Climate and Hydrological Factors Affecting Variation in Chlorophyll Concentration and Water Clarity in the Bahia Almirante, Panama

Rachel Collin, Luis D'Croz, Plinio Gondola, and Juan B. Del Rosario

ABSTRACT. Water clarity and productivity are fundamentally important for the distribution of tropical marine organisms. In the Caribbean, changes in nutrient loading that result from rapid development are thought to have caused increased planktonic productivity, reduced water clarity, and reduced reef and seagrass health. Here we analyze chlorophyll *a* concentration and water clarity from eight years of environmental monitoring in Bocas del Toro, Panama. Chlorophyll *a* concentrations did not vary significantly among the six sampled sites and showed no significant temporal changes, despite the recent rapid development in the region, accompanied by scant wastewater treatment. In contrast, water clarity increased significantly during the study period. Because chlorophyll *a* does not vary closely with water clarity, Secchi depths are likely to reflect changes in suspended particulate matter rather than in phytoplankton biomass. Secchi depths decreased with rainfall and wind speed but increased with solar radiation, supporting the idea that clarity was not tightly linked to phytoplankton biomass. The decrease in annual rainfall, but not wind speed, over the past eight years suggests that the long-term trend in Secchi readings is the result of changes in rainfall patterns.

INTRODUCTION

Water clarity and productivity are fundamentally important to the distribution of tropical marine organisms, especially corals. Ocean primary productivity is also important for global geochemistry and carbon sequestration (Falkowski et al., 1998). Global warming and increase in atmospheric CO_2 are expected to influence the distribution of the biota, as well as its abundance, and the photosynthetic activity of phytoplankton (Falkowski et al., 1998). SeaWiFS satellite imagery shows that worldwide oceanic chlorophyll *a* concentrations are about 0.2 mg/m^3 (Yoder et al., 1993) and can reach 5 mg/m^3 in coastal upwelling zones (Falkowski et al., 1991; Walsh et al., 1978). It is difficult to use this method to obtain information on chlorophyll *a* concentrations for many onshore tropical areas because accurate remote sensing is difficult in coastal areas with large sediment input and because many tropical regions have high frequencies of cloud cover. In such areas field measurements of water clarity and chlorophyll *a* concentrations are vital for assessing short-term variation and ground-truthing remote measurements.

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Coral reef environments are particularly sensitive to changes in water quality, especially changes in nutrients, sediment load, and productivity. The paradigm of coral reef biology is that reef development and coral health are greatest in areas with low sedimentation, low primary productivity, low abundances of zooplankton, and high water clarity. These habitats are most conspicuous in the Indo-Pacific and the offshore islands in the Caribbean. In many locations these habitats are suffering from reduction of water quality associated with coastal development (Bell, 1992; Lapointe, 1992). In the Caribbean, most studies of reefs and their waters are conducted in the Bahamas, Puerto Rico, Netherlands Antilles, and other offshore islands (Gilbes et al., 1996; Otero and Carbery, 2005; van Duyl et al., 2002; Webber et al., 2003). In addition there have been some studies of the unusual upwelling sites along the coast of Venezuela and Colombia (Franco-Herrera et al., 2006) and the strongly freshwater-influenced regions around the Yucatan (Herrera-Silveira et al., 2002). However, few studies have examined heavily terrestrially influenced systems without these unusual features in the Caribbean. Here we report the results of eight years of physical climatic and water quality monitoring in Bahia Almirante, an enclosed Caribbean archipelago that is highly terrestrially influenced.

STUDY LOCATION: BOCAS DEL TORO, PANAMA

Three bodies of water surround the Bocas del Toro Archipelago on the Caribbean coast of Panama: the Bahia Almirante and the Laguna de Chiriquí on the landward side, and the Caribbean Sea on the exposed coastal side (Figure 1). The mainland surrounding the region is largely forested, although the completion of a road linking Costa Rica to Bocas del Toro and the rest of Panama in the year

