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Variability in upwelling along the Pacific shelf of Panama and implications for the distribution of nutrients and chlorophyll

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Abstract

Seasonal dynamics of dissolved inorganic nutrients (NO_3^-, PO_4^{3-}, and $Si(OH)_4$) and chlorophyll *a* were investigated in the Pacific shelf of Panama. The shelf is divided into two large semi-open areas, namely the non-upwelling Gulf of Chiriquí and the upwelling Gulf of Panama. Four research cruises sampled the water column in cross-shelf transects during wet and dry seasons at each region. Hydrological measures varied spatially between regions and also varied temporally on a seasonal basis. Low concentrations of NO_3^- (<0.50 μM), PO_4^{3-} (<0.27 μM), and chlorophyll *a* (<0.34 mg m^{-3}) were typical near the surface in the Gulf of Chiriquí during both rainy and dry seasons, but in the Gulf of Panama nutrients and chlorophyll were low only during the rainy season. In contrast, during the dry season upwelling in the Gulf of Panama, high concentrations of NO_3^- (15 μM) and PO_4^{3-} (1.2 μM) in the upper layer caused surface chlorophyll *a* to peak (1.5 mg m^{-3}). Median $Si(OH)_4$ concentrations in the upper layer ranged from about 4 μM in both regions during the rainy season to nearly 12 μM in the Gulf of Panama during the dry season upwelling. Both the N:P and N:Si molar ratios suggest that phytoplankton is N-limited except in the Gulf of Panama during upwelling. In both regions, a subsurface chlorophyll maximum (>0.5 mg m^{-3}) typically developed close to the usually shallow thermocline during non-upwelling conditions. We found no evidence of significant nutrient input from freshwater runoff. The position of the thermocline is considered to be the main source of nutrients to the euphotic zone in both regions.

Keywords: wind stress; thermocline; nutrients; chlorophyll; Pacific Central America

1. Introduction

The hydrology in the Pacific coast of Central America is highly dynamic and variable in time and space. The region represents the eastern terminus of the warm North Equatorial Counter Current. In response to the high net heat flux and reduced wind mixing, the eastern Pacific warm pool with sea surface temperature (SST) above 27 °C develops in this region (Wang and Enfield, 2001). However, this warm coastal ocean continuum is interrupted when higher pressure systems in the Caribbean and in the Gulf of Mexico promote strong, narrow wind-jets that cross the isthmus through topographic depressions in the Central American cordillera during the boreal winter (Xie et al., 2005). The sea level declines in response to wind forcing and temporary wind-driven coastal upwelling systems develop in the gulfs of Tehuantepec (Mexico), Papagayo (Costa Rica), and Panama (Legeckis, 1988; McCreary et al., 1989). The thermocline shoals during upwelling cooling the sea surface, promoting nutrient enrichment of the euphotic zone, and driving extensive phytoplankton growth. As trans-isthmian winds weaken in the summer, the thermocline deepens and sea-surface waters revert to a warm condition that is nutrient poor and low in chlorophyll. An oceanic wind-driven upwelling system, the Costa Rica Thermal Dome, is also developed west of the Gulf of Papagayo (Kessler, 2006). The large patch of

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chlorophyll roughly superimposed onto the Central American upwelling centers give evidence of high biological production which likely supports productive local fisheries (Fiedler, 2002). The Tropical Surface Water (TSW), a water mass typically present in the tropical eastern Pacific, acquires its lowest salinity near the coast of Colombia due to direct intense rainfall and river discharge from the Andean basin. Part of this water is moved northward by the Panama Bight Gyre reaching Panama (Wyrtki, 1967; Fiedler and Talley, 2006).

The understanding of physical and biological processes in the eastern tropical Pacific Ocean has been enhanced in the past two decades (reviewed by Lavín et al., 2006), especially as satellite image technology and a large compilation of oceanographic data has become available from the World Ocean Database 2001 (Conkright et al., 2002). However, the dynamics of hydrological processes in Central American coastal waters remain understudied.

The Panamanian Pacific Shelf is an example of the biological and hydrological heterogeneity typical of Central America (Fig. 1). This coastal shelf is naturally divided by the Azuero Peninsula into two large areas, the Gulf of Panama (shelf area 27,175 km^2) and the Gulf of Chiriquí (shelf area 13,119 km^2). Evidence suggests that these two regions experience considerably different hydrological regimes. While the Gulf of Panama is known to experience wind-driven upwelling during the boreal winter, corresponding to the Panama's dry season, no evidence exists for a similar process occurring in the Gulf of Chiriquí (Dana, 1975; Kwiecinski and Chial, 1983; Brenes et al., 1995). Satellite images demonstrate that both wind speeds and chlorophyll content of surface waters are lower in the Gulf of Chiriquí than the Gulf of Panama during the dry seasons and do not give evidence of upwelling in this region (Pennington et al., 2006).

Previous studies have emphasized the seasonal dynamics of nutrients and plankton in relation to upwelling in the Gulf of Panama (Smayda, 1966; Kwiecinski et al., 1975; D'Croz and Robertson, 1997). In addition, couplings between nutrients, plankton, and the abundance of pelagic fishes have been reported in this region (Forsbergh, 1969), although comparable biological data is lacking for the Gulf of Chiriquí. The only comparable data between both regions focuses on shallow benthic communities, primarily coral reefs, whose distribution possibly reflects the contrasts of shallow hydrology between upwelling and non-upwelling environments (Glynn and Maté, 1997). Coral reefs are relatively prolific in the Gulf of Chiriquí where temperature records give evidence of warm and relatively stable SSTs, whereas coral growth is highly limited in the Gulf of Panama during upwelling events, possibly by low temperatures and high nutrients (Glynn, 1977; D'Croz and Maté, 2004; Schloeder and D'Croz, 2004).

Here we make a comparable study of the hydrological regimes of shelf waters in both the Gulf of Panama and the Gulf of Chiriquí. We sampled two cross-shelf profiles, from deep to surface waters, during times of upwelling and times of non-upwelling, roughly simultaneously in both regions. The results described herein aim to provide knowledge on the dynamic nature of upwelling events and its influence on the distribution of chlorophyll *a*. We establish if strong coastal upwelling such as is known in the Gulf of Panama also occur in the Gulf of Chiriquí. The data should let us to test what is the source of nutrient and chlorophyll variability in shelf waters in these two regions.

2. Materials and methods

2.1. Field sampling procedures

Comparable north–south, cross-shelf transects were designed in the Gulf of Chiriquí and the Gulf of Panama

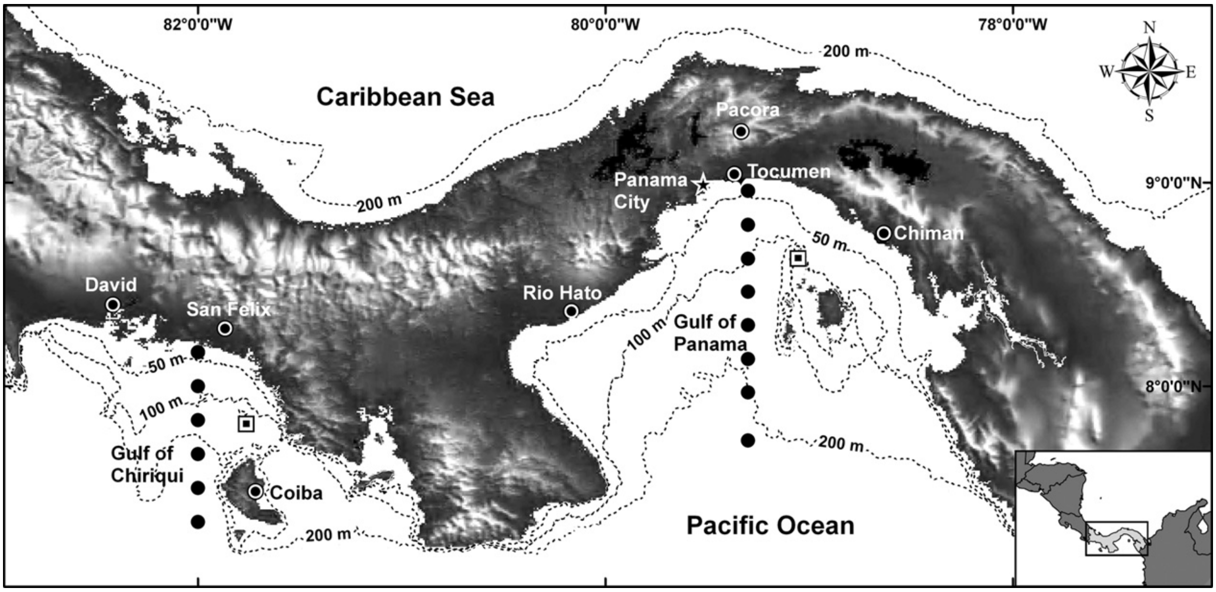

Fig. 1. Map of the Republic of Panama, showing transects in the Gulf of Chiriquí and in the Gulf of Panama. Black circles represent the sampling sites; square symbols indicate the location of the temperature data loggers. Each bulls-eye indicates the location of the meteorological stations.

