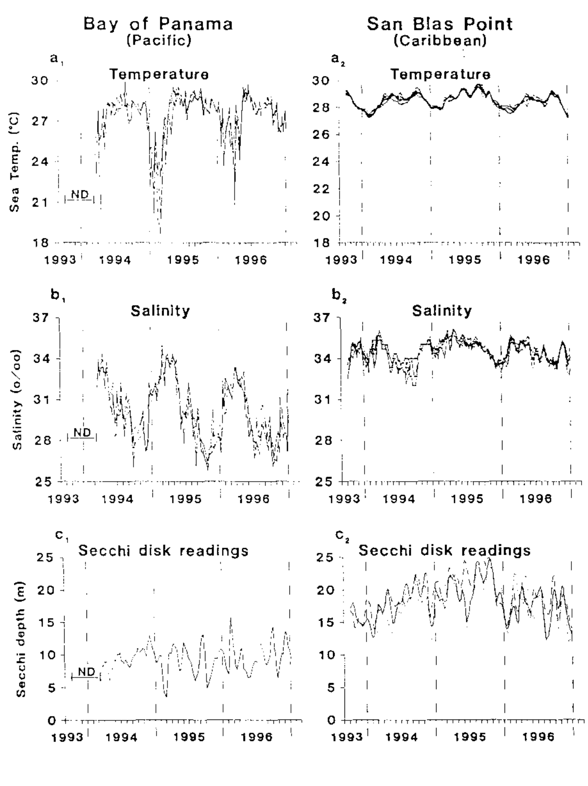

Fig. 4: Weekly measurements of sea temperature (a_1 Pacific; a_2 Caribbean), salinity (b_1 Pacific; b_2 Caribbean), and Secchi disk reading (c_1 Pacific; c_2 Caribbean, from October 1993 to December 1996.

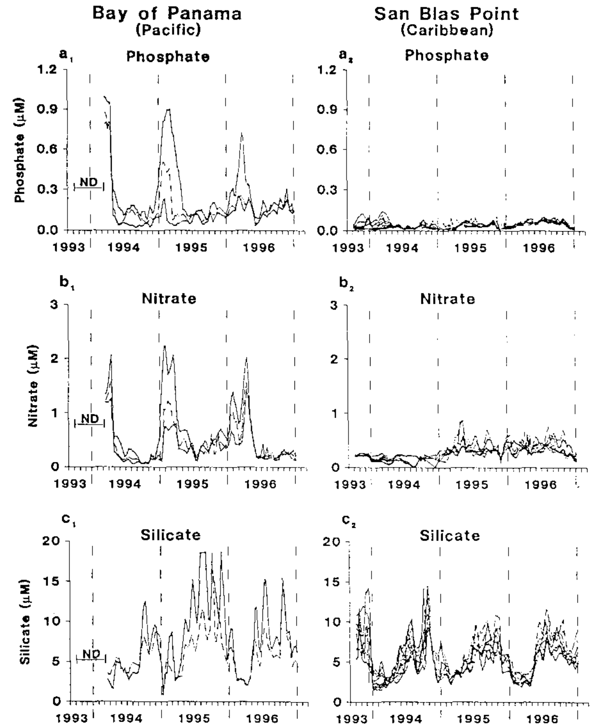

Fig. 5: Time series for phosphate concentration (a_1 Pacific; a_2 Caribbean), nitrate+nitrite concentration (b_1 Pacific; b_2 Caribbean), and silicate concentration (c_1 Pacific; c_2 Caribbean), from October 1993 to December 1996.

in a non-upwelling section of the Pacific coast of Panamá (Gulf of Chiriqui - see Fig. 1) where coral reefs are not abundant. Regardless of the mechanism producing low phosphorus levels in San Blas, phosphorus may well be the primary limiting nutrient for phytoplankton growth (and hence zooplankton production) in our Caribbean study area. Differences between wet season conditions on the Pacific and Caribbean coasts indicate that such limitation is occurring: while nitrate levels are similar on those two coasts, levels of phosphate and phyto- and zooplankton are lower in the Caribbean than the Pacific. What produces higher phosphate levels in the Pacific during wet season is unclear. A much larger watershed (Fig. 1) with higher human populations and much more intensive agriculture may lead to higher phosphate inputs. In addition, a large shallow continental shelf (Fig. 1) swept by strong tidal currents may help retain nutrients in nearshore waters.