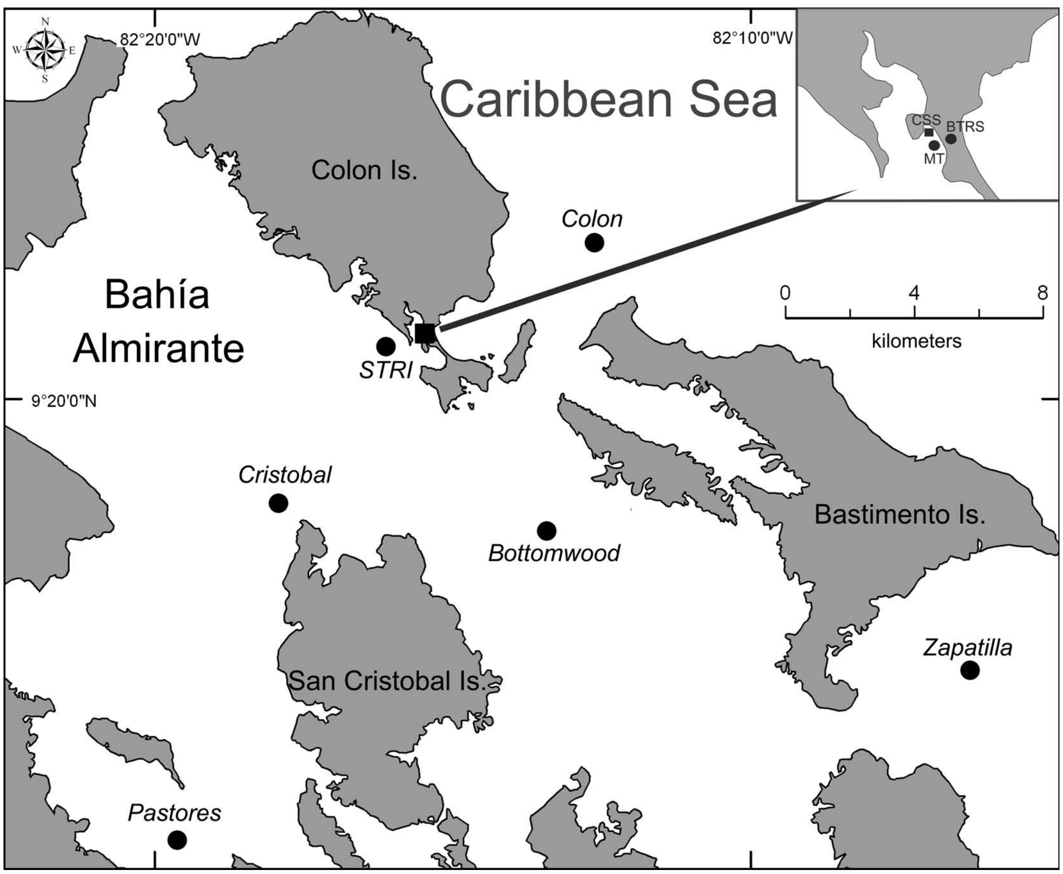

FIGURE 1. Map of the Bahia Almirante region with sampling sites indicated. BTRS = Bocas del Toro Research Station; CSS = CARICOMP seagrass site; MT = instrument platform; STRI = Smithsonian Tropical Research Institute.

2000 has resulted in increased lowland deforestation, as well as land development for small farms and tourism. The landward sides of the islands are fringed with largely intact red mangrove forests, although these are also being cleared from the landward side. The Laguna de Chiriquí, which receives twice the freshwater runoff of Bahia Almirante, has higher nutrient loads and limited coral reef development (D'Croz et al., 2005) and is not discussed further here.

The Bahia Almirante has significantly more oceanic influence than the Laguna de Chiriqui and supports well-developed coral reefs. It receives runoff from only two rivers of any note. High rainfall (about 3 m/year) and runoff from the San San Pond Sac peat swamp forest often result in pronounced haloclines with low-salinity waters (which are often cold) overlying full-salinity bottom waters (Kaufmann and Thompson, 2005). Surface salinities are generally 30–34 PSS (practical salinity scale) but can drop as low as 20 PSS after heavy rains (Kaufmann and Thompson, 2005). Other conditions are relatively aseasonal, with mean sea surface temperatures varying from 27.5°C (January–February) to 29.7°C (September–October). Average wind speed is about 7 km/h but occasionally exceeds 20 km/h (Kaufmann and Thompson, 2005). Despite the high levels of runoff, N:P was always recorded to be below Redfield ratios in a previous survey of the area (D'Croz et al., 2005). This observation suggests that primary productivity could be nutrient limited and that inputs from freshwater runoff or wind mixing could fertilize primary productivity in the Bahia Almirante.

The Smithsonian Tropical Research Institute's Bocas del Toro Research Station is on the Bahia Almirante side of Isla Colon. As part of the development of the scientific knowledge base of the station, and as part of the CARICOMP program, various physical and biological features of the surrounding environment have been monitored since 1999. Here we examine these data (1) to develop a baseline to which future studies can be compared, (2) to determine if the recent rapid development of the region has had an effect on water clarity and phytoplankton biomass, and (3) to explore the physical data to understand what factors influence the variation in these parameters.

MATERIALS AND METHODS

Monitoring History

Isla Colon is the site of the Smithsonian Tropical Research Institute's Bocas del Toro Research Station. At its inception in 1998 a long-term physical and biological monitoring program was initiated. Physical records of air and water temperature, rainfall, salinity, solar radiation, and wind speed have been kept since 1999 (reviewed in Kaufmann and Thompson, 2005). Monitoring of Secchi depths and chlorophyll *a* concentrations was conducted approximately biweekly at five sites (see Figure 1) from 1999 until 2001. The sampling intervals were not equal (ranging from 7 to 28 days), so these data were not appropriate for time-series analyses.

The Secchi depths and chlorophyll *a* monitoring was reinitiated at three of these sites and at an additional site in 2006 and continues to be measured weekly. At one of these, the CARICOMP reef monitoring site (described in Guzmán et al., 2005), the Secchi depths have been recorded weekly since 2000. At the CARICOMP seagrass site, horizontal Secchi readings have been taken weekly since 1999. During the entire period, measurements were made by the same three-person team.

Sampling Localities

Sampling sites (Figure 1; Table 1) were chosen in 1999 to include a range of environments. In 2006 sites were chosen to include an onshore–offshore gradient, in which we expected more oceanic conditions on one end and terrestrially influenced conditions on the other end.

- Colon, 6.3 km northeast of Bocas del Toro Town, is the most exposed site. The bottom at 20.5 m is muddy. Rough conditions occasionally made it impossible to take measurements in this location.
- Cristobal, in the middle of the Almirante Bay, is a site 7 km from the mainland and surrounded by patch reefs. The bottom at 25 m is muddy.
- Pastores is a semienclosed bay, 500 m from the mainland. It is more heavily influenced by continental runoff and creek discharge than the other sites. Depth at the sampling site is 26 m but a nearby coral reef slopes from 5 to 16 m. Jellyfishes are abundant at this site.
- Smithsonian Tropical Research Institute (STRI) is the site closest to the Bocas del Toro Research Station, 500 m from the shore. This site serves as the water monitoring site for the CARICOMP reef site, which is onshore of this location, over a reef that slopes from 5 to 20 m. The bottom is muddy and sandy with isolated patches of coral.
- Bottomwood, between Solarte and San Cristobal Islands, is protected from oceanic influence. The sampling site is near mangrove islets, sand cays, and a shallow coral reef. The reef slopes to a fine sand bottom at 16 m.

- Zapatillas has the highest diversity and abundance of coral and octocoral species of any of our sampling sites. The bottom at about 15 m is mostly covered by patch reefs and fine sand.
- The CARICOMP seagrass site is several hundred meters along the shore to the northwest of the Bocas del Toro Research Station. This shallow (2 m depth) location has extensive *Thalassia* cover, and the small bay is fringed by red mangroves.