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(Fig. 1). Six sampling stations were arranged in the Gulf of Chiriquí and eight in the Gulf of Panama (Fig. 1). Four sampling surveys were conducted along each transect. Samplings were scheduled to correspond with different times of the year, representing contrasting hydrological conditions between the rainy season (non-upwelling) and the dry season (upwelling). Sampling I (S-I) was from August 16 to 22, 1999 (mid-rainy season); sampling II (S-II) was from February 22 to March 1, 2000 (mid dry season); sampling III (S-III) was from January 15 to 21, 2001(early dry season); and sampling IV (S-IV) was from December 14 to 20, 2004 (late rainy season).

The water column was sampled during daylight hours using 2.5 l Niskin bottle casts at each station. Three replicate water samples were collected at discrete depths from surface down to a maximum depth of 200 m. Two liters of each individual replicate sample were immediately sieved through Nitex mesh 350 μm to exclude zooplankton and were vacuum filtered on Whatman GF/F (0.7 μm pore size) for Chl *a* analysis. Chlorophyll filters were wrapped with aluminum foil and stored frozen (−20 °C) for further analysis. For the assay of NO_3^-, NO_2^-, PO_4^{3-}, and $Si(OH)_4$ 40 ml from each filtrate was collected in acid washed 50 ml screw-cap polypropylene test tubes and kept frozen at −20 °C until laboratory analysis. Temperature and salinity were measured with the Ocean Seven 316 multi-parameter probe (Idronaut Srl, Milano, Italy) except during S-IV when reversing thermometers were attached to the Niskin samplers and salinity was measured in the freshly collected water samples with the YSI 85 instrument (Yellow Spring Instruments Inc., Ohio, USA). Salinity is expressed in the Practical Salinity Scale indicated by UNESCO (1981). The depth of the euphotic zone (1% incident radiation) was estimated from Secchi disk readings (Parsons et al., 1984). The light attenuation coefficient was calculated as $K_d = f/z_s$ where z_s is the Secchi depth and $f = 1.4$. In situ water temperature records from both regions were gathered by data loggers (HOBO, Onset Computer, USA). Individual temperature data loggers were positioned at 3 m depth in coral reefs at Uva Island (Gulf of Chiriquí) and Saboga Island (Gulf of Panama), from January 3, 1999 to December 16, 2004. Loggers were set to record temperature at 15–30 min intervals.

2.2. Analysis of water samples

A Teflon pestle was used to grind the filters in 5 ml of a 90% aqueous acetone solution. The slurry transferred to 15 ml polypropylene screw-cap centrifuge tubes, the acetone volume filled to 10 ml, and kept in the dark at −20 °C for 24 h. Extracts were centrifuged at 3000 rpm and the supernatant analyzed for Chl *a* following the non-acidification fluorometric method (Welschmeyer, 1994). Water samples were analyzed for NO_3^-, NO_2^-, PO_4^{3-}, and $Si(OH)_4$ by colorimetric methods (Grasshoff et al., 1983) using an Alpkem automated analyzer. Minimum detection limits for nutrients were: 0.02 μM for NO_3^-, 0.01 μM for NO_2^-, 0.02 μM for PO_4^{3-}, and 0.12 μM for $Si(OH)_4$.

2.3. Climate data

To observe the effect of climate upon hydrological variables we collated data on rainfall, freshwater discharge and wind speeds for both gulfs during times of sampling from various sources. Daily rainfall data was obtained from three meteorological stations in the Gulf of Chiriquí and four stations in the Gulf of Panama (Fig. 1). Data on the monthly mean freshwater discharge into each gulf data was also acquired (Empresa de Transmisión Eléctrica (ETESA)). Daily wind data was obtained from the microwave Quick Scatterometer (QuikScat) (Physical Oceanography Distributed Active Archive Center (PO.DAAC); http://podaac.jpl.nasa.gov/poet).

2.4. Data analysis

Principal components analysis (PCA) was used to ordinate the sample data based on hydrological characteristics (temperature and salinity), nutrient characteristics (NO_3^-, NO_2^-, PO_4^{3-}, $Si(OH)_4$, N:P, and N:Si), and Chl *a* concentration. Average values of wind stress and rainfall at time of sampling, the region, season as non-upwelling (S-I and S-IV) or upwelling (S-II and S-III), geographic variables including region (Gulf of Chiriquí/Gulf of Panama), depth, and distance from shore were applied *a priori* to the ordination to see which factor best explained the variation observed (Lepš and Šmilauer, 2003). Statistical relationships among the variables were tested with Pearson correlations (*r*). Significance differences between the median of variables in the upper layer (top 20 m) were estimated with the Mann–Whitney test (MW) using Systat 9.

3. Results

3.1. Climate

Rainfall patterns across Panama are highly seasonal (Fig. 2a) as they are governed by the position of the Inter-Tropical Convergence Zone (ITCZ). During the course of this study, most rain fell between May and December, when the ITCZ is normally located over or slightly to the north of Panama and winds are light (Amador et al., 2006). The Gulf of Chiriquí was exposed to larger freshwater influence than the Gulf of Panama as rainfall and river discharge was higher (Fig. 2). Average annual rainfall during this study was 3415.12 mm in the Gulf of Chiriquí region and 2158.33 mm in the Gulf of Panama region. September and October were the rainiest months in both regions. The dry season developed between January and March when the ITCZ moves south of Panama, a period characterized by predominating intense northeast trade winds. River discharge into both gulfs typically followed the seasonal trend described for rainfall, but declined on the whole during our study. We currently are unable to explain this pattern, as rainfall does not parallel this tendency (Fig. 2b).

Wind stress on open surface waters was also highly seasonal in both gulfs (Fig. 2c). The Gulf of Panama is subject to intense seasonal northerly winds as the trans-isthmian

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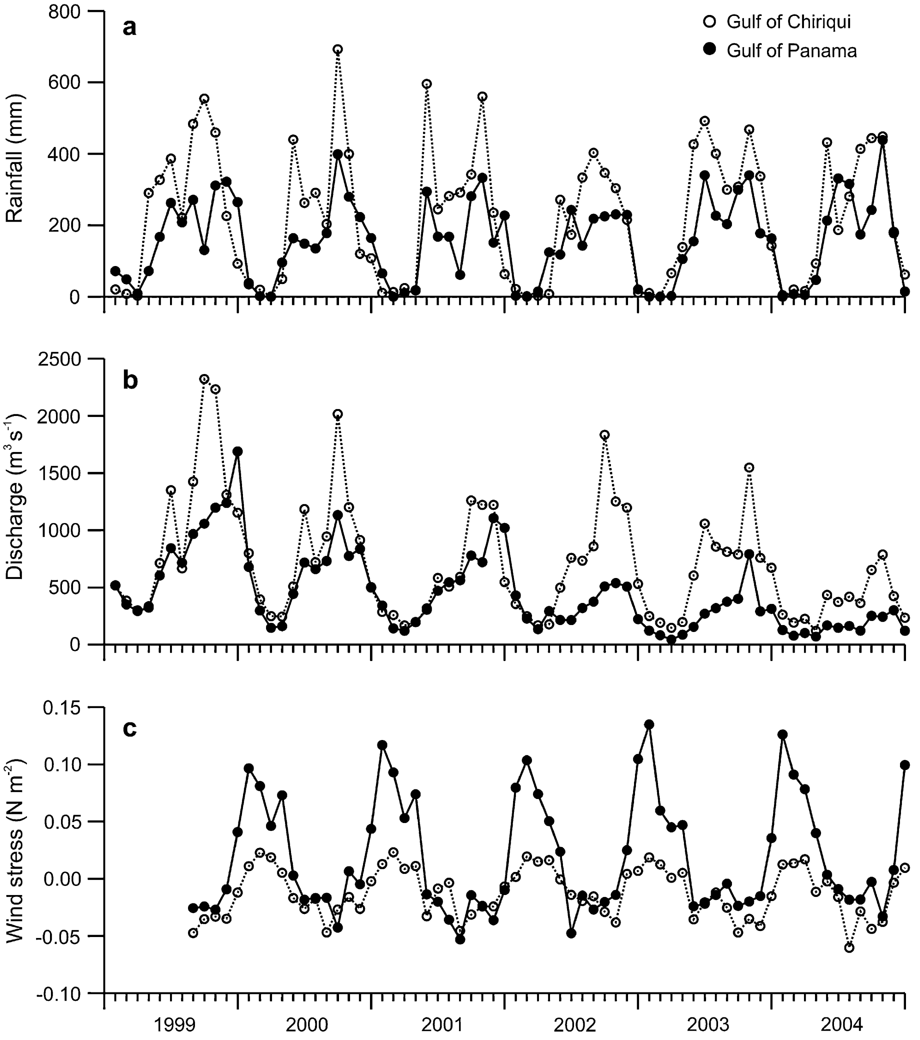

Fig. 2. Monthly means of: (a) rainfall (mm) and (b) freshwater discharge (m^{-3} s^{-1}) from January 1999 to December 2004; (c) wind stress (N m^{-2}) from July 1999 to December 2004. Northerly winds are positive and southerly winds are negative.

wind jet is well developed during the boreal winter (Xie et al., 2005). Although the same trend was observed in the Gulf of Chiriquí the strength of northerly winds never reached values seen in the Gulf of Panama, probably because of the high mountains in the west of the country. Wind stress in both regions was either southerly or mixed during S-I and S-IV. During S-II and S-III, wind stress was predominantly northerly with values in the Gulf of Panama generally being three times as strong as in the Gulf of Chiriquí.

