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# The Effect of Fresh Water Runoff on the Distribution of Dissolved Inorganic Nutrients and Plankton in the Bocas del Toro Archipelago, Caribbean Panama

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**ABSTRACT.—The distribution of dissolved inorganic nutrients (nitrate + nitrite, phosphate, and silicate) and plankton (chlorophyll *a* and zooplankton biomass) was investigated in the Bocas del Toro Archipelago, western Caribbean coast of Panama. The archipelago is naturally divided in two large semi-enclosed lagoons: the Chiriquí Lagoon which is a turbid environment under high influence from runoff, and Almirante Bay that is less affected by runoff. Three surveys were carried out covering both wet and dry months. Hydrological measures varied spatially between regions and temporally on a seasonal basis. High concentrations of nutrients, chlorophyll *a*, and zooplankton biomass coincided with heavy rainfalls. Significant inverse correlations between dissolved inorganic nutrients and salinity during the rainy months confirmed the nutrient contribution from runoff. When compared to the ocean exposed environments high concentrations of chlorophyll and zooplankton biomass were observed in the semi-enclosed lagoons. The episodes of natural eutrophication due to high levels of fresh water runoff in the Bocas del Toro Archipelago contrast to the nutrient and plankton poor waters in coral reef environments along the eastern Caribbean coast of the Isthmus of Panama.**

**KEYWORDS.—Central America, eutrophication, chlorophyll *a*, zooplankton, coral reefs**

## INTRODUCTION

Nitrogen (N), phosphorus (P), and silicon (Si) dissolved in seawater are essential elements for phytoplankton growth and their supply varies greatly in the ocean. The degree of requirement for these nutrients is defined by the Si:N:P atomic ratio (16:16:1) in the phytoplankton biomass and alteration of these proportions often results in physiological limitation of the algae (Redfield 1958). However, exactly which is the most limiting nutrient to algal growth has generated several hypotheses. Nutrient enrichment experiments and field studies have long suggested that phytoplankton productivity in coastal and open oceans is limited by the supply of N (Ryther and Dunstan 1971; Barber and Chavez 1991; Fiedler et al. 1991). Another model predicts that P is the ultimate limiting nutrient for phytoplankton growth in the oceans, since its external supply depends on freshwater discharge from rivers (Tyrrel 1999). Besides, Si is an important requirement for diatom growth and its availability in the coastal ocean primarily depends on freshwater runoff (Falkowski et al. 1998). The ratios among these elements can experience temporal and spatial variation due to ocean processes such as upwelling or due to the effect of heavy fresh water discharge from rivers. These events, therefore, can be critical if the limiting element is altered (D'Elia et al. 1986; Rudek et al. 1991). In coastal areas P limitation is usually related to the discharge of river with high N loads. Whereas N limitation is associated with areas of open ocean water influence (Fisher et al. 1992; Conley 2000; Labry et al. 2002). Coastal plankton food webs are possibly affected by fluctuating Si:N ratios (Turner et al. 1998). Under low Si:N ratios, diatom growth will be Si limited and, therefore, the abundance of copepods, the most important diatom grazers in the mesozooplankton, and main food for planktivore fish, will be reduced.

Nutrient dynamics and plankton production can exhibit great differences in coastal settings along both sides of the Isthmus of Panama (D'Croz and Robertson 1997). Dissolved inorganic nutrients and plankton are at high concentrations in Panama's Pacific coastal environments, mostly due to the seasonal upwelling in the Bay of Panama and also because of the generally large freshwater runoff (Smayda 1966; Forsbergh 1969; Kwiecinski and Chial 1983; D'Croz et al. 1991). In contrast, nutrient— and plankton—poor coastal conditions resulting from strong oceanic influence seem to be the norm on the eastern Caribbean coast of Panama (D'Croz and Robertson 1997; D'Croz et al. 1999).

This paper provides a description of the temporal and spatial patterns of dissolved inorganic nutrients and plankton in the Bocas del Toro Archipelago. Currently there is a dearth of hydrological information from this region of the Panamanian Caribbean coast, particularly given the rapidly developing research being carried out by the Bocas del Toro Research Station operated by the Smithsonian Tropical Research Institute (see Rohwer et al. 2001; O'Dea and Jackson 2002; Carlon and Budd 2002; Tewfik and Guzmán 2003; Guzmán and Guevara 2002; Guzmán et al. 2003; Fukami et al. 2004). We aim to test whether plankton distribution in this area is controlled by dissolved inorganic nutrient inputs from fresh water runoff, or by the incursion of nutrient poor open ocean water.

## MATERIALS AND METHODS

### *Study site*

The Bocas del Toro Archipelago is located in Panama's NW Caribbean coast close to the Costa Rican border and consists of two adjacent semi-enclosed coastal environments bounded by islands, peninsulas, and mainland (Fig. 1). The northern part of the archipelago is subject to ocean-exposed conditions. The Almirante Bay in the NW side of the archipelago has an approximate surface area of 446 Km$^2$, whereas in the SW