Hydrological Measures

Water temperature and salinity were recorded with an YSI 85 multiparameter probe (Yellow Springs Instruments, Yellow Springs, Ohio, USA) at the same time and depth as the seawater was sampled. Measurements were taken at approximately 50 cm. Dissolved oxygen was also measured in 2006–2008. Salinity is expressed in the practical salinity scale (PSS) and dissolved oxygen in milligrams per liter.

Climate Records

Rainfall, solar radiation, and wind speed are monitored continuously at the Bocas del Toro Research Station, as described by Kaufmann and Thompson (2005). These measurements are taken close to the STRI site (see Figure 1). For the purposes of this study average rainfall, solar radiation, and wind speed were calculated for 3 days and 6 days before each sampling day. We chose these periods because Beman et al. (2005) showed that phytoplankton blooms can peak 3 to 5 days after nutrient input from terrestrial runoff.

Annual rainfall was obtained in two ways. First, an hourly tipping bucket measured rainfall from 2002. Because data are incomplete for three of the years (including 2008), we calculated the average daily rainfall to standardize across the years. The second estimates were from the Bocas del Toro airport. These records extend to 1999 and were also converted to annual daily averages.

Secchi Depths

Water clarity was measured by lowering a 30 cm diameter Secchi disk into the water until it was no longer seen and then raised until it reappeared. The Secchi depth was measured according to the length of the submerged rope. This operation was repeated three times at each site during each measurement. At the seagrass site the Secchi was measured horizontally, underwater at 0.5 m depth, and was read with a dive mask.

Chlorophyll *a*

Three replicate water samples were collected by hand at 50 cm below the surface in polyethylene bottles and placed in a cooler for the return to the laboratory. Two liters of each replicate were vacuum filtered on Whatman GF/F (0.7 μm pore size). Filters were wrapped in aluminum foil and stored frozen (−20°C). A Teflon pestle was used

TABLE 1. Study site locations and the data available for each site.

Site	Location	Secchi depths	Chlorophyll *a*
Colon	9°22′37″N	1999–2001	1999–2001
	82°12′37″W	2006–2008	2006–2008
Cristobal	9°18′15″N	2006–2008	2006–2008
	82°17′55″W	–	–
Pastores	9°12′36″N	1999–2001	1999–2001
	82°19′37″W	2006–2008	2006–2008
STRI [a]	9°20′40″N	2000–2008	1999–2001
	82°16′39″W	–	2006–2008
Bottomwood	9°17′47″N	1999–2001	1999–2001
	82°13′25″W	–	–
Zapatilla	9°15′27″N	1999–2001	1999–2001
	82°06′19″W	–	–
CARICOMP seagrass	9°21′06″N	1999–2008	–
	82°15′29″W	Horizontal	

[a] STRI, Smithsonian Tropical Research Institute.

to grind the filters in 5 mL 90% aqueous acetone solution. The slurry was transferred to 15 mL polypropylene screw-cap centrifuge tubes and filled to 10 mL with acetone. The tubes were kept in the dark at −20°C for 24 h. Extracts were centrifuged at 3,000 rpm, and the supernatant was analyzed for chlorophyll *a* following the nonacidification fluorometric method (Welschmeyer, 1994).

Statistical Analysis

Correlation analyses and multiple regression analyses were used to describe the relationships between the variables of interest (Secchi depth and chlorophyll *a* concentration) and the hydrological data and the climate data. Student's *t* test, analysis of variance (ANOVA), and analysis of covariance (ANCOVA) were used to test for differences between sites and sampling periods. Because it is likely that there is a lag in the response of phytoplankton to the input of nutrients from river runoff or turbulence, we looked for correlations between Secchi depths or chlorophyll *a* concentrations and the average of rainfall, solar radiation, and wind speed over the previous 3 and 6 days. Because the 3 day and 6 day results did not differ substantively, only the results using the 3 day average are reported here. Because rainfall and cloud cover are patchy on a local scale, we only examined climatic variables for the STRI and CARICOMP seagrass sites. Time-series autocorrelation analyses were applied to Secchi depth and chlorophyll *a* data. The few weeks of missing data were filled with the averages values for the time series under analysis.

RESULTS

A number of complex relationships were demonstrated between the hydrological parameters, Secchi depths, and chlorophyll *a* concentrations at the different sites. Several of these relationships vary among the sites, and there are a number of interactions between factors; however, the following generalizations can be made. (1) Secchi depths increased with temperature, salinity, and solar radiation, and decreased with rainfall, wind speed, and chlorophyll *a* concentration. (2) Correlations between any hydrological characteristic and Secchi depths or chlorophyll *a* were low (r^2 rarely exceeding 0.10) but were higher for all the climatic variables (rain and solar radiation had r^2 up to 0.22). (3) Chlorophyll *a* concentrations showed no consistent temporal or spatial patterns. (4) Secchi depths were not tightly correlated with chlorophyll *a* concentrations. (5) Secchi depths increased and rainfall decreased throughout the study.

Hydrological Conditions at Each Site

Hydrological parameters varied somewhat among the six sites (Table 2, Figure 2). Salinity was significantly different at all sites (ANOVA with post hoc *t* test; Table 2), with the lowest average salinity in Pastores, the most inland site, and the highest average salinity in Colon, the most oceanic site. For 1999–2001 the average temperature at Pastores was significantly higher than the other sites and the temperature at Colon was significantly lower. The temperature

TABLE 2. Summary of physical and biological data from 1999–2001 and 2006–2008.