Although our sampling surveys were discrete and climatic variations were rapid, our study encompassed the full range of climatic variability that is typically experienced in this region. S-I was carried out in conditions typical of the rainy season when both regions were under the influence from heavy rains, runoff, and low northerly wind stress. S-II took place when freshwater influence was minimal and northerly wind stress was particularly high in the Gulf of Panama, typical of the dry season. S-III and S-IV demonstrated transitional climate conditions between the wet and dry seasons, but S-III was more like a dry season climate, while S-IV was more like a rainy season climate.

3.2. Hydrology

The Gulf of Chiriquí and the Gulf of Panama exhibit the archetypal tropical coastal ocean thermal profile with warm surface waters sitting on the top of cool deep waters. We define the depth of the thermocline in the eastern tropical Pacific Ocean by the position of the 20 °C isotherm (Wyrtki, 1964; Dana, 1975; Fiedler et al., 1991; Xie et al., 2005). During S-I and S-IV, the thermal structure was similar between the two gulfs (Table 1). SSTs were warm (27–28 °C) and a well-defined thermocline was present between 50 and 75 m (Fig. 3). The thermocline rose sharply to the upper layer (top 20 m) in the Gulf of Panama during the dry season samplings. This resulted in a significant cooling of surface waters, particularly during S-II when the thermocline almost broke in the surface. During the dry season, a significant relationship was observed between SST and the northerly wind-stress index in the Gulf of Panama ($r = -0.81$, $p < 0.001$) but not in the Gulf of Chiriquí ($r = -0.125$, $p > 0.05$). A limited shoaling of the thermocline, to nearly 30 m, was also recorded in the Gulf of Chiriquí that compressed warm SSTs into shallow

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Table 1
Median of hydrological variables in the upper layer (20 m) of the Gulf of Chiriquí (GC) and Gulf of Panama (GP). MW, Mann–Whitney *U*-test statistic value; $^{*}p < 0.05$, $^{**}p < 0.01$, $^{***}p < 0.001$, ns, not significant. S-1, mid-rainy season (August 16–22, 1999); S-2, mid-dry season (February 22 to March 1, 2000); S-III, early dry season (January 15–21, 2001); S-IV, late rainy season (December 14–20, 2004)

Hydrological variables	S-I			S-II			S-III			S-IV		
	GC	GP	MW	GC	GP	MW	GC	GP	MW	GC	GP	MW
Temperature (°C)	27.5	27.7	133.0 (ns)	28.0	18.0	238.0***	28.3	23.9	390.5***	28.8	27.7	178.0**
Salinity (psu)	30.6	29.2	311.0**	32.0	33.6	6.5***	32.5	33.3	72.5**	30.5	30.2	109.0 (ns)
NO_3^- (μM)	0.34	0.27	273.5*	0.75	14.45	14.0***	0.45	4.59	39.5***	0.37	0.44	92.0 (ns)
PO_4^{3-} (μM)	0.16	0.14	253.5 (ns)	0.16	1.20	10.0***	0.18	0.46	40.0***	0.24	0.27	99.0 (ns)
$Si(OH)_4$ (μM)	3.67	3.44	194.5 (ns)	5.64	11.63	40.0**	4.17	6.22	130.0 (ns)	4.73	3.78	156.0*
N:P molar ratio	2.25	1.98	230.5 (ns)	7.53	12.46	54.0*	2.40	9.01	67.0**	1.46	1.68	88.0 (ns)
N:Si molar ratio	0.10	0.08	240.0 (ns)	0.14	1.28	10.0***	0.11	0.74	16.0***	0.08	0.11	73.0 (ns)
Chl *a* (mg m^{-3})	0.34	0.27	278.5*	0.29	1.44	23.0***	0.16	0.83	24.0***	0.17	0.24	73.5 (ns)
Euphotic zone (m)	37.1	40.4	12.0 (ns)	54.9	13.8	12.0**	57.5	16.4	20.0**	62.4	36.8	3.5 (ns)

waters during S-II (Fig. 3). This process, however, was not as intense as in the Gulf of Panama and did not result in the notable cooling of SST observed there (Table 1). SST records measured by the temperature data loggers supported these observations by recording warm and relatively stable SST in the Gulf of Chiriquí and seasonal plunges in SST in the Gulf of Panama (Fig. 4). Brief SST cooling events of up to 5 °C were observed in the Gulf of Chiriquí in March 2002.

During S-I and S-IV, both gulfs displayed similar distribution of salinities in the upper layer with values of 30 or less that rose sharply to high salinities (>33) in deeper waters. These results are indicative of a well-stratified water column due to freshwater dilution from rainfall and runoff (Fig. 5). These observations were more pronounced in the Gulf of Panama in S-I where surface salinities dropped below 29 and freshwater discharge was recorded at markedly lower salinities in coastal waters. By the end of the rainy season, the salinity in the upper layer became very similar in both gulfs (Table 1). During S-II and S-III, decreased rainfall led to a rise of salinity in the upper layers of both gulfs. Surface salinity reached 32 in the Gulf of Chiriquí. But the effect was more striking in the Gulf of Panama where deep, high salinity water rose to upper levels, subsequently driving surface salinity above 33.

3.3. Dissolved inorganic nutrients

Both gulfs exhibited low concentrations of nutrients in the upper layers and followed the classic profile of increasing nutrients with increased depth. During S-I and S-IV, values of NO_3^- below 0.5 μM and PO_4^{3-} below 0.3 μM were common in surface waters (Fig. 6). However, surface nutrient concentrations greatly increased in the Gulf of Panama during S-II and S-III when the 15 NO_3^- μM isoline, likely representing the nutricline, moved upward (Fig. 6). Surface waters did not show similar enrichment in the Gulf of Chiriquí, as deep NO_3^- rich waters only reached the 30 m level. Patterns of PO_4^{3-} resembled those of NO_3^- but at lower concentrations (Fig. 7). The concentration of PO_4^{3-} in the upper layer remained low (<0.3 μM) during all sampling cruises in the Gulf of Chiriquí and also in the Gulf of Panama during the S-I and S-IV cruises and during those samplings, was very similar between these regions (Table 1). However, this condition changed in the Gulf of Panama during S-II when the 1.5 μM PO_4^{3-} isoline, which usually sits below 40 m, moved upward and surface PO_4^{3-} increased to nearly 1 μM. On the contrary, PO_4^{3-} rich waters remained at deeper levels in the Gulf of Chiriquí during all samplings and surface waters were not phosphorus enriched. We found that the concentration of NO_3^- in the upper layer was significantly correlated to that of PO_4^{3-} in both regions (Gulf of Chiriquí $r = 0.77$, $p < 0.001$; Gulf of Panama $r = 0.98$, $p < 0.001$). Upper layer concentrations of NO_3^- and PO_4^{3-} were negatively correlated to cold waters in the Gulf of Panama ($r = -0.91$, $p < 0.001$ and $r = -0.87$, $p < 0.001$ respectively) and in the Gulf of Chiriquí ($r = -0.63$, $p < 0.001$ and $r = -0.61$, $p < 0.001$ respectively).

The distribution of $Si(OH)_4$ followed the same pattern as that of NO_3^- and PO_4^{3-} (profiles are not shown). Median $Si(OH)_4$ concentration in the upper layer was approximately 4 μM in the Gulf of Chiriquí during all sampling cruises and in the Gulf of Panama during S-I and S-IV (Table 1). The concentration of $Si(OH)_{4,}$ however, was more than doubled in the upper layer in the Gulf of Panama during S-II. $Si(OH)_4$ concentrations were correlated to cold waters in the Gulf of Panama ($r = -0.78$, $p < 0.001$) but no such correlation was found in the Gulf of Chiriquí.

In general, the NO_3^- to PO_4^{3-} ratios (N:P ratios) in both regions were smaller than the Redfield ratio of 16:1 (Table 1), suggesting that phytoplankton growth is nitrogen-limited (Redfield, 1958). The average N:P profiles showed increasing values with depth and stabilization of the ratio at approximately 50 m. N:P ratios were similarly low (<5:1) in the upper layer of both regions during S-I and S-IV (Fig. 8), but an increase in this N:P ratio was observed in both regions in S-II and S-III. The highest N:P ratios occurred in the Gulf of Panama during S-II, approaching the Redfield value at approximately 40 m. In both regions, the NO_3^- to $Si(OH)_4$ ratios (N:Si ratios) were similar and remarkably low during S-I and S-II (Table 1). N:Si ratios in the upper layer were approximately a tenth of the proposed Redfield ratio (1:1), again suggesting nitrogen limitation for phytoplankton growth (Fig. 8). In the Gulf of Chiriquí, the N:Si ratio increased with depth and became closer to the Redfield value below 30 m. In the Gulf of Panama, N:Si values in surface waters nearly reached the Redfield ratio and gradually increased with depth during S-II.

