Nutrient and Chlorophyll Dynamics in Pacific Central America (Panama)

Luis D'Croz and Aaron O'Dea

ABSTRACT. Strong wind jets from the Caribbean and the Gulf of Mexico cross Central America through topographic depressions in the cordillera during the boreal winter, pushing Pacific coastal waters offshore, lowering sea levels at the coast, and causing coastal upwelling. Where high mountains impede the winds, this phenomenon does not occur. The Panamanian Pacific shelf is an excellent example of this variability. The coast is divided into two large areas, the Gulf of Panama and the Gulf of Chiriquí. To investigate hydrological conditions between the two gulfs, we sampled the water column during upwelling and non-upwelling seasons in each region. In both gulfs during non-upwelling conditions, surface-level nutrients are poor, and the chlorophyll maximum occurs around 30 m where the thermocline intersects the euphotic zone. Oxygen-poor waters (<2 ppm) commonly occurred below the thermocline. During the dry season, wind strength increased and strong upwelling was observed in the Gulf of Panama. The thermocline rose and surface waters became nutrient enriched and chlorophyll a levels increased. Well-oxygenated waters were compressed to shallow depths. In the Gulf of Chiriquí, wind strength was weaker, surface waters did not become enriched with nutrients, and surface chlorophyll a remained low. We did observe a shallowing of the thermocline in the Gulf of Chiriquí, but in contrast to the Gulf of Panama, wind mixing was not strong enough to result in sea-surface cooling and nutrient enrichment. We postulate that the convergence of a shallow thermocline and internal waves in the Gulf of Chiriquí is the likely mechanism that causes pockets of deep water to occasionally migrate into surface waters, leading to restricted and ephemeral upwelling-like conditions. Although its effects upon shallow-water communities remain to be studied, we propose that the process may be more likely to occur during the boreal winter when the thermocline is shallower.

INTRODUCTION

One of the most pervasive hydrological events to influence the shelf waters of Pacific Central America is upwelling. Intermittent or seasonal upwelling develops in the gulfs of Tehuantepec (Mexico), Papagayo (Costa Rica), and Panama (Legeckis, 1988; McCreary et al., 1989; Xie et al., 2005), driving extensive planktonic productivity and shaping the secondary production of biological communities (Jackson and D'Croz, 1997; O'Dea and Jackson, 2002).

The shelf waters along the Pacific coast of Panama are among the most dynamic in the region. Here, the coastal shelf is naturally divided into two large gulfs by the Azuero Peninsula: the Gulf of Panama (shelf area, 27,175 km²) and the Gulf

Luis D'Croz and Aaron O'Dea, Smithsonian Tropical Research Institute, Box 0843-03092, Panama, Republic of Panama. Corresponding author: L. D'Croz (dcrozl@si.edu). Manuscript received 13 May 2008; accepted 20 April 2009.

of Chiriquí (shelf area, 13,119 km²) (Figure 1). The Gulf of Panama experiences strong seasonal upwelling while the Gulf of Chiriquí exemplifies a non-upwelling environment (Dana, 1975; Kwiecinski and Chial, 1983). This distinction is customarily explained using geographic differences between the two gulfs. Seasonal upwelling in the Gulf of Panama develops during Panama's dry season, corresponding to the boreal winter, when northeast trade winds cross to the Pacific over low areas in the isthmian mountain range, pushing warm and nutrient-poor coastal surface water offshore, lowering the nearshore sea level, and causing the upward movement of colder and nutrient-richer deep water (Smayda, 1966; Forsbergh, 1969; Kwiecinski et al., 1975; D'Croz et al., 1991; D'Croz and Robertson, 1997). The established model proposes that because western Panama has higher mountain ranges that block the winds, surface waters in the Gulf of Chiriquí are not displaced out to the Pacific, and no upwelling as such occurs there.

The structure of shallow biological communities between the two regions supports this inference. Coral reefs, which respond poorly to upwelling conditions, are more extensive in size in the Gulf of Chiriquí than in the Gulf of Panama (Glynn, 1977; Glynn and Maté, 1997), whereas small pelagic fish species from the Gulf of Panama represent a large proportion of the total estimated fishery resource in the country (NORAD, 1988). Satellite imagery shows both wind speeds and chlorophyll content of surface waters to be lower in the Gulf of Chiriquí than the Gulf of Panama during the dry seasons (Pennington et al., 2006).

However, the statement that upwelling does not occur in the Gulf of Chiriquí is supported by sea-surface data derived from satellite imagery analysis or from the measurement of properties in the shallow section of the water column. Hydrological profiles of the water column have documented the shoaling of the thermocline in the Gulf of Chiriquí, yet there appears to be no clear association between the physical forcing of this event with the wind-induced upwelling in the Gulf of Panama. Nevertheless, the movement of pockets of cool water that bring nutrients into the upper layer may be a more common occurrence in the Gulf of Chiriquí than previously suspected (D'Croz and O'Dea, 2007).

It is therefore essential that we obtain detailed and comparable hydrological data from both gulfs if we wish to explain variability in biological communities along the Pacific coast of the Isthmus of Panama today and through geologic time (O'Dea et al., 2007). In this paper we expand the information presented in our previous study (D'Croz and O'Dea, 2007), adding new hydrological and biological data from the Gulf of Chiriquí and the Gulf of Panama, and we further discuss the issue of whether upwelling takes place in the Gulf of Chiriquí.
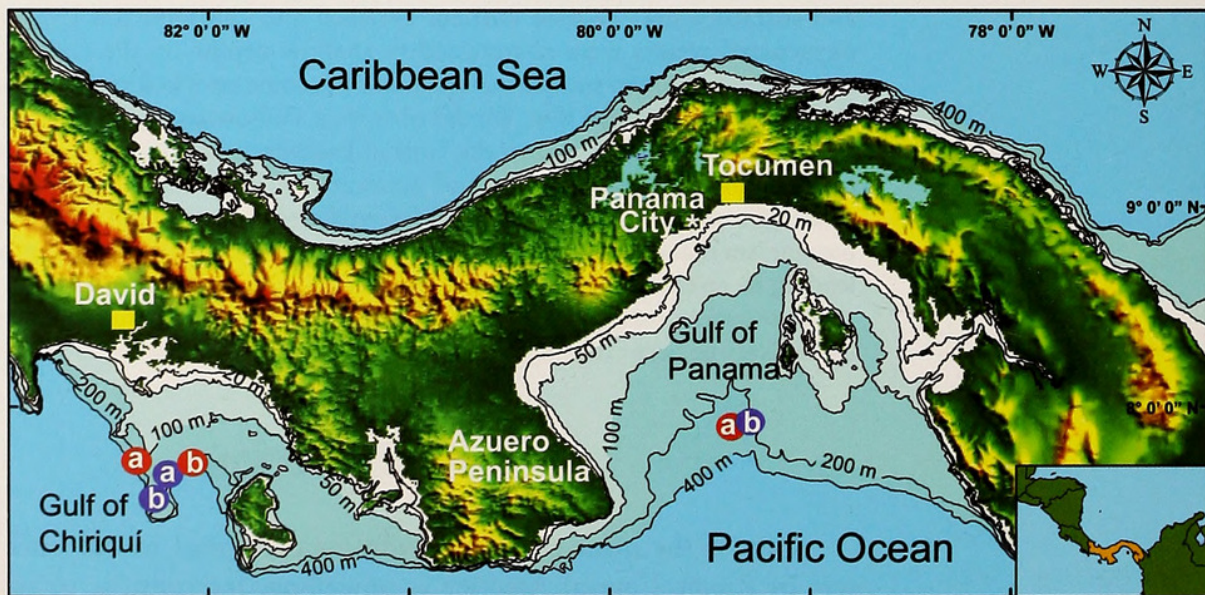