Site	Years	Temperature, °C (SD)	Salinity,[a] PSS (SD)	Dissolved oxygen, mg/L (SD)	Secchi depth, m (SD)	Chlorophyll *a*, mg/m³ (SD)	Significant changes between periods (*t* test)
Colon	1999–2001	28.1 (1.26)	33.0 (1.70)	–	9.1 (3.6)	0.44 (0.19)	Temperature increased
	2006–2008	28.6 (0.89)	33.5 (1.31)	5.80 (0.43)	10.0 (3.6)	0.47 (0.23)	
Cristobal	2006–2008	28.8 (0.95)	32.9 (1.46)	5.83 (0.49)	12.4 (3.2)	0.46 (0.25)	NA
Pastores	1999–2001	28.6 (1.29)	31.9 (2.15)	–	11.0 (3.3)	0.46 (0.24)	Temperature and Secchi depth increased
	2006–2008	29.2 (0.98)	32.4 (1.76)	5.81 (0.51)	13.2 (3.0)	0.49 (0.28)	
STRI	1999–2001	28.3 (1.16)	32.9 (1.33)	–	10.9 (3.9)	0.37 (0.24)	Temperature and Secchi depth increased
	2006–2008	28.7 (0.91)	33.0 (1.34)	5.78 (0.49)	13.2 (3.6)	0.43 (0.23)	
Bottomwood	1999–2001	28.3 (1.24)	32.7 (1.43)	–	11.9 (3.7)	0.36 (0.19)	NA
Zapatillas	1999–2001	28.3 (1.28)	33.0 (2.78)	–	11.3 (2.6)	0.46 (0.22)	NA

[a] PSS = practical salinity scale.

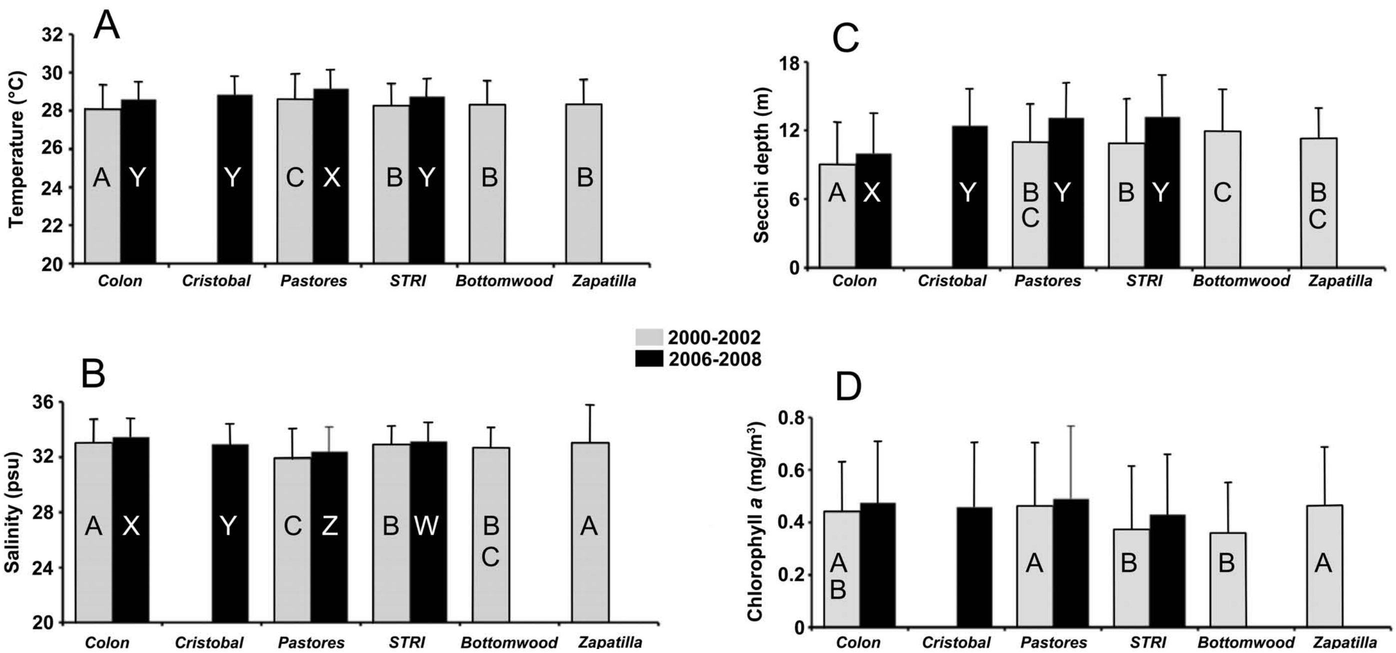

FIGURE 2. Averages of temperature (A), salinity (B), Secchi depths (C), and chlorophyll concentration (D) from the two sampling periods (1999 data excluded). Student's *t* tests showed significant increases in temperature between periods at Colon, Pastores, and STRI and increases in Secchi depth at Pastores and STRI. Single-factor analysis of variance (ANOVA) detected significant ($P < 0.01$) site effects. Significant differences between groups of sites within either sampling period are indicated with letters, so that bars both labeled with "A" are not significantly different from each other but are different from those otherwise labeled with post hoc tests. Specific letters were assigned arbitrarily, but A–C refer to 2000–2002 data and W–Z refer to 2006–2008 data. Bars = one standard deviation (1 SD) of the mean. (Salinity is expressed in the practical salinity scale, PSS.)

at Pastores was also significantly higher than at the other sites in 2006–2008, but there were no significant differences between the remaining sites. Dissolved oxygen did not differ between sites.

Temperature increased significantly between the two time periods at the three sites for which data were available over both periods (*t* test, $P < 0.002$ for each site), despite an overall temperature decrease during the 2006–2008 period. Salinity did not show a significant temporal trend during either time period nor did it differ between the two periods. Dissolved oxygen was only measured for the 2006–2008 period, where it showed no temporal trend. Eight years of data from climatic monitoring at the Bocas Research Station instrument platform shows a downward trend in rainfall, but little change in average solar radiation or average wind speed (Figure 3).