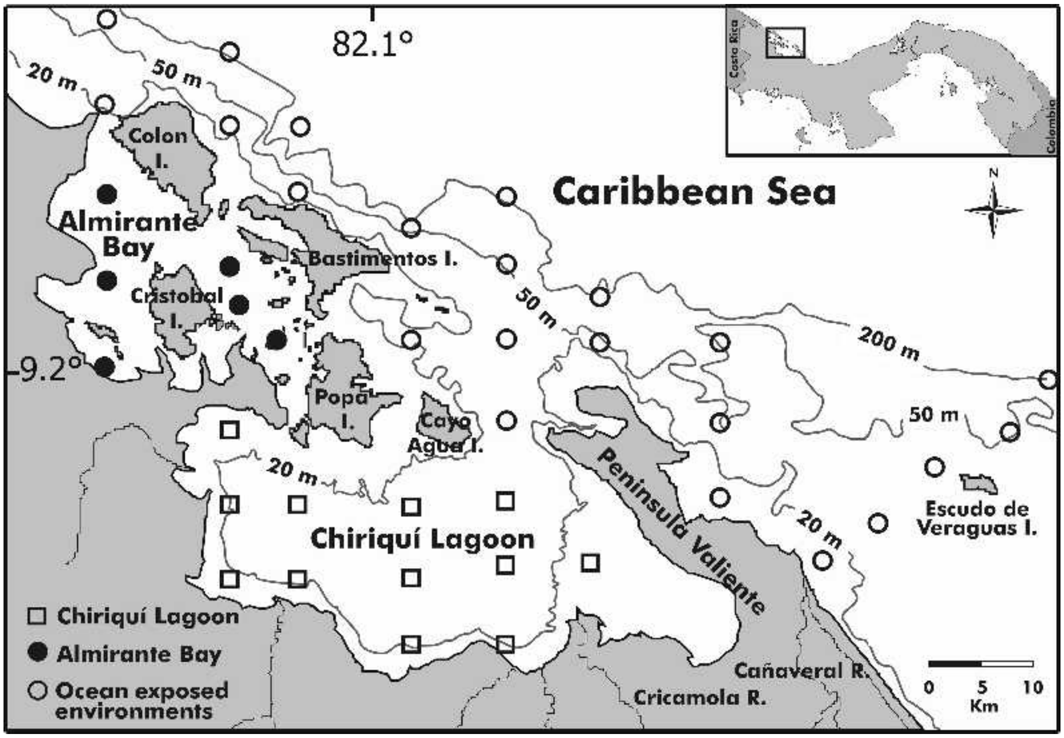

FIG. 1. Location of sampling stations in the Bocas del Toro Archipelago.

the Chiriquí Lagoon is 941 Km$^2$. Water interchange with the open ocean occurs through passages between islands and sand cays. Both zones of the archipelago are communicated by means of numerous mangrove channels. The climate of the archipelago is characterized by frequent and strong rainfalls which averaged 3200 mm per year at Isla Colón for the period from 1972 to 1983 (Instituto Geográfico Nacional Tomy Guardia 1988). Although there is no a clearly defined dry season, periods with less rain typically occur from January to March, and also during September. The rainy season extends from April to December with maximum precipitation during July and December.

The Chiriquí Lagoon is a turbid environment subject to heavy fresh water discharge from several large rivers (see Fig. 1) and runoff geographically varies from 2400 to 2800 mm per year (Instituto Geográfico Nacional Tomy Guardia 1988). Extensive mangrove swamps border the coast in the Chiriquí Lagoon. The Almirante Bay, on the contrary, is under high ocean influence and holds numerous small islands, mangrove islets, and shoaling sand cays. Well developed coral reefs are reported in this area (Guzmán and Guevara 1998). The mean annual runoff is 1600 mm (Instituto Geográfico Nacional Tomy Guardia 1988). The tidal range in the Bocas del Toro Archipelago is small (0.25 m), as typical in the rest of the Caribbean coast of Panama, with complex seasonal patterns of change between diel and semi-diel tides of varying amplitudes (Cubit et al. 1989).

### Sample collections

Three research cruises were conducted in the Bocas del Toro Archipelago aboard the Smithsonian Tropical Research Institute's *R/V Urracá*: Cruise I from the 5th to 10th of May, 1997; Cruise II from the 25th to the 28th of January, 1998; and Cruise III from the 9th to the 13th of October, 1999. Eight cross-shelf sampling transects were made through the archipelago during cruises I and II, and 6 transects during cruise III (Fig. 1). Depending on the length of each transect, from 3 to 7 sampling stations were GPS positioned. Samples were taken between 07:00 and 18:00 h. The closest station to the shoreline was 1.4 Km from the coast and the farthest at 53 Km over the shelf break (approximate depth 200 m). Three replicate surface (1 m depth) water samples were collected at each station and 2 liters from each were immediately sieved through Nitex mesh 350 μm to remove possible zooplankters, and vacuum filtered on Whatman GF/F. Filters with the concentrated phytoplankton were kept for further analyses of chlorophyll *a* (Chl *a*) and an aliquot of 250 mL from each filtrate was set apart for the determination of dissolved inorganic nutrients. Filters and water samples were stored frozen (−20 °C) until analysis. Zooplankton was collected in the upper 10 m of the water column by means of replicate 25 min. oblique tows with twin nets (mouth opening = 1 m and 350 μm Nitex mesh) equipped with flowmeters to calculate the water volume sampled. Zooplankton samples were stored frozen (−20 °C) until processing in the laboratory. *In situ* temperature and salinity measurements were carried out with the YSI 85 instrument (Yellow Spring Instruments Inc., Ohio, USA).

### Chemical and statistical analyses

Not later than two weeks after sampling Whatman GF/F filters were analyzed for total Chl *a*. Filters were transferred to tubes containing 90% aqueous acetone solution, ground with a Teflon pestle, and the Chl *a* extracted in the dark during 24 h. Extracts were then centrifuged at 3000 g for 15 minutes and analyzed by fluorometry (Welschmeyer 1994). Water samples were analyzed manually for nitrite-nitrate (referred to as N) by the standard pink azo-dye method; phosphate and silicate (referred to as P and Si respectively) were determined using the molybdenum-blue method. In all cases the dissolved inorganic nutrient analyses followed the methods of Parsons et al. (1984). For zooplankton organic mass (ash-free dry mass) estimation, samples were thawed at room temperature, rinsed with distilled water to remove salts, oven-dried at 60 °C for 24 hours, weighed, and combusted in a muffle furnace at 500 °C for 12 hrs. The zooplankton organic mass was expressed as $\mu g\ L^{-1}$. For the analyses of spatial patterns the archipelago was arbitrarily divided into three regions: the Almirante Bay, the Chiriquí Lagoon, and the ocean exposed environment (see Fig. 1). Data were analyzed using one-way ANOVA for significance test for spatial comparison and Pearson's correlation analysis to identify possible relationships between dissolved inorganic nutrients, Chl *a*, and zooplankton organic mass.

## RESULTS

Differences in the distribution of hydrological variables were found between the cruises to the Bocas del Toro Archipelago. Descriptive statistics of hydrological variables measured in the archipelago are summarized in Table 1.

### *Temperature*

Warm sea surface temperature in the archipelago was the norm during the three cruises (range from 27 °C to almost 30 °C) and despite this small range, spatial differences were significant in January 1998 ($p < 0.01$) and in October 1999 ($p < 0.001$, see Table 2).