FIGURE 1. Map of the Republic of Panama showing sampling sites. Red dots represent the location of the rainy season samplings in the Gulf of Panama (a = 18 December 2004) and in the Gulf of Chiriquí (a = 13 July 2003; b = 17 December 2004). Blue dots represent the location of the dry season samplings in the Gulf of Panama (a = 29 February 2000) and in the Gulf of Chiriquí (a = 1 March 2000; b = 13 April 2007). Yellow squares indicate the location of the meteorological stations.

MATERIALS AND METHODS

STUDY AREA

Panama's Pacific shelf is located from 07°30′ to 09°01′N and 78°10′ to 82°52′W. The shelf is predominantly occupied by low-salinity surface water, similar to the water mass found over the center of the tropical Pacific Ocean at about 10°N (Wyrtki, 1967; Fiedler and Talley, 2006). The climatology is governed by the Inter-Tropical Convergence Zone (ITCZ), the position of which defines the seasonal pattern of rainfall and winds. The rainy season develops between May and December when the ITCZ is located over or slightly to the north of Panama and winds are light and variable in direction. The dry season develops between January and March when the ITCZ moves south of Panama, a time period characterized by predominating intense northeast trade winds. The mean annual rainfall recorded at meteorological stations near the coast (1999–2004) was 2,760 mm in the Gulf of Chiriquí (David) and 1,880 mm in the Gulf of Panama (Tocumen). Approximately 94% of the annual rainfall in both areas corresponded to the rainy season, the months of September and October being the rainiest in both regions. The estimated sizes of the drainage basins are 11,846 km^2 in the Gulf of Chiriquí and 33,828 km^2 in the Gulf of Panama. River discharges into both gulfs typically follow the seasonal trend described for rainfall. Detailed discussions on wind-stress, rainfall, and river discharge patterns are presented in D'Croz and O'Dea (2007). The tidal regime is semidiurnal, and the sea-level difference during spring tides is 6 m (Glynn, 1972).

SAMPLING PROCEDURES

Sampling research cruises were conducted in the gulfs of Panama and Chiriquí using the Smithsonian Tropical Research Institute's R/V *Urracá* (see Figure 1). Samplings were scheduled to correspond with different times of the year, representing contrasting hydrological conditions (upwelling and non-upwelling). Surface-to-bottom profiles for salinity, temperature, dissolved oxygen, and chlorophyll *a* were recorded with a CTD (conductivity, temperature, depth) multiparameter profiler (Ocean Seven 316, Idronaut Srl, Milano, Italy). Hydrological casts with the CTD corresponding to the dry season were carried out in both gulfs on 29 February 2000 and 1 March 2000 and in the Gulf of Chiriquí on 13 April 2007. Rainy season CTD casts were carried out in the Gulf of Chiriquí on 13 July 2003 and in both gulfs during 17 and 18 December 2004. The water column was sampled at discrete levels to study nutrient and chlorophyll *a* concentrations. Water samples were collected using Niskin bottles during the dry season of the year 2000 (29 February to 1 March) and during the rainy season of the year 2004 (17 and 18 December). Three replicate water samples per selected depth were collected at each site. Two liters of each individual replicate water sample were immediately sieved through Nitex (350 μm) to exclude zooplankton and vacuum filtered on Whatman GF/F filter (0.7 μm pore size) for chlorophyll *a* analysis. An aliquot from each filtrate was set apart for the determination of dissolved inorganic nutrients. Filters and water samples were stored frozen (−20°C) until analysis. Salinity is expressed using the Practical Salinity Scale (pss) indicated by UNESCO (1981). Results from the chlorophyll *a* analyses were used to check the calibration of the CTD's fluorometer. 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 $K_d = f/zs$ where zs is the Secchi depth and $f = 1.4$.

ANALYSIS OF SAMPLES

Not later than two weeks after sampling, filters holding the phytoplankton were analyzed for chlorophyll *a* using the non-acidification fluorometric method (Welschmeyer, 1994). Water samples were analyzed for NO_3^- + NO_2^- (nitrate + nitrite), $Si(OH)_4$ (silicate), and PO_4^{3-} (phosphate) by colorimetric methods using an Alpkem Flow Solution IV automated analyzer. Minimum detection limits were 0.02 μM for nitrate, 0.01 μM for nitrite, 0.12 μM for silicate, and 0.02 μM for phosphate.

ANALYSIS AND PRESENTATION OF DATA

Water quality variables, namely temperature, salinity, dissolved oxygen, dissolved inorganic nutrients, and chlorophyll *a*, are presented graphically as profiles of the samplings. Overall differences in between the two gulfs were assessed with the Mann–Whitney test (U) by taking the median of each variable from samples collected in the top 30 m of the ocean where the highest hydrological variability occurred (Table 1). Water transparency data were compared using the paired t test. We followed the practice of taking the position of the 20°C isotherm to represents the depth of the center of the permanent thermocline in the eastern Pacific Ocean (Wyrtki, 1964; Fiedler et al., 1991; Xie et al., 2005). Pearson correlations with Bonferroni adjustment were used to test statistical relationships among variables.

TABLE 1. Average value of hydrological variables in the top water column (30 m) in the gulfs of Panama (GP) and Chiriquí (GC); SE = standard error of the mean. Statistical tests were either Mann–Whitney U test or paired t test ($^*P < 0.05$, $^{**}P < 0.01$, $^{***}P < 0.001$, ns = nonsignificant).