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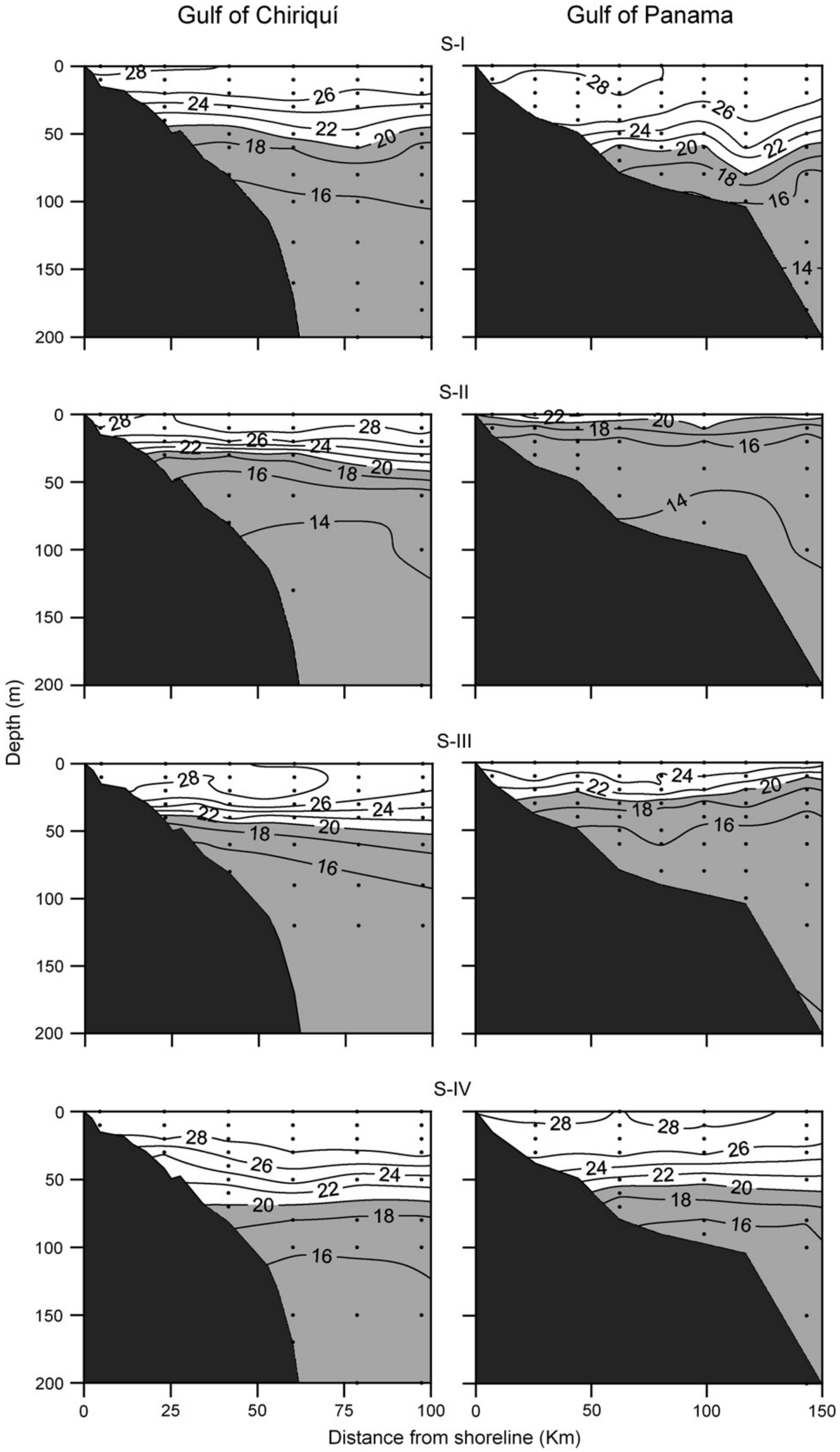

Fig. 3. Depth distribution of isotherms (°C). Contours below the thermocline (20 °C) are shaded gray. Black dots indicate the sampled depths. The shelf profile is shaded black. S-1, mid-rainy season (August 16–22, 1999); S-2, mid-dry season (February 22 to March 1, 2000); S-III, early dry season (January 15–21, 2001); S-IV, late rainy season (December 14–20, 2004).

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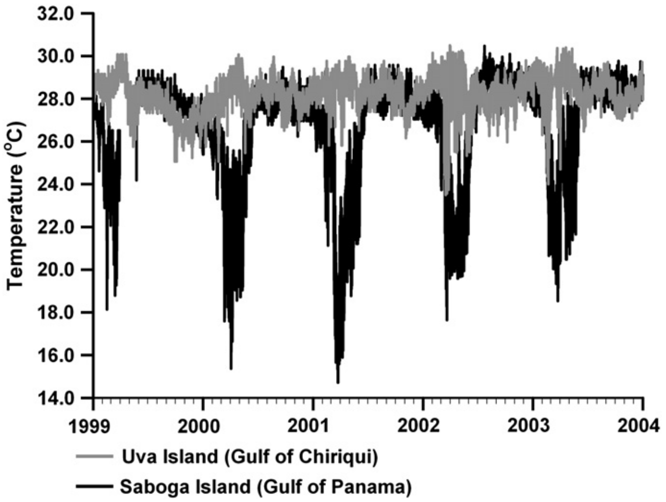

Fig. 4. (a) SST records (°C) from temperature data loggers placed at Uva Island, Gulf of Chiriquí (gray line) and at Saboga Island, Gulf of Panama (black line) from January 1999 to December 2004.

3.4. Chlorophyll *a*

Our findings identify a subsurface chlorophyll maximum (>0.5 mg m^{-3}) during all samplings in the Gulf of Chiriquí and in the Gulf of Panama during the rainy season (Fig. 9). The center of the chlorophyll maximum was typically located between 30 and 50 m, corresponding with waters immediately above the thermocline. The depth of the euphotic zone (average 53 m) in the Gulf of Chiriquí was relatively stable and deeper than in the Gulf of Panama. The depth of the euphotic zone in the Gulf of Panama was highly seasonal and varied from approximately 15 m during the dry season to nearly 40 m during the rainy season (Table 1). The distribution of Chl *a*, however, indicates that the euphotic zone may be deeper than estimates obtained from Secchi disk readings. The overall pattern of Chl *a* distribution changed drastically in the Gulf of Panama when the chlorophyll maximum developed in near-surface waters during dry season upwelling. At that time, the concentration of Chl *a* in the upper layer increased to nearly 1.5 mg m^{-3} during this event and the depth of the euphotic zone was subsequently limited to less than 20 m. In contrast, surface Chl *a* levels in the Gulf of Chiriquí were maintained at low values at all times and the chlorophyll maximum developed at subsurface levels. Enhanced concentration of chlorophyll was observed in nearshore waters in both gulfs during S-I, possibly in response to high freshwater discharge at this time (Fig. 9).

3.5. Ordination of hydrological data

The results of our study reported above are strengthened by the results of PCA. The Gulf of Chiriquí and Gulf of Panama revealed a remarkably similar range of sample scores (Fig. 10a). PCA axis 1 (which accounted for 84.9% of the variation) was driven mostly by temperature and NO_3^- concentration, while PCA axis 2 (which accounted for 4.5% of the variation) was driven mostly by $Si(OH)_4$ concentrations and the N:P molar ratio. Thus, the majority of the variation was explained by samples characterized by warm temperatures and low NO_3^- concentrations on the left to low temperatures and high NO_3^- concentrations on the right (Fig. 10b) which correlates well with shallow and deep waters respectively. Unsurprisingly therefore, the major controlling factor on the PCA axis 1 was depth (Fig. 10c), while a strong effect of distance from shore is probably heavily biased by the increased number of deep water samples that occur in profiles further away from shore. Season was found to be the third most explanatory variable with S-II and S-III being positive while S-I and S-IV being negative. Surprisingly, region was found to explain very little of the variation (Fig. 10c).

Clear patterns emerge when the sample scores of PCA (Fig. 11) are separated into the two gulfs (left and right), depths (top to bottom) and by sampling surveys (labels). Shallow samples tend to be isolated to the left while deep samples to the right, driven by lower temperature and increased NO_3^-. Across the surveys, samples in the Gulf of Chiriquí at 0–20 m do not change while in the Gulf of Panama there is a strong distinction between samples from S-I and S-IV which are similar to shallow water samples in the Gulf of Chiriquí, and S-II and S-III which move towards being more similar to deeper waters.

In mid-level waters from 20 to 50 m, samples in the Gulf of Panama show the same trend. During S-I and S-IV samples are similar to shallow-water samples while during S-II and S-III samples move considerably towards the right. Unlike upper-level waters however, a similar pattern also occurs in the Gulf of Chiriquí, but less pronounced, suggesting that the processes accounting for the divergence in the Gulf of Panama occurs at mid levels in the Gulf of Chiriquí but not in upper-level waters. Deep waters also show a similar distinction, particularly so in the Gulf of Chiriquí.