Factors Affecting Secchi Depths

Secchi depths ranged from 2 to 22 m, and the depths varied substantially from week to week (Figure 4). Secchi depths showed significant effects of site, and significant associations with temperature, salinity and chlorophyll *a* concentrations during both the 1999–2001 and 2006–2008 periods (ANCOVA; Table 3). The correlation of any one variable with water clarity was low, with

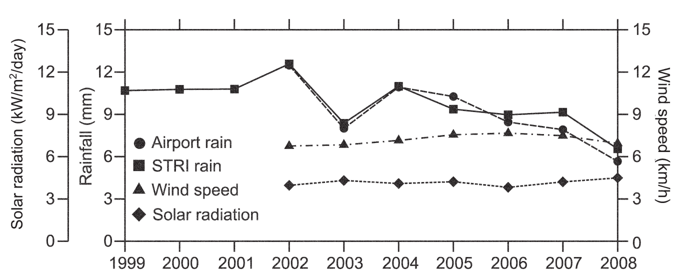

FIGURE 3. Long-term trends in climatic variables. Yearly averages for rainfall, solar radiation, and wind speed during the past 8 years show the decline in average daily rainfall. Daily averages are used because missing data prevent the use of cumulative data. (Rainfall is mm/d.)

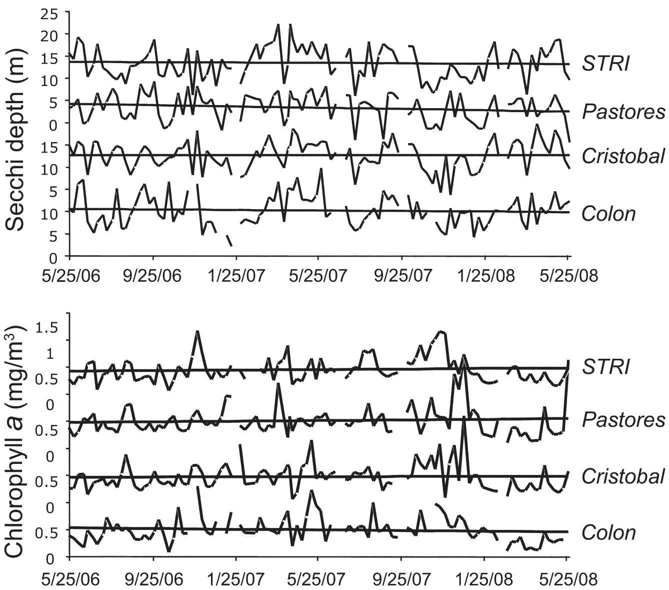

FIGURE 4. Variation in Secchi depths (top graph) and chlorophyll *a* (bottom graph) concentrations over time for the 2006–2008 dataset. Straight line is the trend line of depth or concentration on that date. Superimposed lines show individual variation.

the highest r^2 value for temperature at 0.13–0.17. Secchi depths increased with temperature (Ordinary Least Squares regression [OLS]: 1999–2001, $r^2 = 0.13$, $P < 0.001$; and 2006–2008, $r^2 = 0.17$, $P < 0.001$), and salinity (OLS: 1999–2001, $r^2 = 0.10$, $P < 0.001$; and 2006–2008, $r^2 = 0.06$, $P < 0.001$) and decreased with chlorophyll *a* concentration (OLS: 1999–2001, $r^2 = 0.09$, $P < 0.0001$; and 2006–2008, $r^2 = 0.06$, $P < 0.001$). The average Secchi depth was significantly lower for the exposed Colon site than for the other sites in both time periods (see Table 2, Figure 2). Analysis of the data from the two different periods showed different combinations of interaction effects (see Table 3).

Climatic variables were more tightly correlated with Secchi depth than were the seawater variables. Using the six years of complete climate data from the STRI site, we found that Secchi depths at the STRI site show significant effect of year ($P < 0.0001$), a marginal effect of rainfall ($P = 0.056$), and significant effects of solar radiation ($P = 0.002$) and wind speed ($P < 0.001$), but no significant interactions between these factors. For the CARICOMP seagrass site there was no effect of year, but rainfall and wind speed over the prior 3 days were significant ($P < 0.01$), as well as the interaction between rainfall and solar radiation ($P < 0.0008$). Secchi depth decreased with the amount of rainfall ($r^2 = 0.22$ and 0.23, respectively, with $P < 0.001$) and wind speed ($r^2 = 0.21$; $P < 0.001$) at both sites and increased with solar radiation ($r^2 = 0.21$ and 0.15, respectively, with $P < 0.0001$) at the STRI site but was only significant by its interaction with rainfall in the seagrass site. The interaction at the seagrass site showed that Secchi distances decreased more quickly with rainfall at high levels of solar radiation than at low solar radiation.

Secchi depths increased over the long term: they increased from 1999–2001 to 2006–2008 at Pastores and STRI (*t* test, $P < 0.0001$ for both) but not at Colon. Least squares regression showed a significant increase in Secchi depths ($r^2 = 0.02$; $n = 381$; $P < 0.0002$; slope = 0.3) with date over the 8 years of weekly sampling at STRI. The horizontal Secchi data from the nearby CARICOMP

TABLE 3. Analysis of covariance (ANCOVA) effects of physical variables on chlorophyll *a* concentration and Secchi depth in 1999–2001 and 2006–2008 data after stepwise removal of nonsignificant variables.

Source	*df* [a]	Sum of squares	*F* ratio	*P*
Secchi depth, 1999–2001				
Site	4	235.03	6.78	<0.0001
Temperature	1	100.97	11.65	0.0008
Salinity	1	290.63	33.53	<0.0001
Chlorophyll *a* concentration	1	150.82	17.40	<0.0001
Site*salinity [b]	4	104.02	3.00	0.02
Salinity*temperature [b]	1	67.31	7.76	0.006
Secchi depth, 2006–2008				
Site	3	556.41	21.77	<0.0001
Temperature	1	454.35	53.33	<0.0001
Salinity	1	216.91	25.46	<0.0001
Oxygen	1	2.86	0.33	0.56
Chlorophyll *a* concentration	1	47.15	5.53	0.02
Site*temperature [b]	3	70.34	2.75	0.04
Temperature*oxygen [b]	1	49.58	5.82	0.02
Chlorophyll *a*, 1999–2001				
Site	4	0.38	2.30	0.06
Temperature	1	1.24	30.11	<0.0001
Salinity	1	0.06	1.43	0.23
Site*salinity [b]	4	0.55	3.34	0.01
Salinity*temperature [b]	1	0.31	7.58	0.006
Chlorophyll *a*, 2006–2008				
Temperature	1	0.26	4.90	0.03
Salinity	1	2.41	45.35	<0.0001
Oxygen	1	0.25	4.67	0.03

[a] *df* = Degrees of freedom.
[b] * = Run with only two-way interactions.

seagrass site show no long-term trend. When these values are binned by month, there is a marginal effect of month on the Secchi depths in the seagrass site ($P = 0.07$) and a significant effect of month at the reef site ($P = 0.0007$). Greater Secchi depths were recorded from drier months and sunnier months (Figure 5), a result also found by Kaufmann and Thompson (2005).