	Dry season values			Rainy season values		
Hydrological variables	GP (Mean ± SE)	GC (Mean ± SE)	Statistical value [a,b]	GP (Mean ± SE)	GC (Mean ± SE)	Statistical value [a,b]
Temperature (°C)	17.97 ± 0.92	27.17 ± 0.92	16.0* [a]	26.75 ± 0.54	28.61 ± 0.05	18.0 ns [a]
Salinity (pss) [c]	34.18 ± 0.29	32.98 ± 0.29	12.0* [a]	31.67 ± 0.64	30.48 ± 0.38	3.0 ns
Chlorophyll a (μg L^{-1})	1.82 ± 0.65	0.83 ± 0.65	4.0* [a]	0.23 ± 0.13	0.18 ± 0.06	8.5 ns [a]
Dissolved oxygen (ppm)	3.45 ± 0.27	4.78 ± 0.27	13.0* [a]	3.98 ± 0.16	4.38 ± 0.01	4.0 ns [a]
NO$_3^-$ (μM)	14.37 ± 2.48	3.72 ± 2.48	1.0** [a]	0.99 ± 0.34	0.36 ± 0.02	2.5 ns [a]
PO$_4^{3-}$ (μM)	1.08 ± 0.21	0.39 ± 0.21	1.0** [a]	0.43 ± 0.07	0.24 ± 0.03	4.0 ns [a]
N:P ratio	12.82 ± 1.10	7.77 ± 1.10	1.0** [a]	2.11 ± 0.36	1.49 ± 0.10	3.0 ns [a]
Si(OH)$_4$ (μM)	8.99 ± 1.03	4.40 ± 1.03	5.0* [a]	5.40 ± 0.71	4.87 ± 0.47	13.0 ns [a]
Secchi depth (m)	4.20 ± 0.00	14.80 ± 0.00	−1591.0*** [b]	20.00 ± 0.00	19.00 ± 0.00	2.0 ns [b]
Euphotic zone (m)	13.8 ± 0.00	48.63 ± 0.00	−1394.2*** [b]	65.71 ± 0.00	62.43 ± 0.00	188.4 ns [b]

[a] Mann–Whitney U test.
[b] Paired t test.
[c] pss = practical salinity scale.

RESULTS

THERMOHALINE STRUCTURE

Both the Gulf of Panama and the Gulf of Chiriquí exhibit the typical tropical coastal ocean water structure of cool deep waters leading upward to a shallow thermocline topped by warm surface waters. However, significant differences occur between the two gulfs with respect to climatic variability. During the rainy season, the thermal structure in both gulfs is remarkably similar (see Table 1). Sea-surface temperatures (SSTs) are invariably warm (27°–28°C), and the thermocline sits at approximately 60 m (Figure 2).

During the dry season, thermal conditions become dissimilar between the two regions (Table 1). In our observations, the thermocline in the Gulf of Panama rose sharply and nearly broke at the surface, resulting in a significant cooling of surface waters to 22°C (Figure 3a). Simultaneously, the thermocline in Gulf of Chiriqui rose to around 30 m, compressing warm SSTs into shallow waters (Figure 3b). However, the shoaling of the thermocline in Chiriquí was not as intense as that seen in the Gulf of Panama and did not result in SST cooling.

In general, salinity profiles in both regions revealed a sharp gradient from high-salinity deep water to fresher surface waters. Seasonal variability in surface salinities in both gulfs was very similar (Table 1). During the rainy season, both regions experienced high freshwater dilution in the upper-layer waters, with surface salinities below 30 on the pss (see Figure 2). The halocline was located at 60 m depth, coinciding with the thermocline. During the dry season, lower rainfall led to increased salinities in the surface waters of both gulfs (Figure 3). However, the effect was more striking in the Gulf of Panama as the halocline shoaled and salinity in surface waters reached 34.

In April 2007, the thermohaline structure in the Gulf of Chiriquí departed drastically from the typical condition as the thermocline/halocline shoaled to 20 m. Despite this condition, however, SSTs remained warm (Figure 3c).

CHLOROPHYLL

Concentrations of surface chlorophyll were always below 0.30 μg/L in both gulfs during the rainy season (Table 1), but a deep chlorophyll maximum developed from 30 m to 50 m, lying above the thermocline (Figure 2). The deep chlorophyll maximum contained most of the chlorophyll a in the water column in both gulfs, concentrations reaching 1 μg/L during the rainy season. The dry season upwelling changed this pattern in the Gulf of Panama, as the chlorophyll maximum moved into shallower waters, where concentrations surpassed 4 μg/L (Figure 3a). Surface chloro-
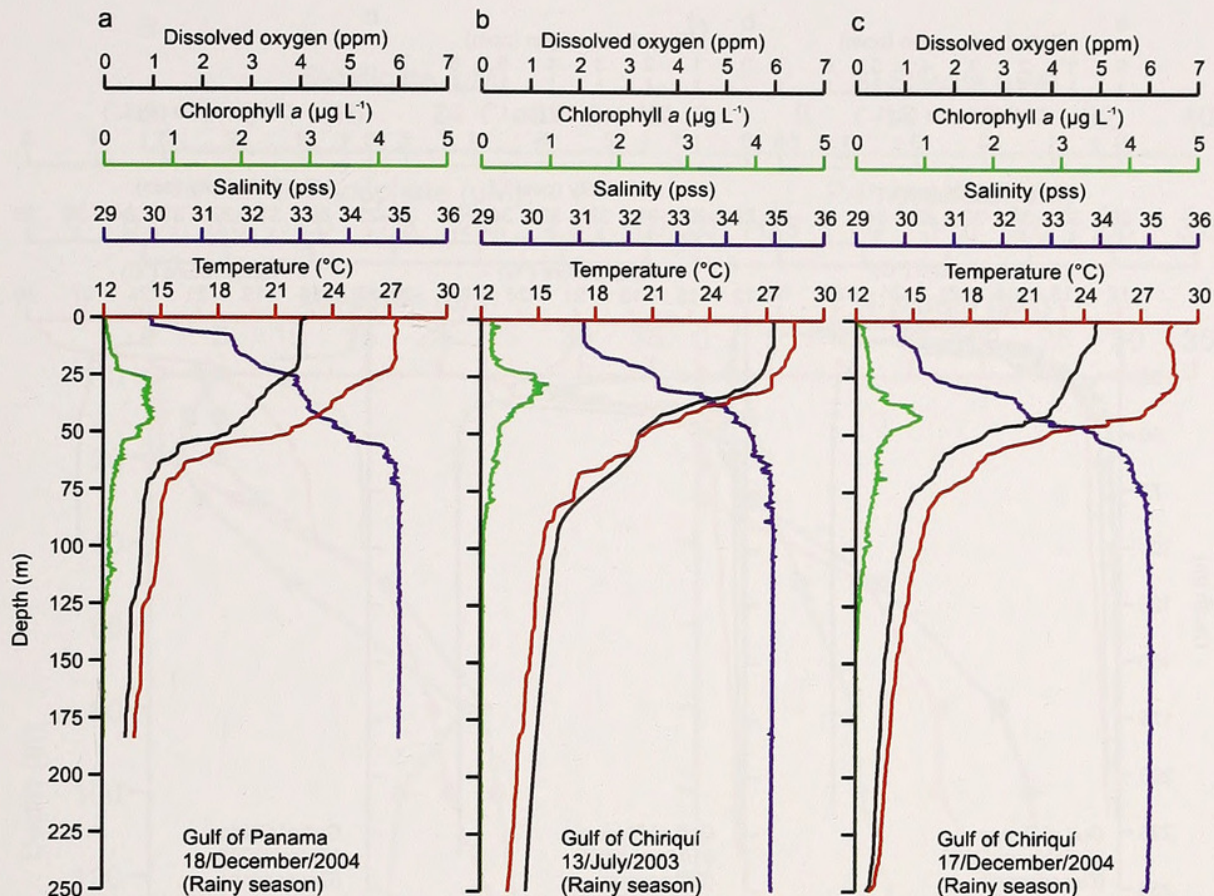
FIGURE 2. Profiles of dissolved oxygen, chlorophyll *a*, salinity, and temperature in the Gulf of Panama and the Gulf of Chiriquí during the rainy season. a = Gulf of Panama, 18 December 2004; b = Gulf of Chiriquí, 13 July 2003; c = Gulf of Chiriquí, 17 December 2004.