### *Salinity*

Surface salinity varied according to season (Fig. 2). Low surface salinities were common during May 1997 coincident with heavy rainfalls. Precipitation measured at the Isla Colón Airport during the 30 days previous to the cruise was 287.7 mm and most of it occurred from May 8 to May 9 coinciding with the collection of the samples (data provided by K. Kaufman). At this time a band of low-salinity water developed along the shoreline, especially at the Chiriquí Lagoon where a plume (< 30 psu) was detected flowing from the SE section of the lagoon (Fig. 2a). This area is subject to strong freshwater discharge from major rivers in the surroundings. However, contemporary surface salinities in Almirante Bay remained at higher values (mean = 30.14 psu) and the distribution of isohalines suggests this environment is under higher influence from open ocean waters. Strong dilution of salinity was also observed in the northern coast of the Valiente Peninsula, possibly related to the fresh water discharge from the Cañaveral River (Fig. 2). During January 1998 high surface salinities were typical in both semi-enclosed lagoons (Fig. 2b). Rainfall recorded during 30 days prior to this cruise was 101.5 mm. Mean salinity was 34.23 psu for the Almirante Bay and 33.91 psu in the Chiriqui Lagoon (Table 1). Full strength salinity was recorded in the ocean exposed environment (35.37 psu). Nevertheless, at the SE section of the Chiriquí Lagoon the 33 psu isohaline developed close to the shoreline indicating moderate dilution from river discharge. The influence of fresh water runoff in the archipelago during October 1999 was not as strong as that recorded during previous cruises (Fig. 2c). Rainfall during the 30 days preceding the October cruise was 82.0 mm. ANOVA corroborated significant differences in the spatial distribution of salinity at all sampling times (Table 2).

### *Water clarity*

Water clarity varied also according to the local climatology. Water clarity was poor during May 1997 when rainfall was heavy and mean Secchi disk depths varied from 4.91 m in the turbid Chiriquí Lagoon to 6.05 m in the ocean exposed environments (Table 1). By early dry season (January 1998) water clarity had doubled and mean values for Secchi disk readings were almost identical between the Almirante Bay and the ocean exposed environments (14 m), providing another indication of offshore water influence in this area. During October 1999 water clarity was reduced and was again very similar between the ocean-exposed environments and the Almirante Bay (Table 1). Water visibility was even less in the Chiriquí Lagoon. However, no significant spatial differences were detected for the different cruises (Table 2).

TABLE 1. Descriptive statistics of water quality and plankton variables (mean ± se). N = number of sampling stations.

| | May 1997 | | | January 1998 | | | October 1999 | | |
|---|---|---|---|---|---|---|---|---|---|
| | Chiriquí Lagoon N = 12 | Almirante Bay N = 6 | Ocean exposed N = 22 | Chiriquí Lagoon N = 12 | Almirante Bay N = 6 | Ocean exposed N = 22 | Chiriquí Lagoon N = 12 | Almirante Bay N = 6 | Ocean exposed N = 14 |
| Temperature (°C) | 27.54 ± 0.14 | 27.72 ± 0.13 | 27.35 ± 0.10 | 28.84 ± 0.10 | 28.73 ± 0.25 | 28.38 ± 0.01 | 29.88 ± 0.22 | 29.85 ± 0.13 | 28.68 ± 0.01 |
| Salinity (psu) | 30.15 ± 0.89 | 31.15 ± 0.99 | 33.62 ± 0.75 | 33.91 ± 0.19 | 34.23 ± 0.06 | 35.37 ± 0.08 | 32.60 ± 0.51 | 33.42 ± 0.10 | 33.86 ± 0.08 |
| Secchi depth (m) | 4.91 ± 0.66 | 5.00 ± 0.68 | 6.05 ± 0.88 | 11.72 ± 1.50 | 14.26 ± 1.02 | 14.20 ± 1.02 | 8.90 ± 1.54 | 10.05 ± 1.30 | 10.50 ± 0.68 |
| Nitrate + Nitrite (μM) | 1.14 ± 0.29 | 0.33 ± 0.05 | 0.61 ± 0.11 | 0.63 ± 0.02 | 0.64 ± 0.06 | 0.64 ± 0.03 | 0.35 ± 0.13 | 0.26 ± 0.09 | 0.33 ± 0.08 |
| Phosphate (μM) | 0.10 ± 0.02 | 0.05 ± 0.01 | 0.07 ± 0.01 | 0.13 ± 0.02 | 0.10 ± 0.03 | 0.08 ± 0.03 | 0.04 ± 0.01 | 0.06 ± 0.02 | 0.03 ± 0.01 |
| Silicate (μM) | 24.56 ± 2.86 | 8.98 ± 1.39 | 7.27 ± 0.75 | 18.64 ± 0.98 | 12.76 ± 1.64 | 7.71 ± 0.48 | 14.64 ± 1.75 | 3.29 ± 0.62 | 10.63 ± 0.86 |
| Nitrate + Nitrite : Phosphate | 11.24 ± 3.39 | 6.50 ± 0.84 | 9.25 ± 0.90 | 5.00 ± 0.89 | 6.33 ± 1.24 | 8.02 ± 1.23 | 7.94 ± 2.00 | 4.20 ± 0.69 | 10.97 ± 3.40 |
| Silicate : Nitrate + Nitrite | 21.51 ± 4.36 | 26.93 ± 1.83 | 11.90 ± 1.08 | 29.74 ± 1.42 | 19.99 ± 4.32 | 12.02 ± 0.91 | 41.67 ± 10.47 | 12.71 ± 3.17 | 32.28 ± 5.36 |
| Chlorophyll *a* (μg $L^{-1}$) | 1.41 ± 0.14 | 1.71 ± 0.15 | 1.21 ± 0.10 | 0.44 ± 0.02 | 0.49 ± 0.08 | 0.34 ± 0.03 | 0.53 ± 0.10 | 0.37 ± 0.06 | 0.26 ± 0.04 |
| Zooplankton organic mass (μg $L^{-1}$) | 3.92 ± 0.73 | 3.00 ± 0.95 | 2.46 ± 0.27 | 4.31 ± 0.90 | 4.52 ± 1.01 | 1.38 ± 0.31 | 3.13 ± 0.72 | 3.35 ± 0.54 | 1.76 ± 0.41 |

### *Nitrogen*

The concentration of N also showed temporal patterns (see Table 1). Nitrogen was especially high in nearshore areas of the Chiriquí Lagoon during rainy May 1997 (mean = 1.14 μM). However, N levels measured at the same time in Almirante Bay and the ocean-exposed environments were much lower (mean = 0.33 μM and 0.66 μM, respectively). Conditions encountered during January 1998 were completely different from May 1997 as concentrations of N were relatively low in the archipelago (circa 0.64 μM). During October 1999, N was found in low concentrations in both Almirante Bay (0.26 μM) and the Chiriquí Lagoon (0.35 μM) (Table 1). The concentration of N was inversely correlated to surface salinities during May 1997 but not during the other samplings (Fig. 3a). The distribution of N isolines, at the SE Chiriquí Lagoon during May 1997, supports the view that discharge from rivers were significantly contributing N (Fig. 4). Spatial differences in N concentrations were significant only in May 1997 (Table 2).