Factors Affecting Chlorophyll *a* Concentrations

Chlorophyll *a* concentration varied between 0.04 and 1.66 mg/m^3. Similar to Secchi depths, concentrations varied substantially from week to week and with no clear seasonal component to the variation (see Figure 4). During the first 14 sampling dates of the 1999–2001 study period, chlorophyll *a* concentrations were measured with a spectrophotometer. An ANOVA testing for effects of site and method showed that the results from the spectrophotometer were significantly higher (site: $F = 3.96$; $df = 4$; $P < 0.005$; method: $F = 26.8$; $df = 1$; $P < 0.0001$; $n = 328$). Therefore values obtained from the spectrophotometer were excluded from the subsequent analyses and this dataset included only data from 2000–2001 or 2006–2008.

Although the average chlorophyll *a* concentrations did not differ between the two periods (*t* test, $P > 0.05$), there were different patterns for the two sampling periods. The only common results were that chlorophyll *a* concentration decreased with temperature, and that the variables examined explained no more than 10% of the variance in chlorophyll *a* concentrations. Data from 2000–2001 showed a significant effect of temperature and a marginal effect of site, but no effect of salinity (ANCOVA; see Table 3). There were significant interactions between site and salinity and between site and temperature (Table 3). Overall, chlorophyll *a* concentrations decreased with temperature (OLS: $n = 328$; $r^2 = 0.06$, $P < 0.0001$). Results from 2006–2008 were different: there were significant effects of temperature and salinity, but not of site or oxygen concentration, nor were there significant interactions (Table 3). Chlorophyll *a* concentrations decreased with temperature (OLS: $n = 402$; $r^2 = 0.03$, $P = 0.002$) and salinity ($r^2 = 0.11$, $P < 0.0001$) but these factors explained very little of the variation.

Climate data were poorly linked to chlorophyll *a* concentrations. Average wind speed for the 3 days before sampling was positively correlated with chlorophyll concentration ($r^2 = 0.19$, $P < 0.005$) but this appeared to be caused by a few periods with extremely high winds. Chlo-

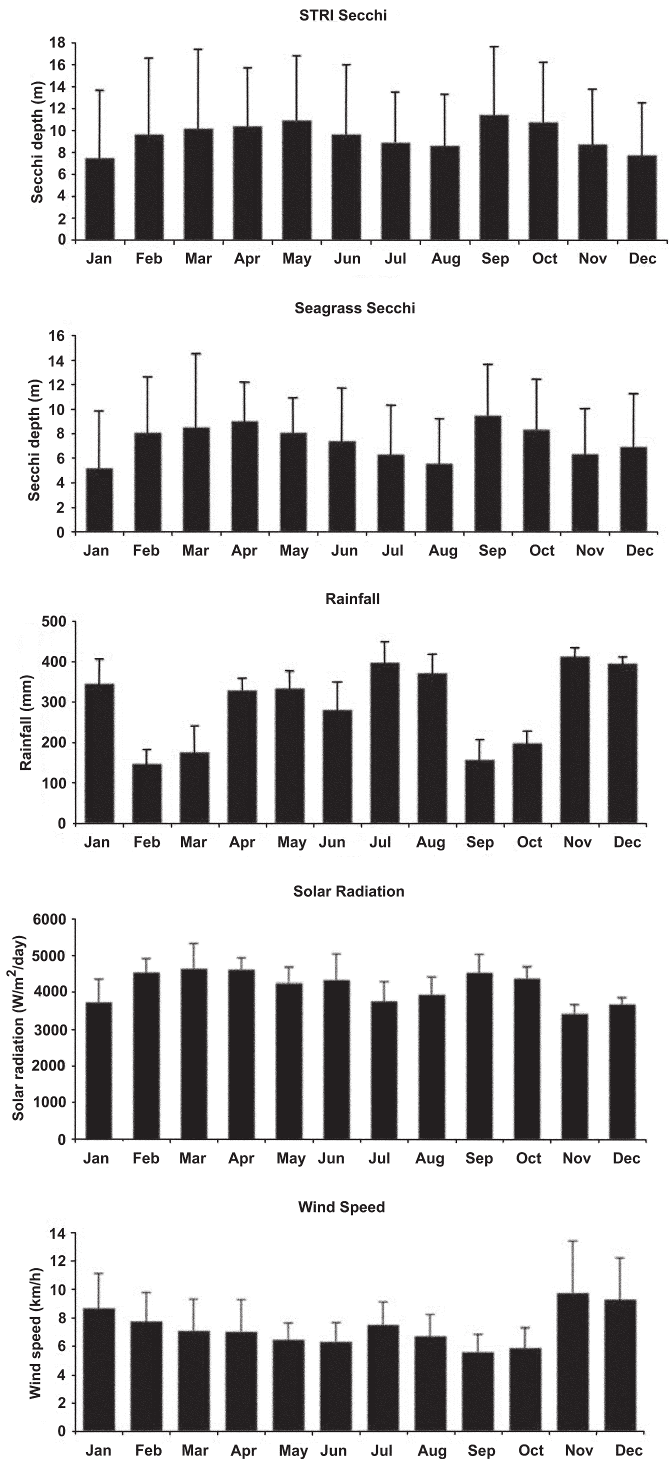

FIGURE 5. Bar graph with monthly averages of Secchi depths, rainfall, solar radiation, and wind speed for the 8-year dataset showing that months with higher average Secchi depths also had lower average rainfall. Bars = 1 SD of the mean.

rophyll *a* concentration was independent of both rainfall over 3 days prior and average solar radiation over the 3 days before the measurements.

