Lagoon Scale Processes in a Coastally Influenced Caribbean System: Implications for the Seagrass *Thalassia testudinum*

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ABSTRACT.—The Bocas del Toro archipelago in the Caribbean sea on the northwest coast of Panama has high annual rainfall (>3000 mm) and a mountainous watershed, resulting in high inflow of fresh water. The two main lagoons have different geologic structure and different inputs; while Bahía Almirante has carbonate sediment and a relatively small watershed, Laguna de Chiriquí has predominantly siliclastic sediment and a very large watershed. The region also has a long history of clearing and agriculture. The purpose of this research was to use the seagrass *Thalassia testudinum* as a bio-indicator of nutrient status of these lagoons, particularly to assess the extent and influence of mainland inputs of freshwater, nutrients and sediments. Leaf tissue nitrogen and phosphorus, as well as surface water quality and porewater nutrients, were measured from 32 sites throughout the archipelago. The Bocas del Toro archipelago showed clear but relatively small differences in these parameters between the carbonate, moderate freshwater input Bahía Almirante and the siliclastic, high freshwater input Laguna de Chiriquí. No evidence of a mainland to offshore (Cayos Zapatillos) gradient in nutrient status was observed in *T. testudinum* meadows. Leaf tissue nitrogen (ca. 2.4%) and phosphorus (ca. 0.25%) as well as chlorophyll *a* concentrations were high throughout the archipelago and higher than many tropical seagrass dominated ecosystems of the Caribbean. It is likely that this is partly a result of the mountainous, volcanic watershed and high rainfall, but the influence of extensive agriculture and land clearing has yet to be explicitly determined.

KEYWORDS.—Nitrogen, phosphorus, sediment, nutrient processes, Bocas del Toro, Panama

INTRODUCTION

The Bocas del Toro archipelago, located on the northwest Caribbean coast of Panama, is bounded on the southwest by the convoluted mainland of Bahía Almirante and Laguna de Chiriquí with an outer lagoon adjacent to the Caribbean Sea that is bounded by the Cayos Zapatillos (Fig. 1). The archipelago contains hundreds of small mangrove cays and seven large forested islands of mostly terrigenous origin, some of which form the northeast boundary of the archipelago (Guzmán and Guevara 1998a). Abundant islands, mangrove cays and coral reefs within the Bocas del Toro archipelago create numerous shallow, calm lagoons that, in combination with a supply of nutrients from river inputs, result in large areas that are ideal habitat for seagrass meadows.