4. Discussion

4.1. Hydrological patterns

Results from this study showed that surface waters that are warm and low in salinity are typical in the Gulf of Chiriquí throughout the year but only during the rainy season in the Gulf of Panama. Properties of surface waters were similar to those of the TSW typical of the surface layer in the tropical eastern Pacific Ocean; the water column is highly stratified, the shallow thermocline is strong and coincident with the halocline (Fiedler and Talley, 2006). Both regions demonstrated strong influence from rainfall and runoff that affected the salinity, column stratification, clarity, and nutrient dynamics of the ocean water. Surface salinity followed climatic patterns, exhibiting higher levels during the dry season and lower levels during the rainy season. Surface salinity, however, was slightly more diluted in the Gulf of Panama than in the Gulf of Chiriquí, although the latter was exposed to more rainfall and river discharge. Probable reasons for this discrepancy may have been regional and local. The TSW reaches its lowest salinity

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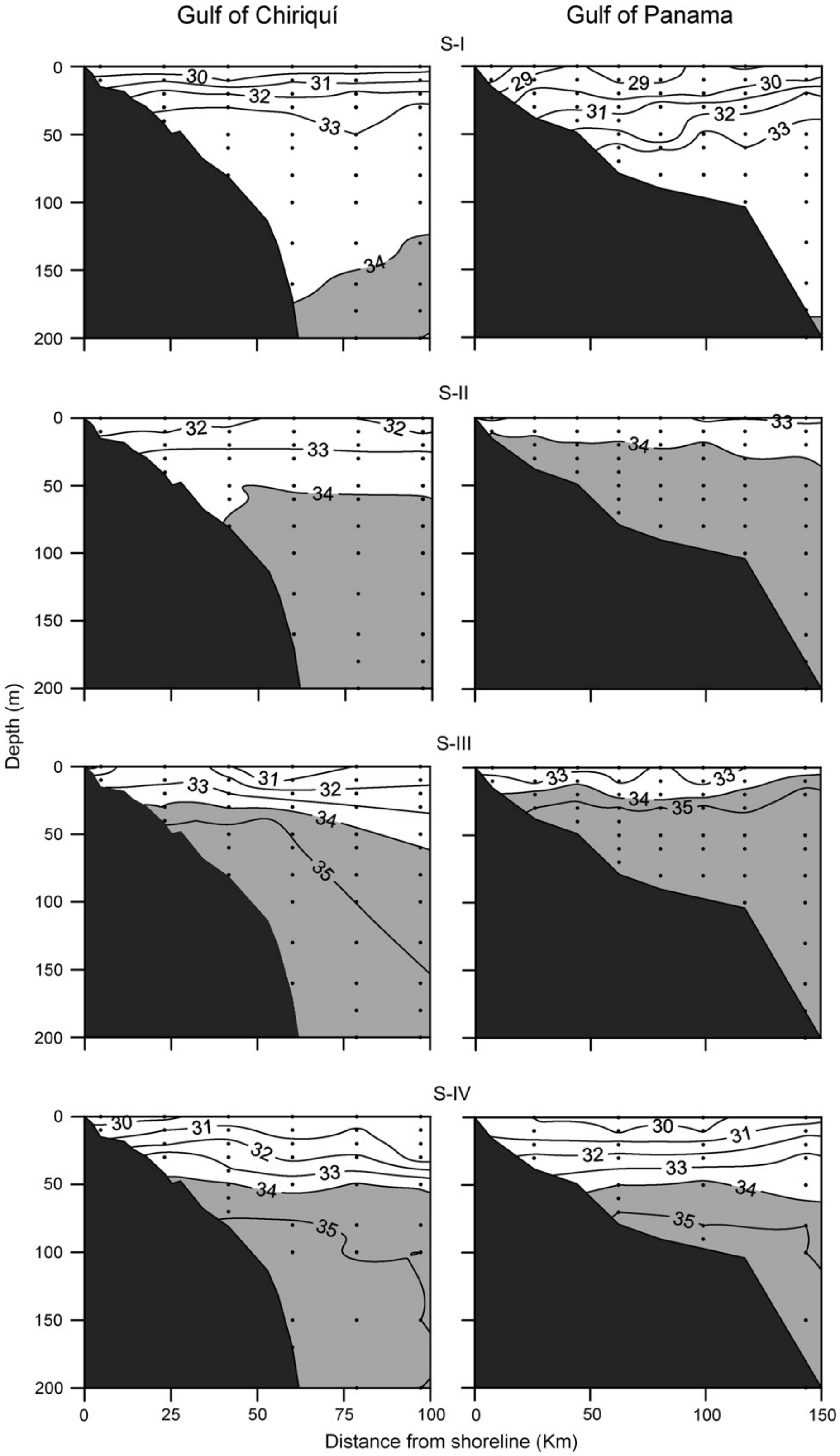

Fig. 5. Depth distribution of salinity. Contours below the 34 isohaline are shaded gray. Black dots indicate the sampled depths. The shelf profile is shaded black. S-1, mid-rainy season (August 16–22, 1999); S-2, mid-dry season (February 22 to March 1, 2000); S-III, early dry season (January 15–21, 2001); S-IV, late rainy season (December 14–20, 2004).

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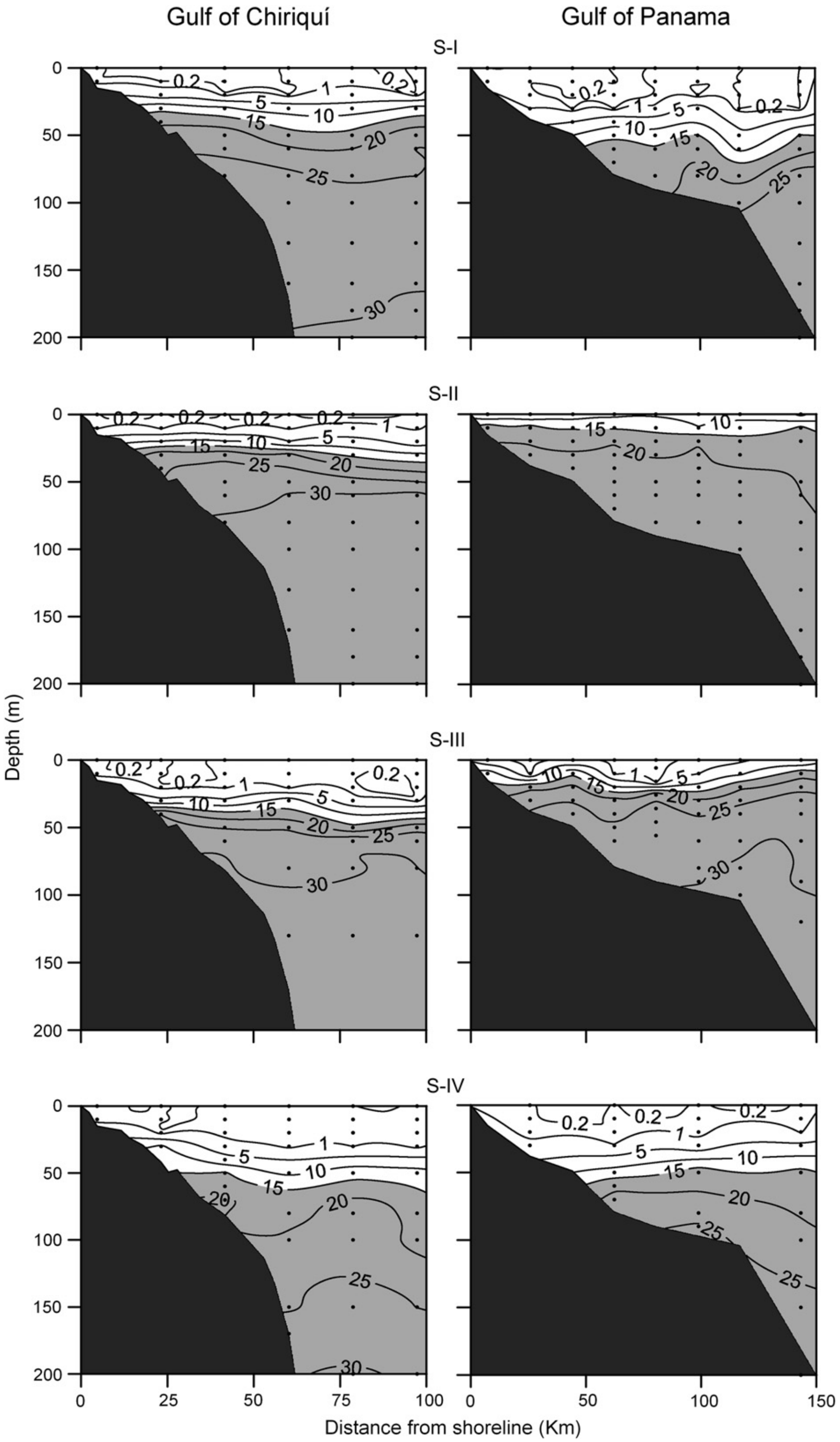

Fig. 6. Depth distribution of NO_3^- (μM). Contours below the 15 μM isoline are shaded gray. Black dots indicate the sampled depths. The shelf profile is shaded black. S-1, mid-rainy season (August 16–22, 1999); S-2, mid-dry season (February 22 to March 1, 2000); S-III, early dry season (January 15–21, 2001); S-IV, late rainy season (December 14–20, 2004).