Time Series

Both the Secchi depths and chlorophyll *a* concentrations varied considerably from week to week (see Figure 4). To determine if this variation has a temporal autocorrelation, we conducted a time-series analysis. For 1999–2008 Secchi depth is temporally auto-correlated at both the CARICOMP seagrass and the STRI sites (seagrass: Fisher's kappa = 9.9, $P < 0.01$; for coral: Fisher's kappa = 12.2, $P < 0.001$). Over the shorter period, 2006–2008, Secchi depth was temporally auto-correlated at Colon (Fisher's kappa = 8.59, $P < 0.01$), Cristobal (Fisher's kappa = 7.39, $P < 0.02$), and STRI (Fisher's kappa = 6.91, $P < 0.04$) but not Pastores ($P > 0.05$). Chlorophyll *a* concentrations, on the other hand, showed an autocorrelation only for Colon ($P < 0.005$). Examination of the autocorrelation function shows that, over the short term (lag of up to several months), the autocorrelation function appears stationary (Figure 6). However, a peak around the 52 week lag (Figure 6) is evidence of seasonal externally driven periodicity and suggests an annual cycle that is not obvious from plots of the raw data (see Figure 4).

DISCUSSION

The overall values for the data presented here are similar to those reported for the Bahia Almirante by D'Croz et al. (2005), Kaufmann and Thompson (2005), and Carruthers et al. (2005). We report some long-term trends that were not detected by Kaufmann and Thompson, who closely examined the patterns of daily

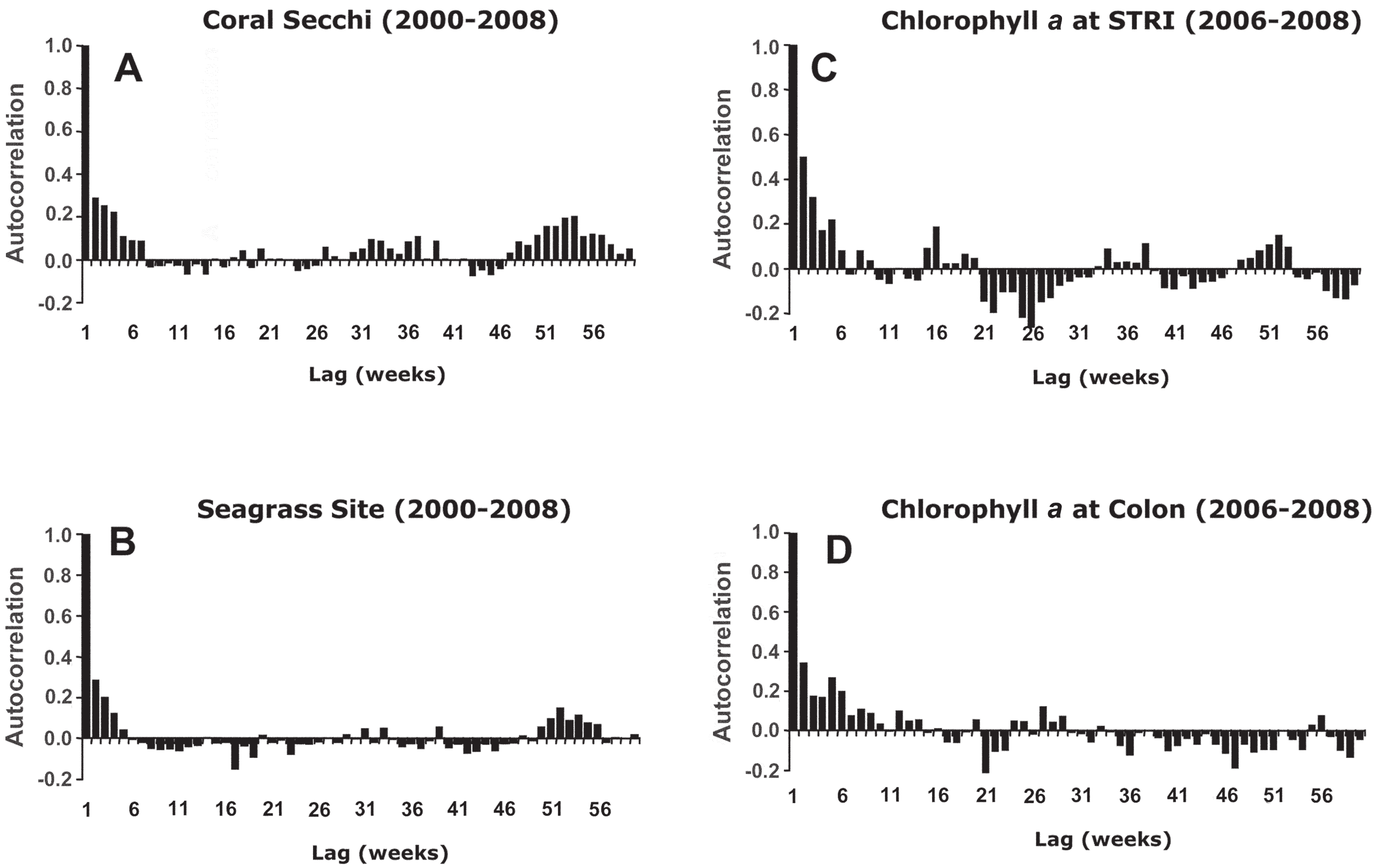

FIGURE 6. Autocorrelation function for 8 years of Secchi data for STRI and CARICOMP seagrass sites and chlorophyll *a* concentrations for 2 years for Colon (significant autocorrelation) and STRI (no significant autocorrelation) sites.

and monthly variation in physical parameters. Comparing the YSI 85 probe measures of temperature and salinity between the 2000–2002 sampling period and the 2006–2008 period, we found significant increases in water temperature and salinity. This finding appears to be associated with the recent trend toward lower rainfall in the region.