The results of our study clearly illustrate the ample differences that exist between the coastal environments on the Pacific and Caribbean sides of the Isthmus of Panamá. These differences are consistent with what previous workers have suggested about factors influencing the development of coral reefs in the TWA and TEP. Coral reefs are best developed in warm seas. Sea surface temperature in the Caribbean side proved to be high, and very stable over the studied period, with a maximum seasonal shift of 2° C. In the Bay of Panamá, however, sea surface temperatures are subjected to substantial seasonal fluctuation (up to 15° C) between the rainy and the dry season, due to seasonal upwelling. Such variation in sea temperature apparently has strong limiting effects on the growth of corals such as *Pocillopora damicornis*, the most important reef builder coral species in the TEP: This species has a much lower rate of growth in the Gulf of Panamá than in the adjacent Gulf of Chiriqui (see Fig. 1), which lacks upwelling and experiences little seasonal change in temperature (Glynn 1977).

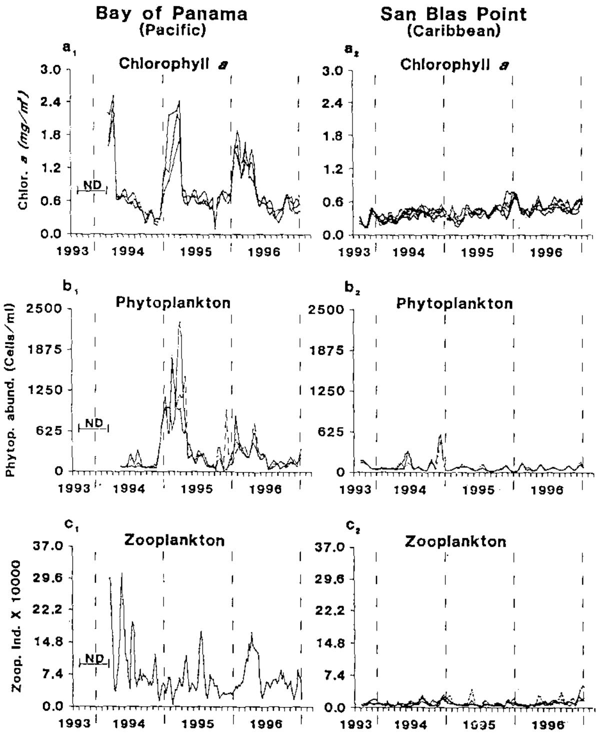

Fig. 6: Weekly concentration of chorophyll *a* (a_1 Pacific; a_2 Caribbean), abundance of phytoplankton (b_1 Pacific; b_2 Caribbean) and zooplankton (c_1 Pacific; c_2 Caribbean), from October 1993 to December 1996.

However, corals are not limited only by low temperatures. Extensive coral bleaching and mortality occurred in the TEP during the strong 1982-83 ENSO, when sea surface temperature rose substantially (Glynn 1984; Glynn et al. 1988). Experimental work with *Pocillopora damicornis* suggests that high temperatures had greater negative effect on corals from the Gulf of Panamá, than on corals from the non-upwelling Gulf of Chiriquí (Glynn and D'Croz 1990). However, a major coral bleaching event also occurred at San Blas Point (and many other areas in the Caribbean) during the summer of 1983, during a period of unusually high sea surface temperatures. This bleaching affected 25 species of coelenterates and mortality reached 35% in some coral reefs (Coffroth et al. 1990). Bleaching associated with high temperatures also affected reefs in San Blas from June to October 1995, but apparently not in the TEP. Thus mortality associated with coral bleaching may negatively affect reef development on the Caribbean and Pacific coasts of Panamá.

Although both high and low sea temperatures are important in limiting coral's growth and the development of coral reef, other evidence indicates that concentrations of dissolved nutrients also directly and indirectly affect coral growth and survival and the development of coral reefs. Highly eutrophic systems may be antagonistic to the development of coral reef in several ways: (a) Light penetration, which affects the growth of algal symbionts of autotrophic corals, can be limited by an abundance of plankton (Lewis 1977). (b) High concentrations of dissolved nutrients promote the growth of macroalgae and other benthic organisms that can outcompete corals for space, and prevent the accumulation of reef structure (Birkeland 1977). (c) Elevated concentrations of phosphorus may inhibit calcification in corals (Kinsey and Davies 1979). (d) High nutrients leads to an abundance of plankton that supports large populations of planktotrophic bioeroding organisms that limit growth of massive corals in the TEP (Highsmith 1980). Strong relationships between sea temperature, dissolved nutrients and phytoplankton in the Bay of Panamá confirmed that enhanced physical seasonality and eutrophic conditions in the Bay of Panamá, conditions that may be unfavorable to the development of coral reefs for a variety of reasons, derive mainly from seasonal upwelling. Stable, tropical, oligotrophic conditions that are favorable to the growth of coral reefs on the Caribbean coast are associated primarily with a lack of upwelling. Thus our data support the idea (Porter 1974) that many of the fundamental controls on the distribution of coral reefs on both coast of the Isthmus of Panamá are purely physical.

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