phyll *a* remained at very low values in the Gulf of Chiriquí during the dry season, but the deep chlorophyll maximum became remarkably intense at 30 m where concentration reached 3 µg/L (Figure 3b).

DISSOLVED OXYGEN

Dissolved oxygen profiles followed the typical pattern of well-oxygenated surface waters lying on top of deeper oxygen-poor waters. During the rainy season, severe hypoxic conditions (<2 ppm) were recorded below the strong oxycline, at 50 m and nearly coincident with the thermocline (see Figure 2). Oxygen concentrations in waters above the thermocline were strongly correlated with temperature in both the Gulf of Panama ($r = 0.91$; $P < 0.001$) and the Gulf of Chiriquí ($r = 0.89$; $P < 0.001$) during the rainy season. This arrangement, however, had strong seasonal variation in the Gulf of Panama during the dry season, as the oxycline rose to 25 m and

compressed the oxygenated waters into shallow depths (Figure 3). Dissolved oxygen below this depth rapidly declined to less than 1 ppm (Figure 3a), whereas waters in the Gulf of Chiriquí only became hypoxic below the 50 m oxycline (Figure 3b). No correlations were confirmed between dissolved oxygen and temperature in any of these regions during the dry season.

DISSOLVED NUTRIENTS

Both gulfs exhibit a strong vertical gradient of upwardly decreasing nutrient concentrations. Nitrate in surface waters was depleted in both gulfs during the rainy season, with values below 0.5 µM (Figure 4). During the dry season, nitrate concentrations at the surface were observed to increase 10 fold in the Gulf of Panama when the nutricline shoaled to around 10 m (Figure 5a). No similar surface enrichment was detected in the Gulf of Chiriquí, where a strong nutricline was developed at 60 m (Figure 5b).
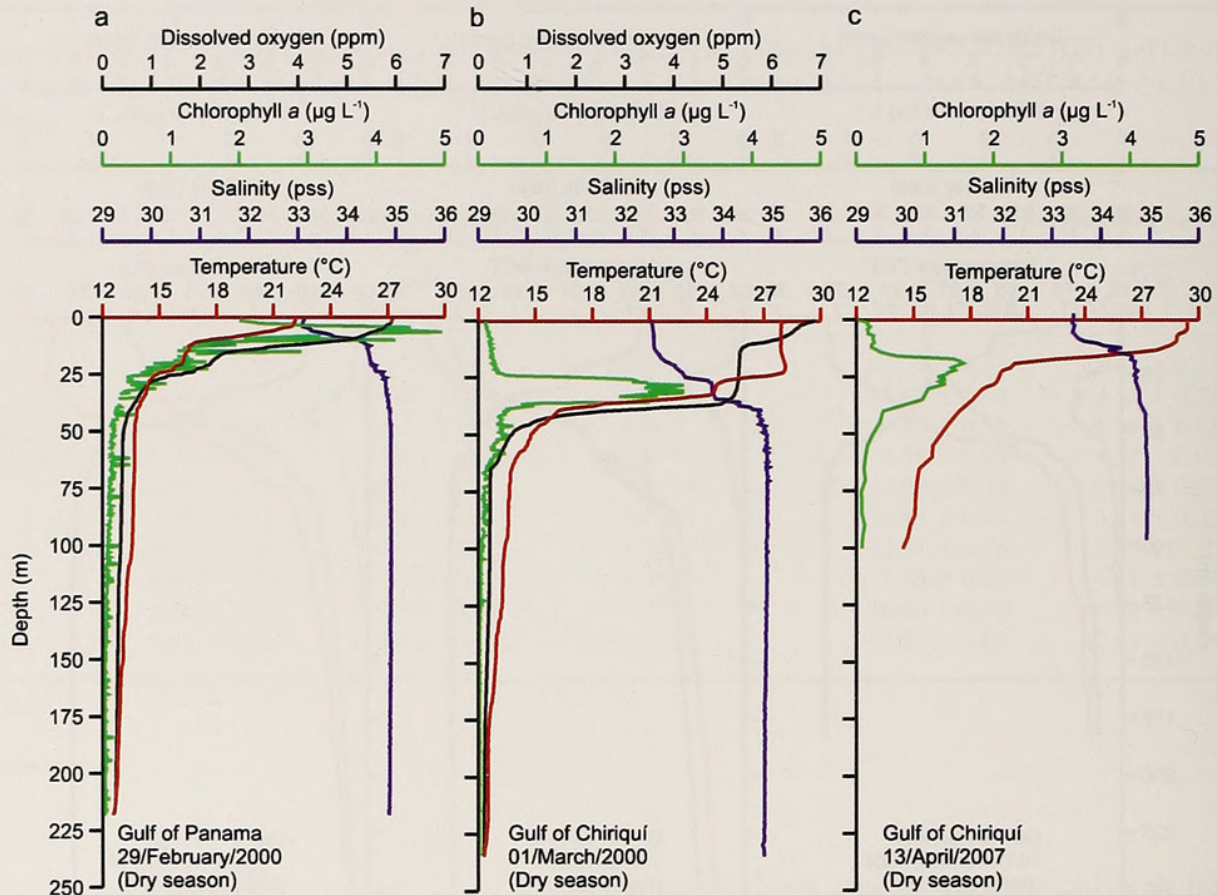
FIGURE 3. Profiles of dissolved oxygen, chlorophyll *a*, salinity, and temperature in the Gulf of Panama and the Gulf of Chiriquí during the dry season. a = Gulf of Panama, 29 February 2000; b = Gulf of Chiriquí, 1 March 2000; c = Gulf of Chiriquí, 13 April 2007.