off the Gulf of Panama as precipitation rates exceed evaporation rates beneath the ITCZ (Amador et al., 2006). Part of this water is moved to the Gulf of Panama by the northward flow of the Colombia Current and additional freshwater input is received from local rain and river discharge (Stevenson, 1970; Kessler, 2006). Also, the influence of runoff may be greater in the wider, more laterally-enclosed shelf of the Gulf of Panama than in the smaller, more open shelf of the

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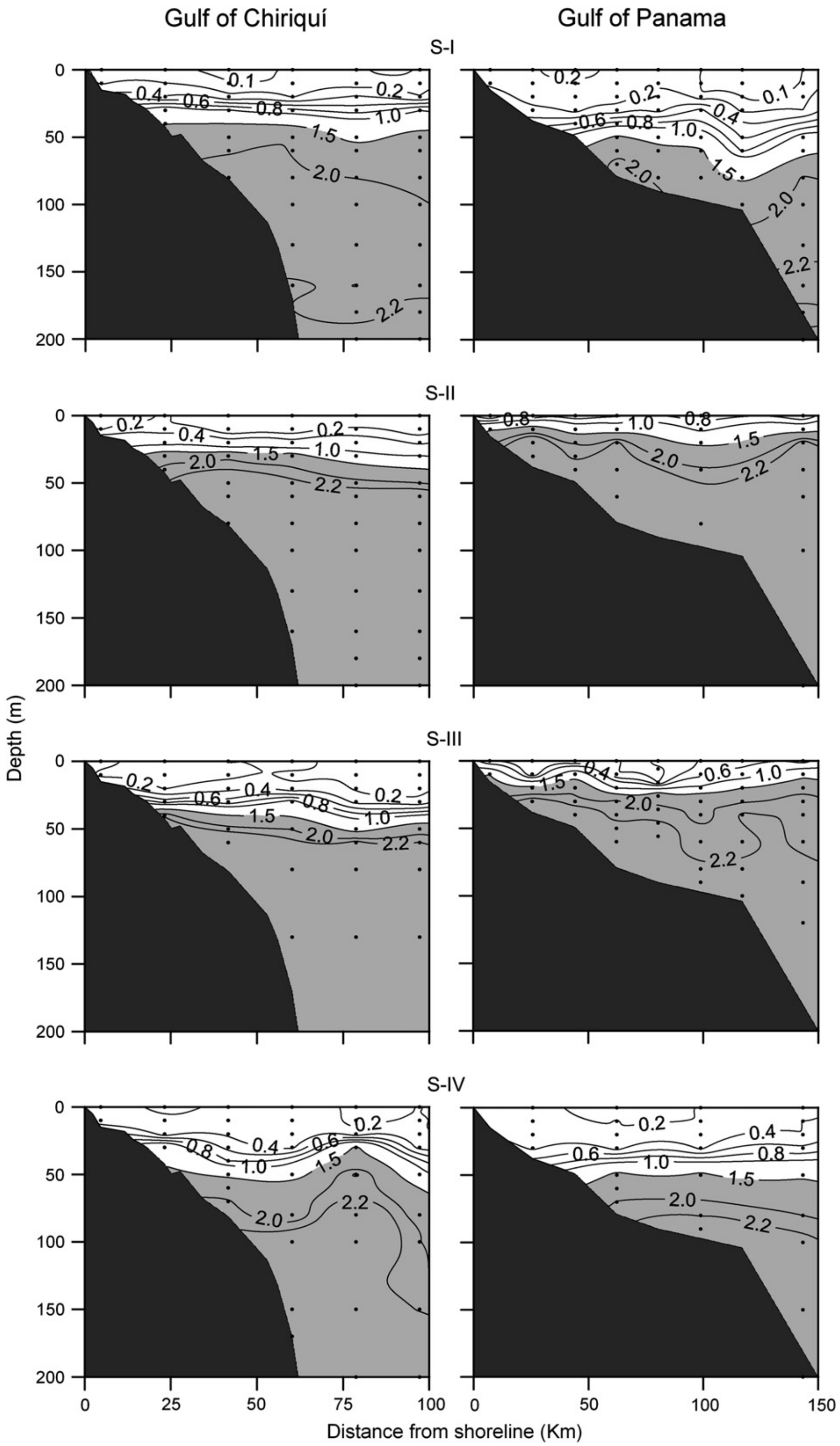

Fig. 7. Depth distribution of PO_4^{3-} (μM). Contours below the 1.5 μM isoline are shaded gray. Black dots indicate the sampled depths. The shelf profile is shaded black. S-1, mid-rainy season (August 16–22, 1999); S-2, mid-dry season (February 22 to March 1, 2000); S-III, early dry season (January 15–21, 2001); S-IV, late rainy season (December 14–20, 2004).

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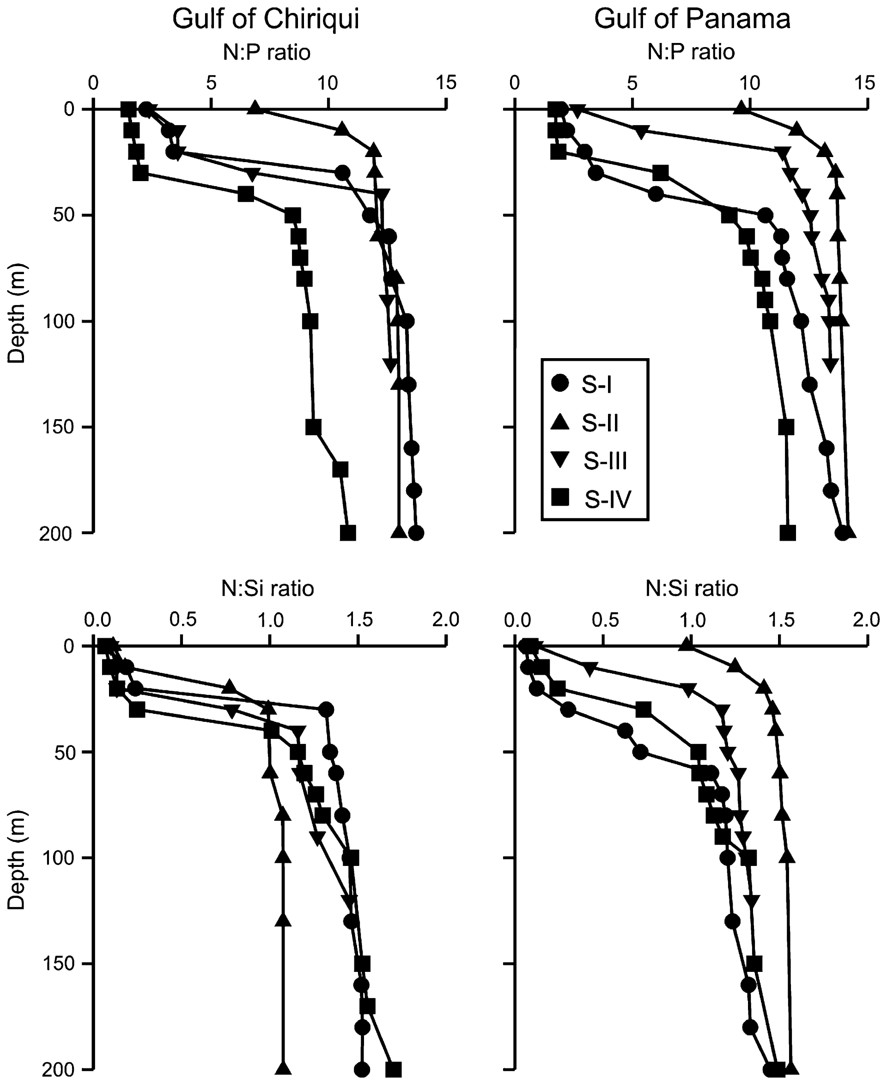

Fig. 8. Profiles of average N:P and N:Si molar ratios. S-1, mid-rainy season (August 16–22, 1999); S-2, mid-dry season (February 22 to March 1, 2000); S-III, early dry season (January 15–21, 2001); S-IV, late rainy season (December 14–20, 2004).

Gulf of Chiriquí where oceanic and shelf waters are more likely to exchange (D'Croz and Robertson, 1997). All of these factors likely contribute to the low surface salinities (<30) and the highly stratified water column in the Gulf of Panama during the rainy season.

During the dry season, surface waters in the two gulfs became dissimilar. Surface salinity increased because of reduced precipitation and SST remained warm in the Gulf of Chiriquí. In the Gulf of Panama, however, the trans-isthmian wind jet displaced the warm and nutrient poor surface waters offshore, inducing the upwelling of deep waters into coastal and surface layers in the Gulf of Panama, as previously described (Forsbergh, 1969; Kwiecinski et al., 1975; D'Croz et al., 1991). A significant relationship between wind-stress and sea-level provides the mechanism responsible for upwelling in the Gulf of Panama (Schaefer et al., 1958; Legeckis, 1988; Xie et al., 2005). Our results, in agreement with previous studies in the Panama Bight (Forsbergh, 1969; Rodriguez-Rubio and Stuardo, 2002), prove that wind stress is inversely related to SST in the Gulf of Panama during the dry season but not during the rainy season. Upwelling caused the thermocline to nearly break in the surface, leading to the cooling of SST and the increase of surface salinity in the Gulf of Panama (Fig. 3). Properties of surface water during periods of upwelling corresponded to those of water close (from approximately 60 m) to the thermocline during the rainy season. Upwelling, however, did not occur in the Gulf of Chiriqui because surface waters were not displaced offshore as the flow of northerly winds is partially blocked by the high cordillera running along western Panama. Wind stress in the Gulf of Chiriquí is less than a third of that in the Gulf of Panama during the dry season. A similar pattern was reported by Kwiecinski and Chial (1983). On the contrary, mountain ranges are low in central Panama and allow a strong wind jet toward the Gulf of Panama (see Fig. 1), thus accounting for the lack of correlation between wind stress and SST in the Gulf of Chiriquí.