The dominant seagrass throughout the archipelago is *Thalassia testudinum*, growing on a wide range of sediment types. Composition of sediments supporting seagrass meadows ranges from 99% carbonate to 73% siliclastic, organic content ranges from 49% to less than 1% organic content and sediment grain size ranges from mostly granule and pebbles to sediments with a high percentage of fine sand, silt and clay (Barnes and Carruthers unpublished data). The sediments in the region are comprised of a mixture of ancient tropical deep-bed marine sediments (20 million years old), igneous and sedimentary rock from abundant volcanic activity (10-16 million years old) and more recent coral reef for-
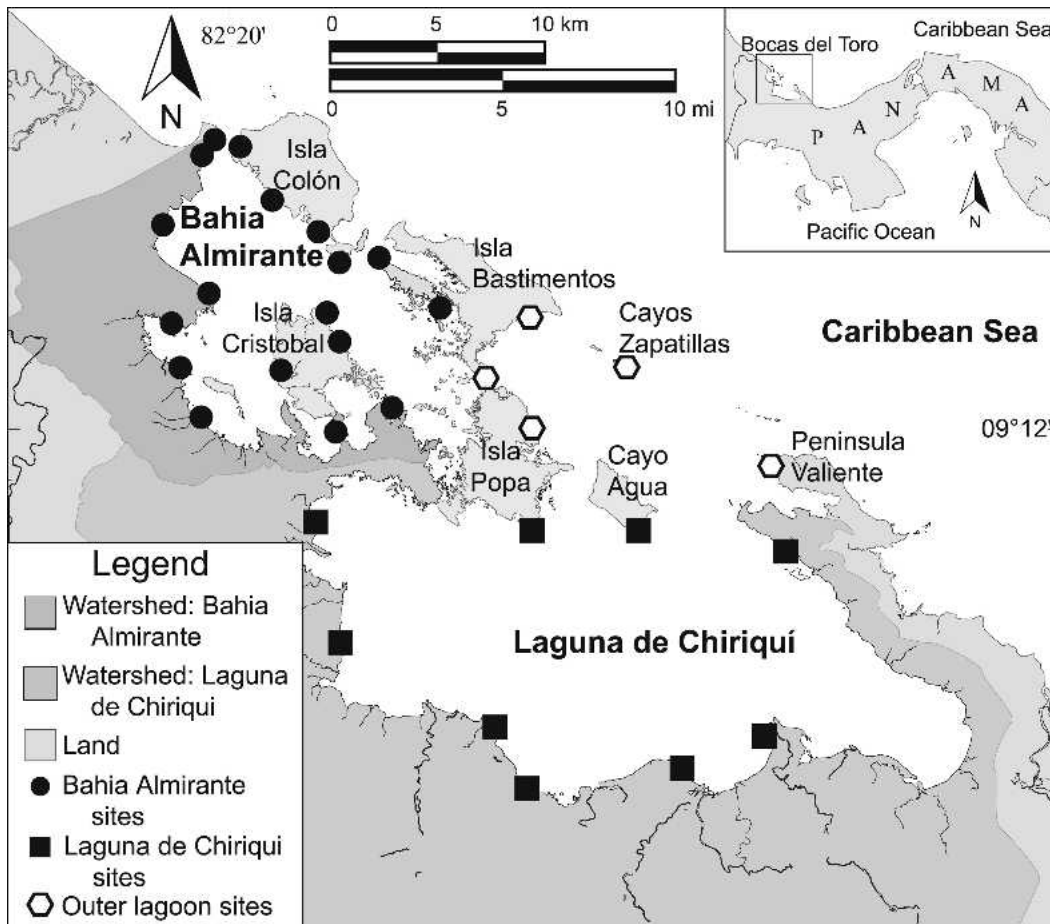
FIG. 1. Location of sampling sites throughout Bocas del Toro archipelago, divided into the three main water bodies.

mation including the two coral atolls, the Cayos Zapatillos (Coates and Jackson 1998). While the Bahía Almirante and outer lagoons are Neogene sedimentary basins, most of the Laguna de Chiriquí and its watershed are pre-Pleistocene undifferentiated volcanic rock (Coates and Obando 1996).

The watersheds of the Bocas del Toro archipelago have historically been used for subsistence agriculture, as well as intensive banana plantations on both the mainland and larger islands between 1820 and 1920, and an expansion of cacao farming from 1920-1980 (Heckadon-Moreno 1997). The decline of each of these major crops has been caused by disease, with the most recent being the *Monilia* fungus that has led

to a reduction in cacao production. There has been a corresponding increase in timber extraction and cattle rearing in the Bocas del Toro archipelago (Heckadon-Moreno 1997).

The lagoons of the Bocas del Toro archipelago are highly influenced by river flow from the mainland and have low flushing rates. The archipelago has high rainfall, with annual mean rainfall being 3.3 m between 1972 and 1983 (Phillips et al. 1997), and is surrounded by mountains from 50 to 400 m located within 3 km of the coast (Guzmán and Guevara 1998a). The result is frequent and abundant inflow of freshwater through a series of large and small rivers and wetlands into the coastal regions of the archipelago. Although the watersheds

of both Laguna de Chiriquí and Bahía Almirante contain high mountains resulting in rapid delivery of rainfall to the archipelago, the watershed of Laguna de Chiriquí is much larger with a greater number of larger rivers and thus has greater potential for river inflow. Consequently, Laguna de Chiriquí and Bahía Almirante are defined as high and intermediate runoff, respectively (Guzmán and Guevara 2002). Bahía Almirante has three channels that allow flushing from the Caribbean sea, while Laguna de Chiriquí has two very large openings to the Caribbean sea (Fig. 1). However, the tidal range in this region is small (<0.5 m), current flow is generally slow (Glynn 1972; Ballou et al. 1989), and the archipelago is outside the hurricane belt, so flushing is limited and the system has thus been described as semi-lagoonal (Guzmán and Guevara 1998a).