Overall, the patterns of phosphate resembled those of nitrate, but concentrations were lower by an order of magnitude. Concentrations of phosphate in excess of 1 μM were usually found below 30 m depth. Phosphate concentrations in surface waters remained relatively low (<0.3 μM) in the Gulf of Chiriquí during both climatic seasons (Figures 4b, 5b). However, phosphate enrichment of surface waters clearly occurred in the Gulf of Panama during the dry season when the nutricline shoaled and phosphate concentrations in the top of the water column reached about 1.0 μM (Figure 5a).

Silicate profiles followed similar trends to that of the nitrate and phosphate (Figures 4, 5). Although silicate concentrations were similar in surface waters in both gulfs during the rainy season, they doubled in the Gulf of Panama during the dry season (Table 1).

Dissolved nutrients in the upper 50 m had a high degree of relationship with temperature and salinity. During the rainy season, nitrate concentrations were inversely cor-

related to temperature in both the Gulf of Chiriquí ($r = -0.78$; $P < 0.001$) and the Gulf of Panama ($r = -0.97$; $P < 0.002$). In the dry season, nitrate in the Gulf of Panama was negatively correlated to temperature ($r = -0.98$; $P < 0.044$) and directly related to salinity ($r = 0.98$; $P < 0.049$). Nitrate was negatively correlated to temperature in the Gulf of Chiriquí during the dry season ($r = -0.89$; $P < 0.016$), but not to salinity ($r = 0.67$; $P > 0.159$). Phosphate was negatively correlated to temperature during the dry season in the Gulf of Panama ($r = -0.98$; $P < 0.038$) and in the Gulf of Chiriquí ($r = -0.97$; $P < 0.036$). Dry season phosphate was also correlated to salinity in the Gulf of Chiriquí ($r = 0.98$; $P < 0.05$).

The extremely low nitrate to phosphate ratios (N:P) suggest that phytoplankton growth in both regions was under severe nitrogen limitation during the rainy season (Figure 6). The N:P ratio was below 2:1 in surface water and increased with depth, surpassing the value of 10:1 below the depth of 50 m. During the dry season, N:P ra-
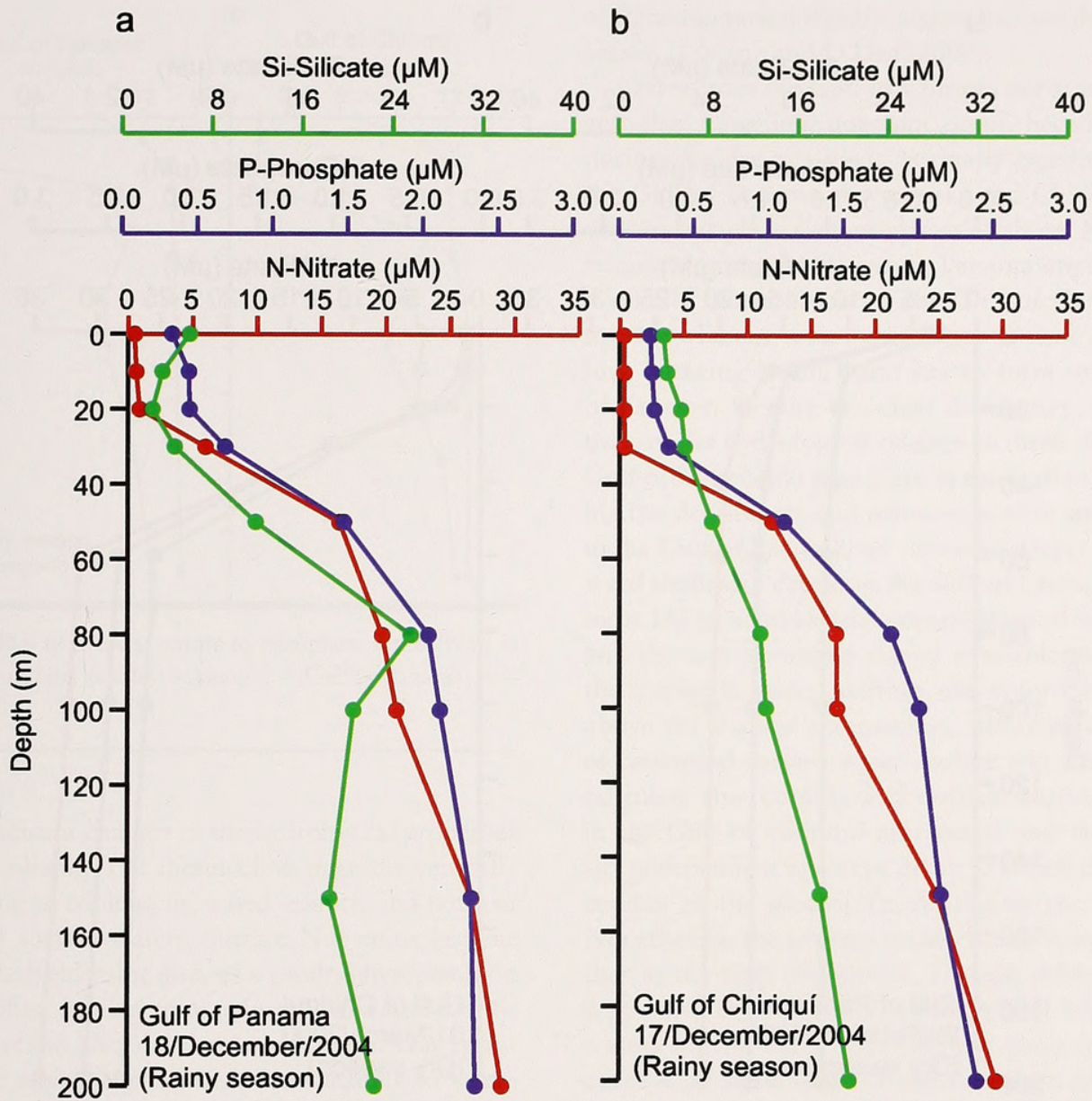
FIGURE 4. Mean profiles of silicate (Si), phosphate (P), and nitrate (N) in the Gulf of Panama and the Gulf of Chiriquí during the rainy season. a = Gulf of Panama, 18 December 2004; b = Gulf of Chiriquí, 17 December 2004.

tios within the euphotic zone largely increased in both regions, becoming closer to the N:P ratio of 16:1 suggested as favorable for phytoplankton growth (Redfield, 1958).