### *Phosphorus*

During the three cruises mean P concentrations were generally low (< 0.15 μM), as illustrated by the P isolines (Fig. 5). However, P levels in the Chiriquí Lagoon were slightly higher during May 1997 and showed significant inverse correlation with salinity (Fig. 3b). Significant spatial differences in the distribution of P were only found in October 1999 (Table 2). The N:P ratios in the archipelago were always below the Redfield value (Table 1). The ANOVA test did not confirmed spatial N:P differences during May 1997 and October 1999. However, significant differences in N:P were found in January 1998 when the ratio in the Chiriquí lagoon was half that measured in the other environments (Table 2).

### *Silicon (Silicate)*

Very high Si concentrations were measured in the Chiriquí Lagoon during May

TABLE 2. Summary of the results from ANOVA/F spatial comparison. Significance levels: $^{*}P < 0.05$, $^{**}P < 0.01$, and $^{***}P < 0.001$.

| | May 1997 | January 1998 | October 1999 |
|---|---|---|---|
| Temperature (°C) | 1.77 | 6.31** | 19.50*** |
| Salinity (psu) | 4.60** | 44.42*** | 3.75* |
| Secchi depth (m) | 0.56 | 1.06 | 0.39 |
| Nitrate + Nitrite (μM) | 3.70* | 0.06 | 0.13 |
| Phosphate (μM) | 2.50 | 0.52 | 3.30* |
| Silicate (μM) | 31.98*** | 53.73*** | 13.63*** |
| Nitrate : Phosphate | 1.00 | 3.55* | 0.99 |
| Silicate : Nitrate | 13.22*** | 38.68*** | 3.92* |
| Chlorophyll *a* ($\mu g\ L^{-1}$) | 2.98* | 3.55* | 2.69 |
| Zooplankton organic mass ($\mu g\ L^{-1}$) | 2.38 | 8.82** | 2.14 |

TABLE 3. Pearson's correlation coefficients between dissolved inorganic nutrients, Chl *a*, and zooplankton organic mass. Data (log + 1) transformed. Significance levels: * $p < 0.05$; ** $p < 0.01$.

| | Chlorophyll *a* ($\mu g\ L^{-1}$) | Phosphate (μM) | Nitrate + Nitrate (μM) | Silicate (μM) |
|---|---|---|---|---|
| Phosphate (μM) | 0.07 | — | | |
| Nitrate + Nitrite (μM) | 0.19 | 0.31* | — | |
| Silicate (μM) | 0.20 | 0.18 | 0.43** | — |
| Zooplankton organic mass ($\mu g\ L^{-1}$) | 0.36* | 0.28 | 0.35* | 0.21 |

1997 and nearshore concentrations were from 4 to 8 times higher than in the ocean exposed environment (Table 1). Even during the dry season cruise (January 1998) mean Si concentrations in both semi-enclosed lagoons remained high (12 to 18 μM) double that of the ocean-exposed stations (Fig. 6). The concentration of Si was inversely correlated to salinity in all the samples (Fig. 3c). Spatial Si differences were highly significant (Table 2). The Si:N ratios were very high (12 to 42) due to the elevated Si concentrations (Table 1) and significantly varied between regions at all times (Table 2).

### Chlorophyll *a*

Mean Chl *a* reached highest levels in May 1997, ranging from 1.21 $\mu g\ L^{-1}$ in the ocean exposed environments to 1.71 $\mu g\ L^{-1}$at the Almirante Bay (Fig. 7a). During subsequent cruises concentrations of Chl *a* were approximately half of this level with the highest levels always within the semi-enclosed lagoons (Figs. 7b and 7c). Significant spatial differences in the concentration of Chl *a* occurred in the archipelago during May 1997 and January 1998 (Table 2).

### Zooplankton

Highest zooplankton organic mass was measured in the Chiriquí Lagoon and smallest in the ocean exposed environment (Fig. 8). However, significant spatial differences in organic mass were confirmed only for January 1998 data (Table 2). Mean zooplankton organic mass data, from the three cruises, were fairly close yet slightly higher during January 1998 when ranged from 4.5 $\mu g\ L^{-1}$ in the semi-enclosed lagoons to 1.76 $\mu g\ L^{-1}$ in the ocean exposed environments (Table 1).

In order to identify possible relationships between dissolved inorganic nutrients and plankton we applied the Pearson's correlation analysis and results are presented in Table 3. Only a few significant correlations were obtained. Significant correlation occurred between the concentration of Chl *a* and the zooplankton organic mass ($p < 0.05$), but not between Chl *a* and dissolved inorganic nutrients. Levels of N were significantly correlated to Si ($p < 0.01$)

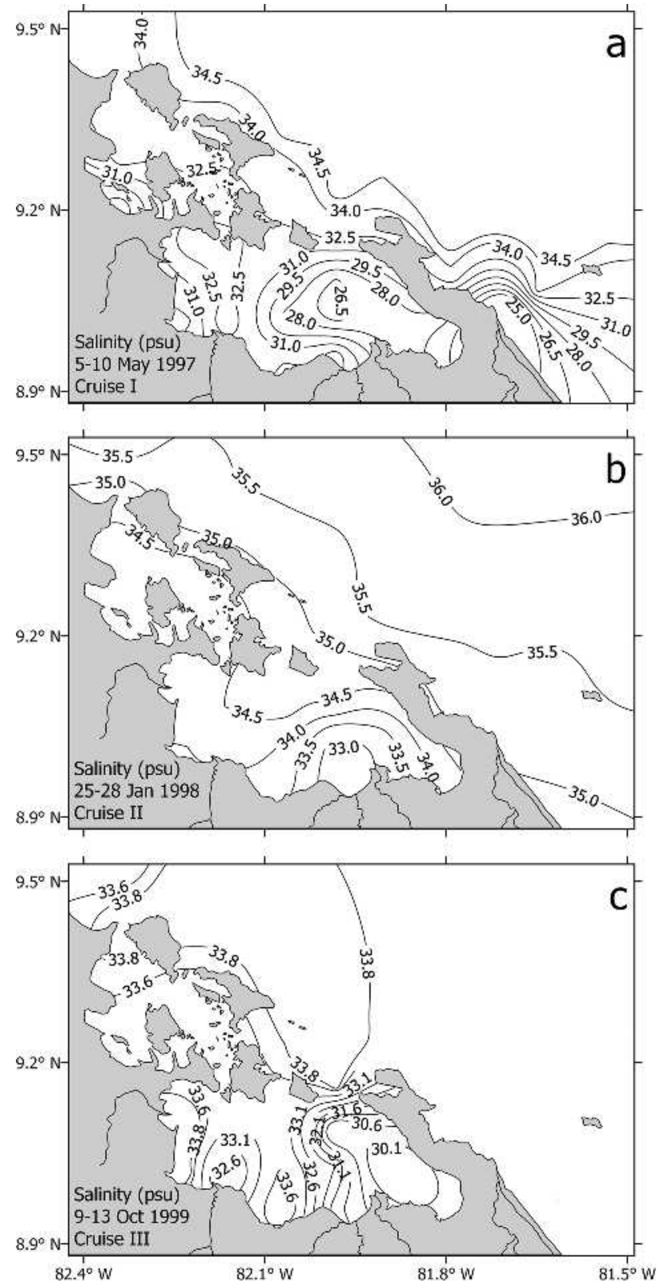

FIG. 2. Surface distribution of salinity (psu) in the Bocas del Toro Archipelago during (a) 5-10 May 1997, (b) 25-28 January 1998, and (c) 9-13 October 1999.

and to the zooplankton organic mass ($p < 0.05$).