Annual rainfall is typically high, in excess of 3,000 mm, in the Bahia Almirante, and the mean freshwater runoff is approximately 1,600 mm per year (IGNTG, 1988). However, average daily rainfall per year dropped from 12.48 mm in 2002 to 7.91 mm in 2007 (see Figure 3). Reduced rainfall likely affected the hydrological conditions in Bahia Almirante, which result from the interaction between river discharge and ocean intrusion (D'Croz et al., 2005). During the 1999–2001 sampling period, rainfall was high and salinity showed the typical increasing trend from Pastores, the site nearest the mainland, to the ocean-exposed sites at Colon and Zapatilla. This pattern in surface salinity is consistent with the expected high dilution at nearshore sites resulting from river discharge into the bay. The inshore-to-offshore salinity gradient was not apparent during the 2006–2008 sampling period, presumably because of the reduction of river discharge and consequent greater influence of salinity from open ocean waters (see Figure 2).

Long-Term Trend in Secchi Depths

The most striking long-term trend we detected was the surprising increase in Secchi disk depths. During the 8 years of monitoring, visibility has increased by 2 m (a rate of 0.25 m/year) for several of the sites. Long-term trends of *decreased* Secchi depths have been reported for monitoring in other areas. For example, in a dataset from the Baltic Sea spanning 77 years, Secchi depths have decreased 0.05 m/year (Sandén and Håkansson, 1996), and a decrease of 0.03 m/year was reported in the Menai Strait in Wales (Kratzer et al., 2003). The few reports of increased Secchi depths were associated with bioremediation or efforts to reduce untreated sewage outfall. For example, Secchi depths increased at 0.05 m/year in Narragansett Bay, Rhode Island, coincident with reductions in anthropogenic total suspended solids (Borkman and Smayda, 1998), as at one of several sampled sites in the Southern California Bight (Convers and McGowan, 1994). Our measures show a much more rapid change in Secchi depths than these previous studies.

The observed changes in Secchi depths were not in the expected direction. A number of complicated, interacting factors can influence water clarity, as measured by Secchi disk, but many of them would indicate a decrease in Secchi depth. The ongoing rapid development of tourism in Bocas del Toro, particularly on Isla Colon, is accompanied by an increase in wastewater input to the Bahia Almirante. Changes in Secchi readings can reflect changes in particulate matter (from runoff or wind-induced turbidity) but can also be caused by changes in phytoplankton biomass or yellow pigments (mostly humic and fulvic acids) in the water. Deforestation and coastal development can affect all three of these factors. Inputs from untreated wastewater as well as runoff from deforested areas can increase the nutrients, particulate matter, and yellow pigments in the water. In addition, increased nutrients often lead to increased primary productivity, which can result in higher standing phytoplankton biomass. These anthropogenic effects have been increasingly affecting coral reef habitats throughout the Caribbean, where wastewater disposal is the leading cause for eutrophication and decreased water clarity (Szmant, 2002). We had expected to see a long-term reduction in water clarity as a result of similar changes in Bocas del Toro.

Secchi depth is often strongly correlated with chlorophyll *a* concentration and has been used as a proxy for productivity in highly seasonal upwelling zones or temperate lakes. This method is often favored because it is cheaper, faster, and easier to obtain than a quantification of chlorophyll *a* concentration. Sandén and Håkansson (1996) reviewed four studies as well as their own data that showed a relationship between Secchi depths and chlorophyll *a* concentrations. The relationships are reported as power functions and show chlorophyll *a* to scale with Secchi depth to the 1.47–2.6 power. Megard and Berman (1989) showed that the proportion of light attenuation caused by chlorophyll concentration differed between neritic and pelagic seawater, but there were clear relationships nonetheless. Here we found that chlorophyll *a* concentration explained only 6%–9% of the variance in Secchi depths. In addition, mean chlorophyll *a* concentrations were relatively low in the Almirante Bay, near 0.5 mg m^{-3}, which is the suggested threshold value for oligotrophic conditions required for coral reef development (Bell, 1992). Therefore, these measures are not consistent with the presence of phytoplankton blooms resulting from anthropogenic nutrient enrichment. They do, however, suggest that even small increases in nutrients or chlorophyll *a* concentrations in this region could result in a shift from coral-dominated to algal-dominated benthic communities.

It seems unlikely to us that there has been a drop in the load of anthropogenic suspended solids and/or nutrients during the past eight years, despite the probable decrease in the volume of runoff. In fact, it appears that, if anything, these inputs have increased. So, what is the cause of the long-term trend in Secchi depth? The correlation analysis and the monthly trends (see Figure 5) both suggest that rainfall and solar radiation are the most closely associated with Secchi depth. However, rainfall is the only variable showing a strong annual trend consistent with the increased Secchi depths, and rainfall over the three days before the measurements was the variable most highly correlated with Secchi depths of any hydrological or climate variable examined. Solar radiation, although it is positively correlated with Secchi depths on the reef, does not show the pronounced long-term trend that rainfall does. The effect of wind on Secchi depth similarly does not explain the long-term trend. It could, however, explain the fact that Colon, the most exposed site, with the highest winds had consistently lower Secchi depths than the other sites. Wind-induced turbidity, which resuspends bottom sediment, is the likely cause of the limited water clarity at this site.

CONCLUSION

The baseline data reported here will be useful for future studies of anthropogenic effects in the unique Bocas del Toro archipelago. Rapid local development is progressing in the face of little information on the impact of such development and the factors affecting such impacts (e.g., water residence time or currents in the Bahia Almirante). It is likely that anthropogenic inputs of nutrients and suspended particulate matter will contribute to eutrophication of some areas. This study suggests that despite the impact of development, patterns of water clarity and chlorophyll *a* concentrations in the region are currently driven mainly by large-scale climate patterns. There is little evidence of a tight relationship between these measures and features of the local water mass, nor is there evidence of eutrophication at the sites we sampled. Future sampling closer to highly developed areas is necessary to document and monitor the impact of development on water quality.

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