WATER TRANSPARENCY

Water transparency was seasonably stable in the Gulf of Chiriquí but varied considerably in the Gulf of Panama (see Table 1). Water transparency in both gulfs was higher during the rainy season when the euphotic zone was approximately 60 m deep, in contrast to the limited trans-

parency and shallow euphotic zone (14 m) observed in the Gulf of Panama during the dry season upwelling.

DISCUSSION

Our data on bottom-to-surface profiles reveal the dynamics of hydrological conditions along the Pacific coast of Panama during times of both upwelling and non-upwelling. During the non-upwelling rainy season, both gulfs exhibit extremely similar hydrological structures dominated by the
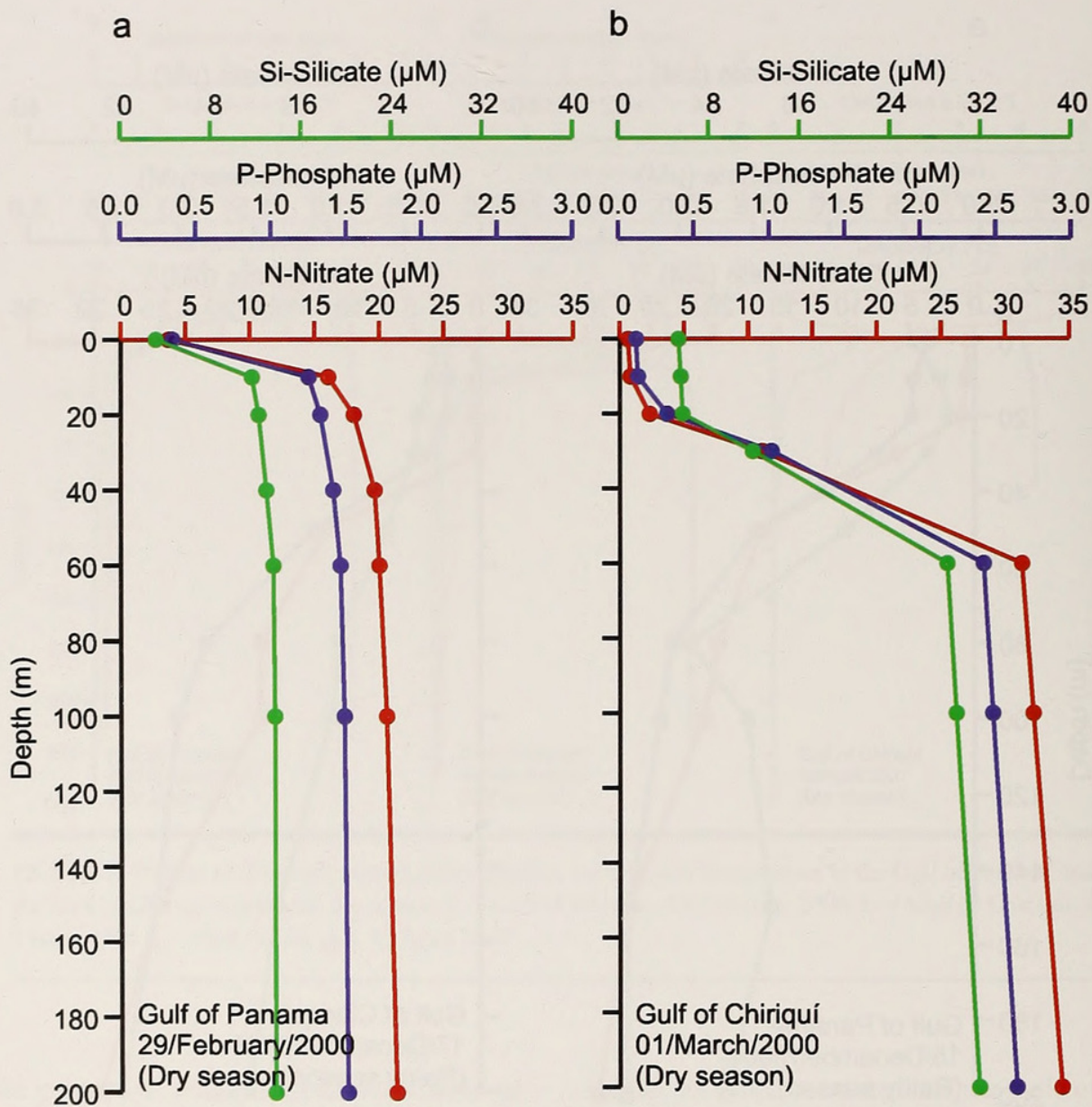
FIGURE 5. Mean profiles of silicate (Si), phosphate (P), and nitrate (N) in the Gulf of Panama and the Gulf of Chiriquí during the dry season. a = Gulf of Panama, 29 February 2000; b = Gulf of Chiriquí, 1 March 2000.

development of an intense thermocline at approximately 60 m. Surface waters tend to have low salinities and are warm and nutrient depleted. Low N:P ratios in surface waters during the rainy season suggest that phytoplankton growth is strongly nitrogen limited. Consequently, the standing stock of chlorophyll *a* is maintained at relatively low levels in surface waters. Phytoplankton does however peak at subsurface levels as the nutrient-rich thermocline waters intersect the euphotic zone, increasing N:P ratios and favoring algal growth. The strong inverse correlation between nutrients and sea temperature is consistent with the coincidence of a shallow thermocline and strong nutri-

cline typical of the eastern tropical Pacific Ocean (Enfield, 2001). As such, the seasonal movement of the thermocline represents a key source of nutrients for phytoplankton. Our sampling sites were far offshore and therefore silicate concentrations were not as high as previously reported for the inner shelf (D'Croz and O'Dea, 2007) even though the concentration of silicate in the Gulf of Panama is reported to be the highest in the eastern Pacific as a consequence of the intense runoff in the area (Pennington et al., 2006).