Another factor that may contribute to differences in strength of surface water displacement between the two gulfs

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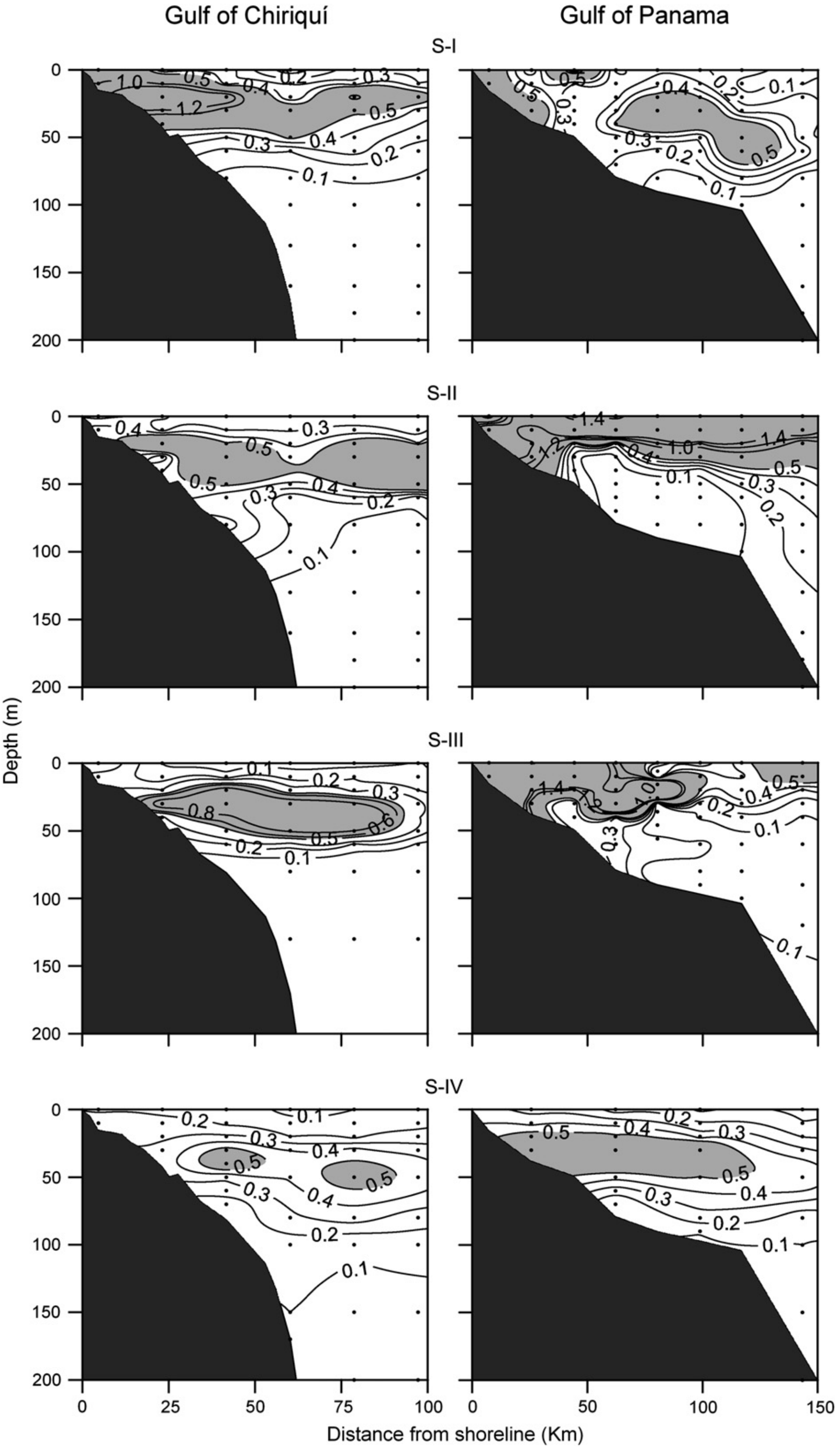

Fig. 9. Depth distribution of chlorophyll *a* (mg m^{-3}). The maximum chlorophyll *a* concentration zone is shaded gray. The shelf profile is shaded black. S-1, mid-rainy season (August 16–22, 1999); S-2, mid-dry season (February 22 to March 1, 2000); S-III, early dry season (January 15–21, 2001); S-IV, late rainy season (December 14–20, 2004).

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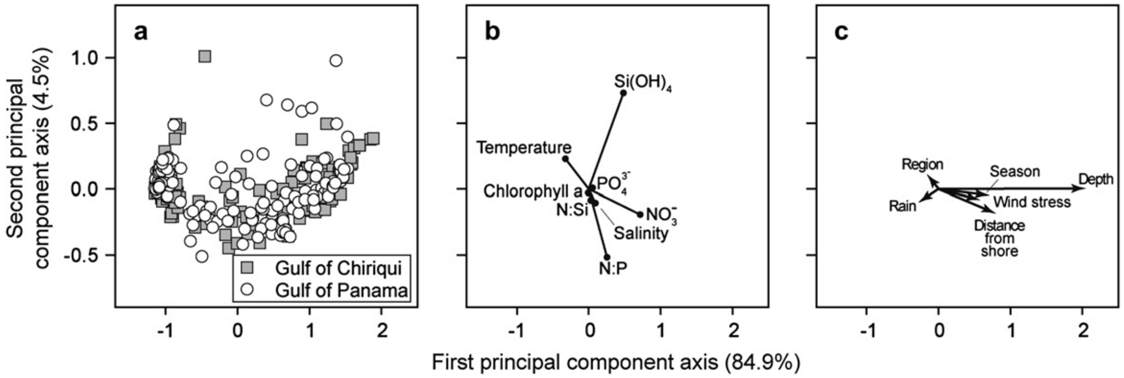

Fig. 10. Hydrological structure of the Gulfs of Chiriquí and Panama. (a) Ordination of all samples using PCA based upon water quality factors; (b) temperature, salinity, NO$_3^-$, PO$_4^{3-}$, Si(OH)$_4$, N:P, N:Si, chlorophyll *a*; (c) environmental and geographical variables that best explain the ordination.

is shelf geography. The Gulf of Panama is enclosed by land to the north, east, and west while the Gulf of Chiriquí is enclosed to the north and east but only semi-enclosed to the west (Fig. 1). Consequently, northerly winds are much more effective at displacing surface waters in the Gulf of Panama. According to the mean surface circulation from surface drifters in the eastern tropical Pacific (Kessler, 2006), we deduce that surface waters enter the Gulf of Chiriquí from the west, replacing any wind-displaced waters that move south. Daily records from the data loggers confirmed seasonal SST