## DISCUSSION

The influence from fresh water runoff varies greatly along the Caribbean coast of Panama. Although signals from fresh water runoff were evident from near shore to ocean exposed environments in the Bocas del Toro Archipelago, in the San Blas Archipelago, eastern Panama, fresh water runoff is low and restricted to a narrow

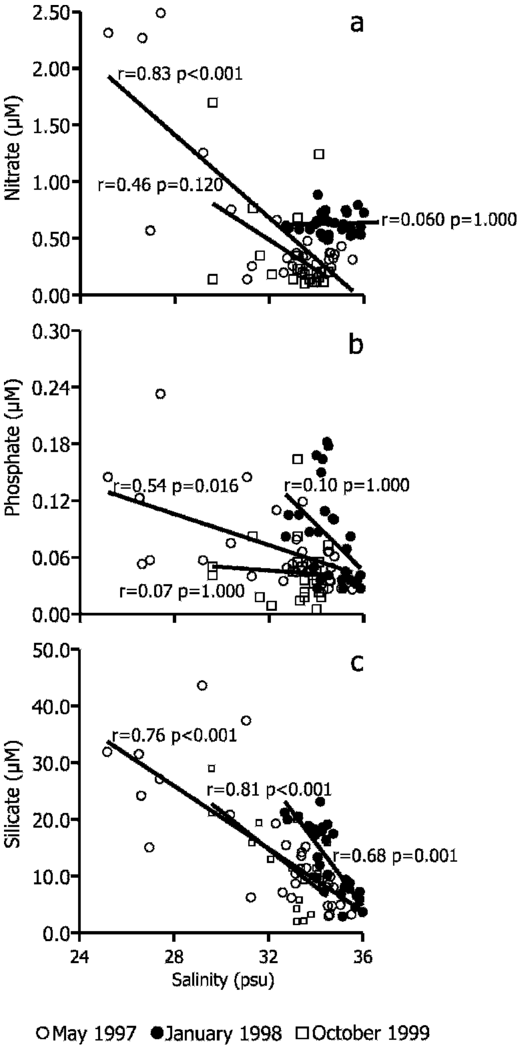

FIG. 3. Correlations between dissolved inorganic nutrients (µM) and surface salinity (psu). (a) nitrate + nitrite, (b) phosphate, and (c) silicate. r = Pearson's correlation coefficient; p = significance level.

zone close to the coast (D'Croz and Robertson 1997). River discharge in Bocas del Toro affected most of the hydrological variables measured during this study, yet the degree of mixing between ocean and fresh waters varied along the inshore-offshore gradient in the archipelago. In particular, sea surface salinity was significantly reduced because of mixing with fresh water in the Chiriquí Lagoon. Fresh water mixing, however, was less intense in Almirante Bay and salinity was closer to that of the ocean exposed environments. Isohaline patterns across the region suggest a general flow of high salinity water from the open sea into the Almirante Bay whereas low salinity water streamed off the Chiriquí Lagoon (Fig. 2). Also, limited eastward flow of high salinity water from Almirante Bay to the Chiriquí Lagoon should be expected by means of the passages between the islands.

Overall, the data support the idea that fresh water discharges contribute to significant amounts of nutrients to the Bocas del Toro Archipelago. This condition was particularly apparent in the Chiriquí Lagoon which is heavily affected by the drainage from the Cricamola River and others (Figs. 4 to 6). The significant inverse correlations between dissolved inorganic nutrients and surface salinities during May 1997 support this conclusion (Fig. 3). High N levels (> 1 µM) were measured in the archipelago during May 1997 when there were indications of strong river discharge, such as low surface salinities and debris from aquatic plants floating in the lagoon. We believe this to be the reason for the significant difference in N concentration between the Chiriquí Lagoon and the Almirante Bay at this time. However, P levels in the archipelago were usually low (less than 0.13 µM) which is comparable to other locations in Central America, such as mangrove and coral reef environments in Belize (Lapointe et al. 1992). The inverse correlation between P and salinity in the Chiriquí Lagoon in May 1997 also indicates P contribution from runoff during times with high rainfall (Fig. 3b). High nutrient and chlorophyll concentrations in coastal areas under strong influence from fresh water discharges are not unusual in the Caribbean. The effect of the Orinoco River plume reaches Puerto Rico and the Dominican Republic, affecting hydrological conditions in a large section of the Caribbean Sea (Rivera-Monroy et al. 2004; Corredor and Morrel 2001). Central American coastal areas are also subject to heavy river discharge (Hallock and Elrod 1988; Roberts and Murray 1983). In addition, nutrification episodes are related to upwelling off Venezuela (Muller-Karger et al. 1989); and