During the dry season, the hydrological patterns of the two gulfs become dissimilar. In the Gulf of Panama strong upwelling of cold deep waters into coastal and surface wa-
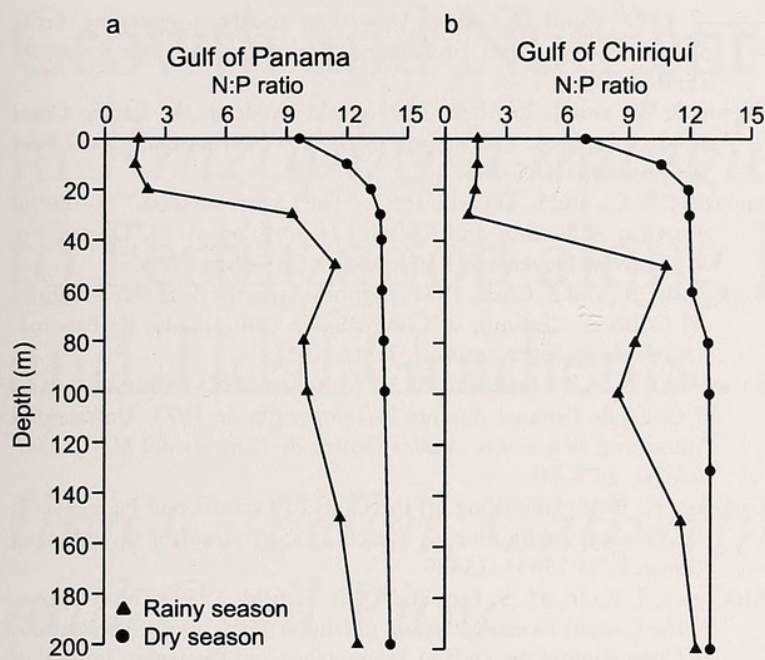
FIGURE 6. Profiles of average nitrate to phosphate ratios (N:P) in rainy (triangles) and dry (circles) seasons: a = Gulf of Panama; b = Gulf of Chiriquí.

ters drives significant changes in the hydrological properties of the water column. The thermocline migrates vertically upward, leading to cooling, increased salinity, and nutrient enrichment on surface waters. Surface N:P ratios become closer to the Redfield value and, as a result, phytoplankton growth intensifies, leading to a reduction in water clarity. A shallow oxycline also develops and oxygen concentration below the oxycline is reduced, often leading to severe hypoxic conditions. In contrast, the oxycline in the Gulf of Chiriquí is deeper and deep water remains hypoxic. Low oxygen minima are nonetheless typical in the eastern tropical Pacific as a combination of high algal growth at the surface, a strong pycnocline that impedes the ventilation of waters below, and the sluggish circulation of deep waters (Fiedler and Talley, 2006). The report of large filamentous *Thioploca*-like sulfur bacteria on shallow sediments in both regions strongly suggests that the inner shelf is exposed to episodes of reduced oxygen (Gallardo and Espinoza, 2007).

A significant relationship between wind-stress index (calculated from the sum of northerly winds) and sea level provides an explanatory mechanism for upwelling in the Gulf of Panama (Schaefer et al., 1958; Legeckis, 1988; Xie et al., 2005). Surface waters are displaced into open ocean by strong northerly winds during the dry season, and deep waters move vertically upward to replace them (Fleming, 1940; Smayda, 1966; Forsbergh, 1969). Consequently, wind stress is inversely related to SST in the Gulf

of Panama during the dry season but not during the rainy season (D'Croz and O'Dea, 2007).

Data from the Gulf of Chiriquí are scant but did suggest that upwelling does not occur, because wind stress during the dry season is normally one-third of that of the Gulf of Panama (Kwiecinski and Chial, 1983) and it does not displace surface waters offshore. High mountain ranges running along western Panama impede the flow of northerly winds across to the Gulf of Chiriquí (see Figure 1), whereas mountain ranges in central Panama are low, allowing strong wind jets to form toward the Gulf of Panama. Despite this clear distinction, our data show that similar hydrological changes to those that occur in the Gulf of Panama do take place in the Gulf of Chiriquí. During the dry season, and concurrent with strong upwelling in the Gulf of Panama, we observed deeper waters rise toward shallower depths in the Gulf of Chiriquí. This movement led to a substantial compression of the mixed layer and the corresponding rise of available nutrients within the euphotic zone, shifting the chlorophyll maximum above the shallow thermocline. Although direct evidence of prolonged surface water cooling was not observed, we postulate that cooling and nutrient-enrichment episodes in the Gulf of Chiriquí may occur and that their intensity is dependent upon the depth to which the thermocline reaches in the eastern Pacific during the boreal winter. Nonetheless, the process is clearly much less intense than that in the Gulf of Panama. Despite substantial shifts in deeper water conditions in the Gulf of Chiriquí, surface waters remain warm and nutrient poor, presumably because wind stress is not strong enough to cause the advection of deep, cool, and nutrient-rich waters to the surface (D'Croz and O'Dea, 2007). However, ocean forces such as internal waves might change the oceanographic structure in the Gulf of Chiriquí, causing brief periods of advection of deep cold water to the surface layer (Dana, 1975). Long-term records from data loggers deployed in coral reefs give evidence of such brief SST drops in the Gulf of Chiriquí that are possibly related to internal waves (D'Croz and O'Dea, 2007). This effect might be more evident as the internal waves approach the shallow coasts around the islands in the Gulf of Chiriquí and may be more likely to occur during times of thermocline shallowing.

In conclusion, although the Gulf of Chiriquí does not experience the intense seasonal upwelling characteristic of the Gulf of Panama, deeper waters do migrate upward in synchrony with Gulf of Panama upwelling. This movement is probably caused by an overall shallowing of the thermocline across Central America. The difference in intensity of upward movement of the thermocline between

the two gulfs strongly influences the phytoplankton community, with seasonal blooms occurring in the Gulf of Panama but not in the Gulf of Chiriquí. Deeper waters do nonetheless experience similar patterns of seasonal hydrographic change, and shallow waters of the Gulf of Chiriquí can be exposed to brief pulses of cold and nutrient-rich waters by advection. However, the effects of thermocline migration and advection on the shallow-water communities of the Gulf of Chiriquí remain to be studied in detail.