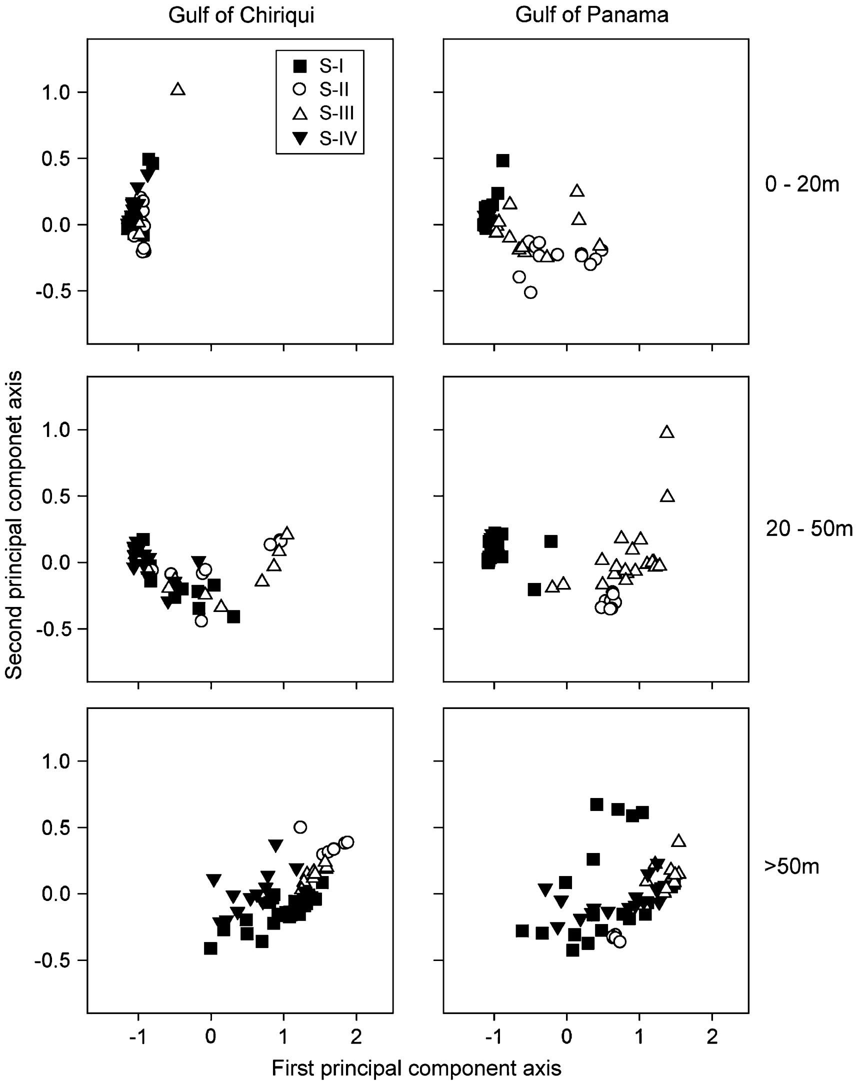

Fig. 11. Sample scores from ordination presented in Fig. 10 separated into Gulf of Chiriquí (left) and Gulf of Panama (right), surface waters (top), mid-level waters (middle) and deep waters (bottom), and within each plot by sampling surveys. See text for details.

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plunges in the Gulf of Panama but thermal stability in the Gulf of Chiriquí (Fig. 4). SST warmed in the Gulf of Panama after the relaxation of the trans-isthmian wind jet in April (Fig. 2). Upwelling was not observed in the Gulf of Chiriquí nor in the Gulf of Panama during the rainy season and surface waters remained invariably warm. Our hydrological profiles, in accordance with previous studies (Brenes et al., 1995), agree that the thermocline in the Gulf of Chiriquí sits at a much deeper level than the Gulf of Panama during the entire year. We did however see some evidence that the thermocline can shoal in the Gulf of Chiriquí, as occurred during S-II, although this may be have been a result of region-wide changes in thermocline depth throughout the tropical eastern Pacific, and not related to seasonal wind-forcing as seen in the Gulf of Panama. PCA suggests that the hydrological divergence between both regions is limited to upper levels of the water column (Fig. 11). Therefore, a small change in the oceanographic structure such as that produced by internal waves (Dana, 1975), or the intensification of wind mixing, could be the cause of these brief periods of advection of deeper cold temperatures to the surface layer, as recorded by data loggers (Fig. 3).

4.2. Nutrient dynamic

The near-surface concentration of nutrients was low in the Gulf of Chiriquí during the entire year and in the Gulf of Panama only during the rainy season. Nutrients clearly increased in the upper layer in the Gulf of Panama during dry season upwelling. We found that the upward movement of the thermocline was an unquestionable source of nutrients for near-surface waters. This condition was justified as the thermocline in the eastern Pacific is typically shallow, coinciding with a strong nutricline (Enfield, 2001; Fiedler and Talley, 2006). Only during upwelling did the N:P and N:Si ratios approach the Redfield values considered suitable for the growth of phytoplankton. These ratios remained below the Redfield values in the upper layer during non upwelling conditions in the Gulf of Panama and during the entire year in the Gulf of Chiriquí. Fiedler et al. (1991) suggested that open-ocean phytoplankton in the tropical eastern Pacific is nitrogen-limited when temperature is above 25 °C. The N:Si ratio in this study, though, indicates that NO_3^- became depleted when temperatures were warmer than 20 °C, corresponding with water above the thermocline.

The role of rainfall and runoff on nutrient dynamics was not entirely clear. We observed a strong decline of surface salinity during the rainy season when rainfall and river discharges were high. In addition, a large supply of $Si(OH)_4$ to shelf waters, presumably from runoff, was particularly evident in the Gulf of Panama as the average concentration in the top 100 m was approximately 10 μM during the rainy season (profile is not presented). Nevertheless, this value is about a third of that presented by Pennington et al. (2006) who suggests that the top 100 m in the Gulf of Panama exhibit the highest $Si(OH)_4$ concentration and lowest salinity in the entire eastern Pacific. All of these arguments are unequivocal indications of strong freshwater influence on shelf waters. The concentrations of NO_3^- and PO_4^{3-} in the upper layers in both transects, however, were correlated to cold and saline waters, thus not supporting the notion that freshwater was an important source of nutrients. Instead, nutrients may become depleted by freshwater dilution during periods of maximum rainfall (Fiedler et al., 1991). We found the N:P ratio in the top 50 m to be drastically reduced in both regions during the rainy season. This nutrient decline was particularly evident by the end of the year when both regions had been subjected to large inputs of freshwater during the rainy season. Although this condition could be partially explained as nutrient depletion by phytoplankton uptake in the euphotic zone, it may also reflect freshwater dilution. Nutrient contribution from runoff, though, is probably significant nearshore. We observed a drastic peak of Chl *a* in both regions at the beginning of the rainy season, when nutrients derived from land were presumably flushed into the coast. As it is mostly nutrient-limited, phytoplankton growth was promoted (Pennington et al., 2006). According to Kwiecinski (1986), freshwater inputs, mostly from river discharges, may supply 3.3% of the phosphorus and 2.3% of the nitrogen annually required by phytoplankton in the Gulf of Panama. Similarly, this author indicates that in the Gulf of Chiriquí, nutrient contribution from freshwater is even larger, comprising 5% of the nitrogen and almost 20% of the phosphorus demand from phytoplankton. However, Kwiecinski also suggests that the influence from river discharge is not evenly distributed in both gulfs, but mostly constrained to near-shore waters by the strong tidal current. This may explain why our results suggest that the overall contribution of river discharge along the cross-shelf transects was minimal.

4.3. Chlorophyll

The dynamics of the standing stock of chlorophyll reflect the different environmental regimes of the two gulfs. Concentrations of Chl *a* were significantly higher in the Gulf of Panama during the dry season when strong upwelling took place, while both gulfs exhibited similar Chl *a* patterns during the non-upwelling rainy season. The seasonal pattern of chlorophyll in the Gulf of Panama is in agreement with previous studies (Smayda, 1966; D'Croz et al., 1991; D'Croz and Robertson, 1997). Phytoplankton growth was generally nitrogen-limited, except in the Gulf of Panama during upwelling conditions when surface Chl *a* intensified and the depth of the euphotic zone was greatly reduced. The suppressed chlorophyll in the upper layer was probably related to the NO_3^- deficiency which persisted throughout the year in the Gulf of Chiriquí and in the Gulf of Panama during the rainy season. The latter is deduced from the significantly low N:P and N:Si ratios observed at these times. Phytoplankton uptake of NO_3^- comes close to the saturation concentration of 4 μM (MacIsaac and Dugdale, 1969). But NO_3^- concentration in the upper layer was consistently below 1 μM, except in the Gulf of Panama during upwelling when it rose above 10 μM. On the contrary, $Si(OH)_4$ concentration in the upper layer was relatively high (Table 1) during all cruises and

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surpassed the 2 μM considered as the half-saturation constant for diatom Si uptake (Del Amo and Brzezinski, 1999). Therefore, this data does not support that $Si(OH)_4$ was a limiting factor for phytoplankton growth.

The concentration of Chl *a*, however, peaks in subsurface levels which usually corresponded to water close to the thermocline. This pattern may be justified by two possible reasons: (a) the relatively deep euphotic zone in the Gulf of Chiriquí throughout the year and in the Gulf of Panama during the rainy season and, (b) the presence of a shallow nutricline and thermocline that intersect the euphotic zone. This model might be of common occurrence in coastal environments in the eastern tropical Pacific (Pennington et al., 2006). As N:P and N:Si ratios increase with depth, NO_3^- becomes more available at the lower euphotic zone, thus promoting phytoplankton growth. Subsurface chlorophyll maximum may be important in supporting plankton food webs in non-upwelling environments in Central America.

5. Conclusions

Our data on cross-shelf, bottom to surface profiles, reveals the seasonal upwelling-associated hydrological and biological processes that take place along the Pacific coast of Panama. During the non-upwelling rainy season, both gulfs exhibit similar hydrological profiles dominated by the stratification of the water column and the development of an intense thermocline. A subsurface chlorophyll maximum was then developed following the shallow thermocline topography. During the dry season, however, wind-induced upwelling becomes the central hydrological process in the Gulf of Panama, bringing nutrients to the upper layer and promoting phytoplankton growth near the surface. Our data demonstrates that similar processes to those in the Gulf of Panama also take place in the Gulf of Chiriquí. These important processes in the Gulf of Chiriquí are related to the shoaling of the thermocline which is much less pronounced than in the Gulf of Panama and that exists without the widespread movement of deep, cool, nutrient-rich waters to the sea surface. Nevertheless, we postulate that the movement of small pockets of cool, deep water that brings nutrients into the upper layer may be a more common occurrence in the Gulf of Chiriquí than previously suspected. There appears to be no association, however, between the physical forcing and timing of these events with the wind-induced upwelling in the Gulf of Panama.

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