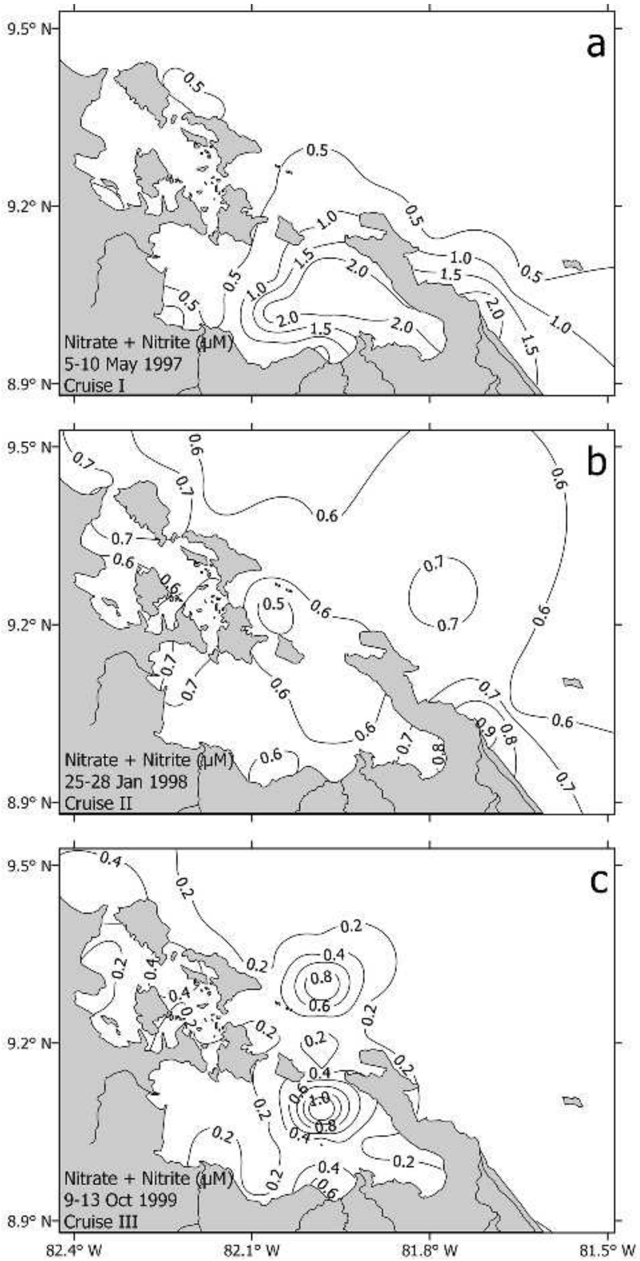

FIG. 4. Surface distribution of nitrate + nitrite (μM) in the Bocas del Toro Archipelago during (a) 5-10 May 1997, (b) 25-28 January 1998, and (c) 9-13 October 1999.

anthropogenic enrichment is increasingly affecting coral reef habitats all over the Caribbean (D'Elia et al. 1981; Tomasick and Sander 1985; Littler et al. 1992). However, the large input of nutrients from fresh water runoff detected in the Chiriquí Lagoon is opposite to the nutrient dynamics observed at San Blas, where oligotrohy results from the combination of a small watershed and low human impact (D'Croz and Robertson 1997; D'Croz et al. 1999). Also, the semi-enclosed nature of the Chiriquí La-

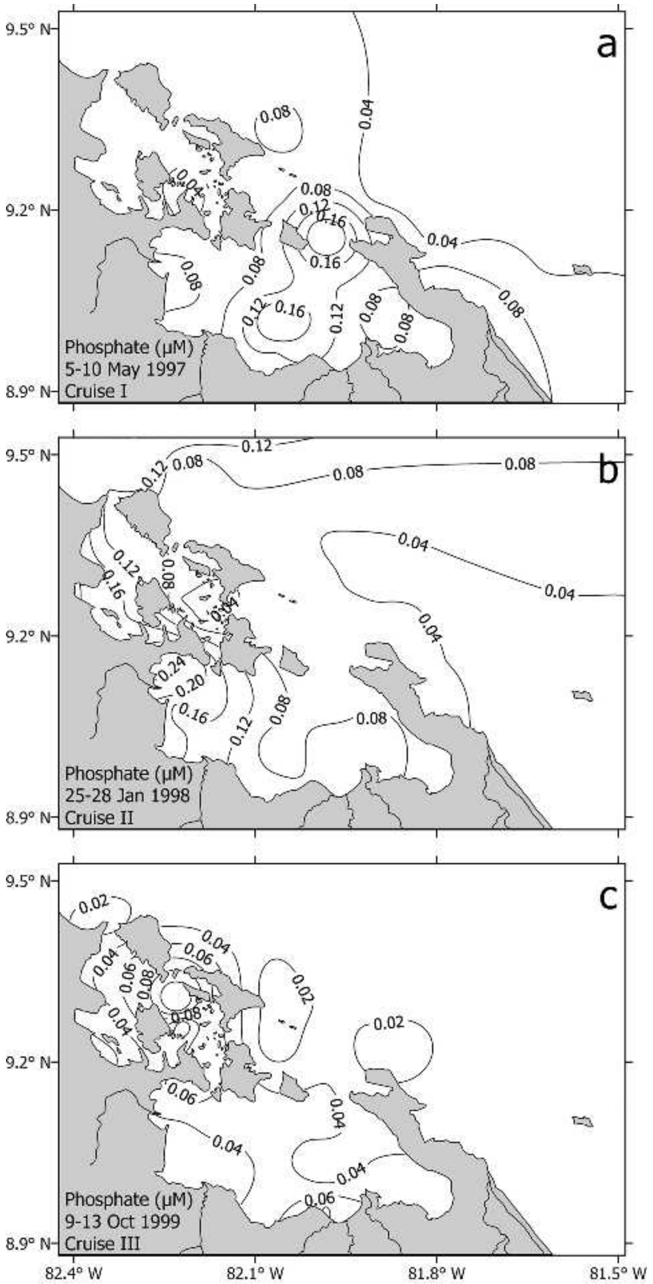

FIG. 5. Surface distribution of phosphate (µM) in the Bocas del Toro Archipelago during (a) 5-10 May 1997, (b) 25-28 January 1998, and (c) 9-13 October 1999.

goon promotes large nutrient levels during episodes of increased river discharge. The relatively high residence time of the water mass in the Chiriquí Lagoon, approximately140 days according to Kwiecinski and Chial (1984), may also contribute to keep nutrient levels high. Open coastal zones, on the contrary, are generally well flushed which minimizes the effect of land derived nutrients (Pastorok and Bilyard