To assess broad scale system patterns, this paper summarizes patterns in water column and sediment characteristics within seagrass meadows in the three main water bodies in the Bocas del Toro archipelago (Bahía Almirante, Laguna de Chiriquí and the outer lagoon). Specifically, the following questions were addressed for *T. testudinum* meadows in these three lagoons: Were there differences in water quality and sediment type between the three lagoons with varying river inflow?; Did nutrient status of the *Thalassia testudinum* meadows reflect variations in water column and sediment characteristics between lagoons with different river inflow?; What inferences could be drawn with regard to system dynamics from observed patterns and relationships in water column, sediment and seagrass parameters?

MATERIALS AND METHODS

Study site

The Bocas del Toro archipelago is located on the northwest Caribbean coast of Panama. The region is divided into Bahía Almirante in the north and Laguna de Chiriquí in the south (Fig. 1). In addition, there is an outer lagoon between Valiente Peninsula, the Cayos Zapatillos and Isla Bastimentos. The archipelago is approximately 60 km along the coast and 40 km wide from the mainland shoreline, located north to south from 9°25′05.6″ N to 8°56′23.1″ N and east to west from 82°23′00.2″ W to 81°55′10.5″ W.

Sampling

Between 18 February and 1 March 2003, 32 sites were sampled throughout the Bocas del Toro archipelago (Fig. 1). Sites were chosen in continuous seagrass meadows greater than 50 m by 50 m and at a water depth of approximately 1.5 m, where possible. Sites were chosen to represent a diversity of carbonate and siliclastic sediments and also to include areas influenced by the outflow from major rivers. Sampling was carried out during an unusually long period of low rainfall (Fig. 2) and no major rainfall events occurred during sampling.

Water column samples.—At each site, salinity, temperature, pH and dissolved oxygen (DO) were measured 10 cm below the surface using a WTW Multi 340i probe. Secchi depth was measured, and three 2-liter water samples were taken from 0.5 m below the surface for later determination of total suspended solids (TSS) following the method of Erftemeijer and Koch (2001). Three additional 2-liter water samples were taken for later chlorophyll determination. Chlorophyll samples were stored on ice in the dark, filtered immediately on return to the laboratory through 0.45 μm cellulose acetate membrane filters and frozen before
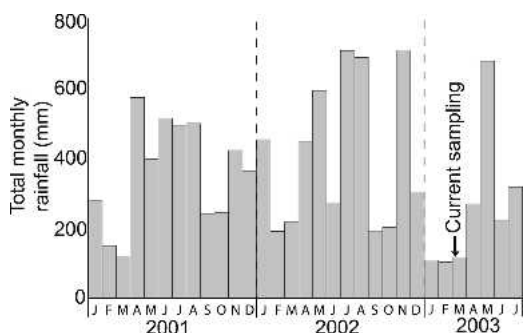

FIG. 2. Total monthly rainfall (mm) at Bocas del Toro airport on the south end of Isla Colón, current sampling date is indicated.

analysis using 90% acetone extraction and spectrophotometry (Jeffrey and Humphrey 1975).

Sediment samples.—At each site, three sediment core samples (10 cm diameter and 10 cm deep) were taken haphazardly at least 5 m apart. Samples were maintained on ice until they could be frozen upon return to the lab. After drying at 60°C for 4 days, sediment aggregates were broken up and subsamples taken for grain size analysis and sediment composition. For grain size analysis, a sample of 10 g was placed into a tower of sieves with the following mesh sizes from 0.063, 0.13, 0.25, 0.5, 1.0 and 2.0 mm. Following shaking, the sediment sample fraction retained on each sieve was weighed separately. For sediment composition, a 10 g subsample was weighed and then treated with concentrated HCl to remove carbonates, rinsed and placed in a 60°C oven until dry. After reweighing, the dried sample was heated in a muffle furnace to 600°C for 10 hours to remove organics, leaving the silicate portion (Barnes 1994). Percent composition of the sediment samples was then determined as carbonate, mineral (largely siliclastics) and organic components.