Acknowledgments

LITERATURE CITED

Dana, T. F. 1975. Development of Contemporary Eastern Pacific Coral Reefs. *Marine Biology*, 33:355–374.

D'Croz, L., J. B. Del Rosario, and J. A. Gómez. 1991. Upwelling and Phytoplankton in the Bay of Panamá. *Revista de Biología Tropical*, 39:233–241.

D'Croz, L., and A. O'Dea. 2007. Variability in Upwelling Along the Pacific Shelf of Panama and Implications for the Distribution of Nutrients and Chlorophyll. *Estuarine, Coastal, and Shelf Science*, 73:325–340.

D'Croz, L., and D. R. Robertson. 1997. Coastal Oceanographic Conditions Affecting Coral Reefs on Both Sides of the Isthmus of Panama. *Proceedings of the 8th International Coral Reef Symposium*, 2:2053–2058.

Enfield, D. B. 2001. Evolution and Historical Perspective of the 1997–1998 El Niño–Southern Oscillation Event. *Bulletin of Marine Science*, 69:7–25.

Fiedler, P. C., V. Philbrick, and F. T. Chavez. 1991. Oceanic Upwelling and Productivity in the Eastern Tropical Pacific. *Limnology and Oceanography*, 36:1834–1850.

Fiedler, P. C., and L. D. Talley. 2006. Hydrography of the Eastern Tropical Pacific: A Review. *Progress in Oceanography*, 69:143–180.

Fleming, R. H. 1940. A Contribution to the Oceanography of the Central American Region. *Proceedings of the 6th Pacific Science Congress*, 3:167–175.

Forsbergh, E. D. 1969. On the Climatology, Oceanography and Fisheries of the Panamá Bight. *Inter-American Tropical Tuna Commission Bulletin*, 14:49–259.

Gallardo, V. A., and C. Espinoza. 2007. New Communities of Large Filamentous Sulfur Bacteria in the Eastern South Pacific. *International Microbiology*, 10:97–102.

Glynn, P. W. 1972. "Observations on the Ecology of the Caribbean and Pacific Coast of Panamá." In *The Panamic Biota: Some Observations Prior to a Sea-Level Canal*, ed. M. L. Jones. *Bulletin of the Biological Society of Washington*, 2:13–30.

———. 1977. Coral Growth in Upwelling and Non-upwelling Areas off the Pacific Coast of Panamá. *Journal of Marine Research*, 35:567–585.

Glynn, P. W., and J. L. Maté. 1997. Field Guide to the Pacific Coral Reefs of Panamá. *Proceedings of the 8th International Coral Reef Symposium*, 1:145–166.

Jackson J. B. C., and L. D'Croz. 1997. "The Ocean Divided." In *Central America: A Natural and Cultural History*, ed. A. G. Coates, pp. 38–71. New Haven and London: Yale University Press.

Kwiecinski, B., and B. Chial. 1983. Algunos Aspectos de la Oceanografía del Golfo de Chiriquí, su Comparación con el Golfo de Panamá. *Revista de Biología Tropical*, 31:323–325.

Kwiecinski, B., A. L. Jaén, and A. M. Muschett. 1975. Afloramiento en el Golfo de Panamá durante la Temporada de 1973. Universidad Autónoma de México. *Anales Centro de Ciencias del Mar y Limnología*, 2:73–80.

Legeckis, R. 1988. Upwelling off the Gulfs of Panamá and Papagayo in the Tropical Pacific during March 1985. *Journal of Geophysical Research*, 93:15485–15489.

McCreary, J. P., Jr., H. S. Lee, and D. B. Enfield. 1989. The Response of the Coastal Ocean to Strong Offshore Winds: With Applications to Circulation in the Gulf of Tehuantepec and Papagayo. *Journal of Marine Research*, 47:81–109.

NORAD. 1988. *Surveys off the Pacific Coast of Central America*. Reports on Surveys with R/V Dr. Fridtjof Nansen. Institute of Marine Research, Bergen, Norway: NORAD/UNDP/FAO.

O'Dea, A., and J. B. C. Jackson. 2002. Bryozoan Growth Mirrors Contrasting Seasonal Regimes Across the Isthmus of Panama. *Palaeo*, 185:77–94.

O'Dea, A., J. B. C. Jackson, H. Fortunato, J. Travis-Smith, L. D'Croz, K. G. Johnson, and J. A. Todd. 2007. Environmental Change Preceded Caribbean Extinction by 2 Million Years. *Proceedings of the National Academy of Sciences of the United States of America*, 104(13):5501–5506.

Parsons, T. R., M. Takahashi, and B. Hargrave. 1984. *Biological Oceanographic Processes*, 3rd ed. Oxford: Pergamon Press.

Pennington, J. T., K. L. Mahoney, V. S. Kuwahara, D. D. Kolber, R. Calienes, and F. P. Chavez. 2006. Primary Production in the Eastern Tropical Pacific: A Review. *Progress in Oceanography*, 69:285–317.

Redfield, A. C. 1958. The Biological Control of Chemical Factors in the Environment. *American Scientist*, 46:205–221.

Schaefer, M. B., Y. M. Bishop, and G. V. Howard. 1958. Some Aspects of Upwelling in the Gulf of Panama. *Inter-American Tropical Tuna Commission Bulletin*, 3:77–132.

Smayda, T. J. 1966. A Quantitative Analysis of the Phytoplankton of the Gulf of Panamá. III. General Ecological Conditions, and the Phytoplankton Dynamics at 8°45′N, 79°23′W from November 1954 to May 1957. Inter-American Tropical Tuna Commission Bulletin, 11:353–612.

UNESCO. 1981. *The Practical Salinity Scale 1978 and the International Equation of State of Seawater 1980*. UNESCO Technical Papers in Marine Science No. 36. Paris: UNESCO.

Welschmeyer, N. A. 1994. Fluorometric Analysis of Chlorophyll a in the Presence of Chlorophyll b and Pheopigments. *Limnology and Oceanography*, 39:1985–1992.

Wyrtki, K. 1964. Upwelling in the Costa Rica Dome. *Fishery Bulletin*, 63:355–372.

———. 1967. Circulation and Water Masses in the Eastern Equatorial Pacific Ocean. *International Journal of Oceanology and Limnology*, 1:117–147.

Xie, S.-P., H. Xu, W. S. Kessler, and M. Nonaka. 2005. Air–Sea Interaction over the Eastern Pacific Warm Pool: Gap Winds, Thermocline Dome, and Atmospheric Convection. *Journal of Climate*, 18:5–20.