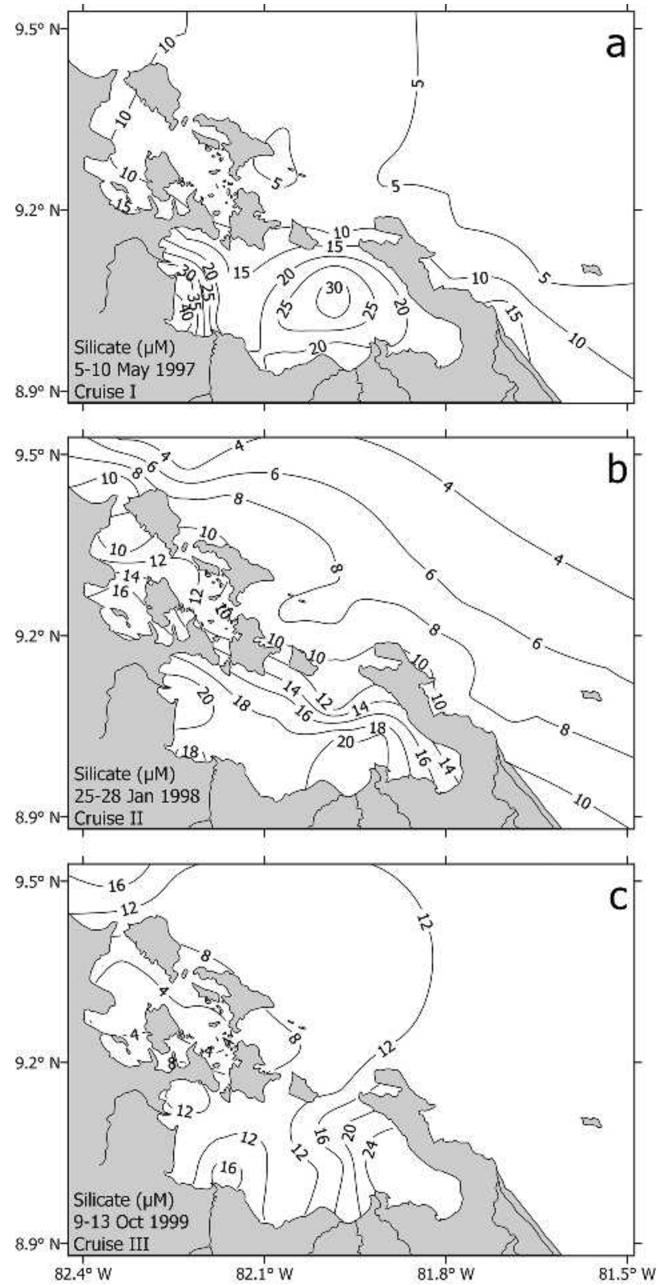

FIG. 6. Surface distribution of silicate (μM) in the Bocas del Toro Archipelago during (a) 5-10 May 1997, (b) 25-28 January 1998, and (c) 9-13 October 1999.

1985). As the Almirante Bay is less exposed to runoff, nutrient levels are lower than in the Chiriquí Lagoon.

Coral reef distribution in the Bocas del Toro Archipelago tend to mirror the hydrological differences observed between the Almirante Bay and the Chiriquí Lagoon. Suggested threshold nutrient levels for coral reef development in the Caribbean is P below 0.10 μM and N under 1 μM

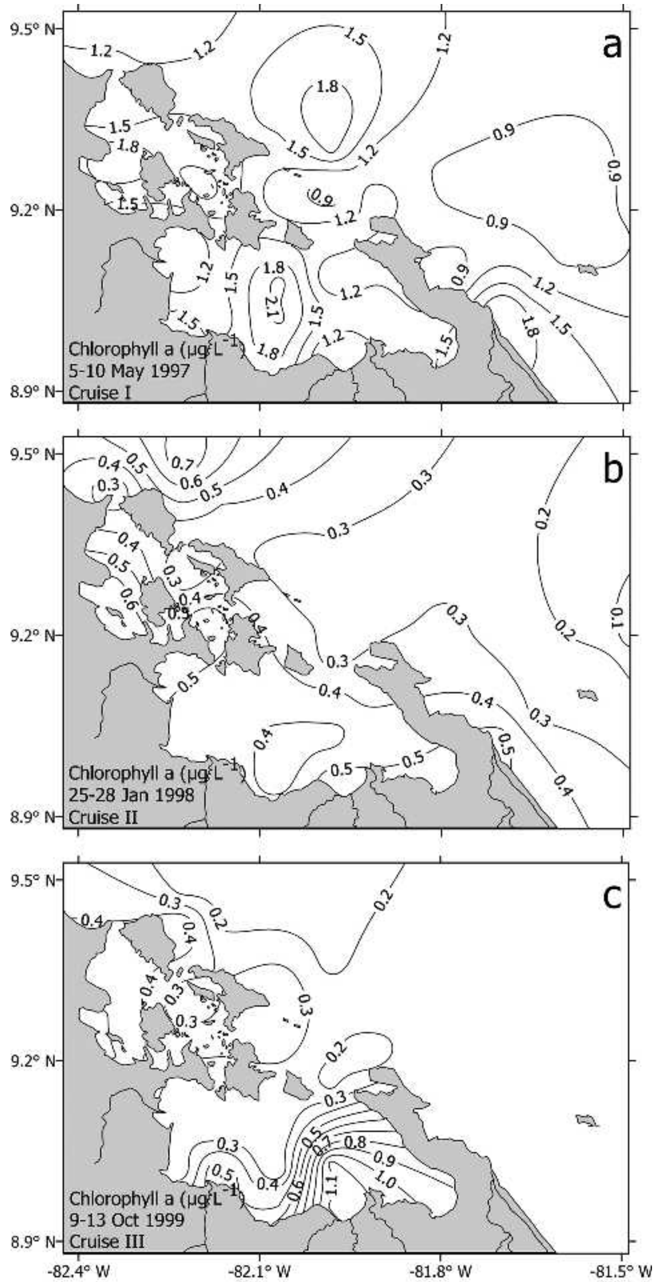

FIG. 7. Surface distribution of chlorophyll *a* (μg $L^{-1}$) in the Bocas del Toro Archipelago during (a) 5-10 May 1997, (b) 25-28 January 1998, and (c) 9-13 October 1999.

(Lapointe et al. 1992). High-nutrient water will induce the rapid growth of macroalgae rather than seagrasses and corals. Low-nutrient waters, in contrast, may promote high benthic diversity through complex food webs, environmental stability, and spatial heterogeneity (Hallock 1988). The relatively clear and nutrient poor waters in the Almirante Bay likely promote the development of coral reefs down to 20 m. In

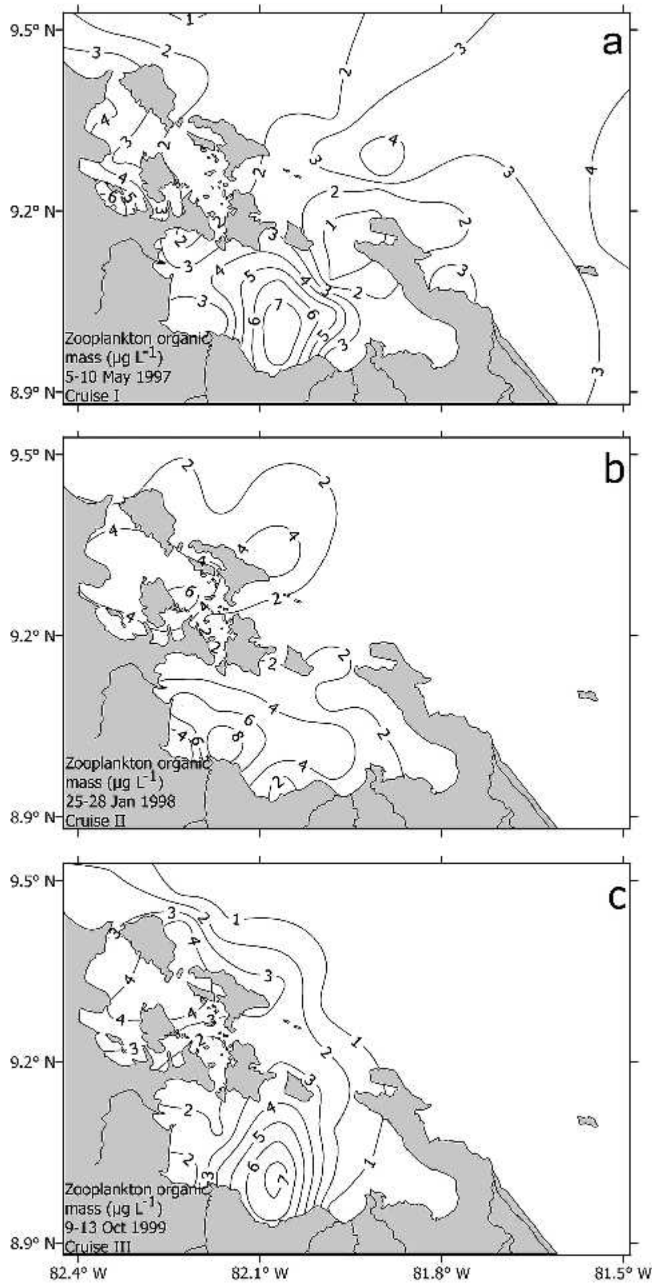

FIG. 8. Surface distribution of zooplankton organic mass (µg L$^{-1}$) in the Bocas del Toro Archipelago during (a) 5-10 May 1997, (b) 25-28 January 1998, and (c) 9-13 October 1999.

the Chiriquí Lagoon high fresh water runoff fosters turbid environments and coral distribution and diversity is very restricted. While 14 coral reefs are reported in the Almirante Bay, only one is in the Chiriquí Lagoon (Guzmán and Guevara 1998). Coral reefs in the Almirante Bay have 33 scleractinian species and living coral covers up to 50%, whereas in the Chiriquí Lagoon seven coral species are reported and coral growth is limited to 3 m depth (Guzmán and Guevara 1998). Notwithstanding, coral growth in Bocas del Toro is not as high as in the San Blas Archipelago, where clearer water promotes coral distribution down to 40 m.

In general, river runoff greatly modifies the N:P and Si:N ratios in coastal zones (Fisher et al. 1992; Labry et al. 2002; Wu and Chou 2003). However, the spatial or temporal patterns in N:P ratios in the Bocas del Toro Archipelago were not clear. Mean N:P ratios were mostly below 8 and, at all cases, below the Redfield value (16:1) suggesting N-limited phytoplankton growth. However, incubation experiments to examine nutrient limitation in phytoplankton growth have often rendered different N:P thresholds according to different environments. For instance, N-limited phytoplankton growth was reported when N:P ratios ranged from 6 to 17 in the western North Atlantic (Menzel and Ryther 1964). Whereas, in the estuary of Changjiang River, China, N limitation occurred when N:P ratios was below 8 and P limitation when N:P was larger than 30 (Wang et al. 2003).

The large supply of Si in the Bocas del Toro Archipelago resulting from runoff was particularly evident in the Chiriquí Lagoon. Continental weathering is the primary source for the usually high Si levels in river discharges (Falkowski et al. 1998). We found Si concentrations in the archipelago ranging from 7 μM to 25 μM (except 3.29 μM in the Almirante Bay during October 1999). Therefore, Si limitation on phytoplankton growth is not likely to have occurred in the archipelago as these concentrations surpass the half-saturation constant for diatom Si uptake of 2 μM (Del Amo and Brzezinski 1999). The input from land derived Si, clearly visible from the distribution of Si isolines in the Chiriquí Lagoon, affected a large section of the archipelago (Fig. 5). The Si:N ratios in the Chiriqui Lagoon were high (12 to 42) exceeding the Redfield Si:N (1:1) and possibly confirming N-limited phytoplankton growth.

High chlorophyll *a* values during May 1997 suggest that phytoplankton growth was greatly enhanced when the archipelago became exposed to high runoff (Fig. 6). However, we were unable to monitor the particular types of autotrophs responsible for these high chlorophyll levels. Eutrophy may foster the proliferation of small ciliates but may correspondingly inhibit diatom growth, the main food for copepods, and a condition that would also lead to high chlorophyll levels (Turner et al. 1998). Besides the high chlorophyll levels found in May 1997, mean chlorophyll *a* concentrations were relatively low in the Almirante Bay and at the ocean exposed environments, and close to 0.5 $\mu g\ L^{-1}$ the suggested threshold value for oligotrophic coral reef environments (Bell 1992). The distribution of the zooplankton organic mass may also be connected to water runoff as higher values occurred in the semienclosed lagoons, particularly near the areas most affected by river discharges (Fig. 8). Increased zooplankton biomass with elevated eutrophication has been reported in lakes (Bays and Crisman 1989, Pace 1986). The ecological significance of high organic mass within the plankton food web in Bocas del Toro can not be answered with this study as we did not assessed the structure of the zooplankton community. Eutrophication in coastal environments has increased the relative proportion of microzooplankton in the zooplankton biomass making small zooplankters, such as oligotrichs and rotifers, dominant while decreasing the relative number of microcrustacean nauplii and copepods in the mesozooplankton (e.g., Park and Marshall 2000). As copepods are the main food for planktivore fish, fish-yields might be small if their proportion in the plankton becomes impoverished (Turner et al. 1998). Whether runoff affects plankton food webs in the Bocas del Toro Archipelago is an issue that will have to be approached in further studies.

In summary, hydrological changes in the Bocas del Toro Archipelago were influenced from both the fresh water runoff and the oceanic waters. While the Almirante Bay was more influenced by the intrusion of clear and nutrient poor oceanic waters, fresh water runoff was the overriding source for hydrological changes in the

Chiriquí Lagoon typically causing elevated nutrient concentrations. The highest plankton concentrations also coincided with runoff affected areas.

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