Six sediment core samples of 5 cm diameter and 2 cm depth were taken at each site, at least 1 m apart, for determination of chlorophyll attributable to benthic microalgae. These samples were immediately stored on ice in the dark and frozen on return to the lab, before using acetone extraction and a spectrophotometer to determine chlorophyll (Granger and Iizumi 2001), using the equations of Jeffrey and Humphrey (1975).

Sediment porewater samples.—Lysimeters (McGlathery 1992) were used to collect porewater at each site. Each lysimeter was purged with water column water and then placed into the sediment so that the sampling ports were at 5 cm depth into the sediment. Twenty milliliters of porewater was then immediately drawn through and discarded to purge the lysimeter, followed by collection of a 60 mL sample. Porewater samples were kept frozen until immediately prior to analysis for PO_4^{3-}, NH_4^+ NO_2^- and NO_3^- using an Alpkem Flow Solution IV (O-I Analytical).

Seagrass samples.—At each site, seven shoots were sampled from three areas at least 5 m apart. Evidence of fish grazing was recorded when observed. Shoots were stored on ice, and then scraped of epiphytes and dried at 60°C before grinding in a mortar and pestle (Anderson and Fourqurean 2003). Subsamples of approximately 3 mg were weighed into tin capsules and used for stable isotope analysis using a Europa Hydra 20/20 continuous flow IRMS. The remaining ground tissue sample was used for analysis of CHN and P. Tissue nutrients were analyzed using a CHN analyzer (Fisons NA1500). Dry oxidation and acid hydrolysis extraction followed by colorimetric analyses were used to determine phosphate concentration of the extract (Fourqurean et al. 1992a). Elemental content of leaf tissue was calculated on a dry weight basis and elemental ratios on a molar basis. Algal epiphytes were classified according to functional groups (Steneck and Dethier 1994) and epiphyte cover was recorded using a Braun-Blanquet scale (Sidik et al. 2001). At all sites with an appropriate depth gradient, the water depth at the deepest edge of the seagrass meadow was recorded as an estimation of Maximum Depth Limit (MDL) (Carruthers et al. 2001; Dennison et al. 1993).

Data analyses

To assess potential patterns in water quality between the three water bodies, ordination analysis was performed on chlorophyll *a*, Secchi depth, pH, salinity, temperature, dissolved oxygen, phosphate, ammonia, nitrite, nitrate and total suspended solids. Data were range standardized and the Bray–Curtis association measure was used to produce a distance matrix. Non-metric multidimensional scaling (non-metric MDS) was used to produce an ordination of the distance matrix, using PATN (Belbin 1993). Analysis was performed in three dimensions with 10 random starts, and the resulting ordination had an acceptable stress level (0·15) (Clarke and Warwick 1994). To assess which of the physical variables were influencing patterns in the non-metric MDS, principal axis correlation

(PCC) was carried out. Principal axis correlation determines the direction and correlation coefficient of the best fit of each variable used in the ordination to the summary variables in ordination space (Belbin 1993). The significance of differences in water quality between water bodies was assessed using ANOSIM analysis on Primer (Clarke and Warwick 1994), a non-parametric procedure that uses permutations of the calculated similarity matrix to test *a priori* pairwise comparisons (Clarke and Warwick 1994).

One-way ANOVAs were used to test for statistically significant differences in seagrass epiphytes, and sediment parameters between the three water bodies. Homogeneity of variances was checked using Cochran's test (Winer 1971) and in all cases variances were homogenous. Tukey's test was used to assess the nature of significant differences between lagoons (Winer 1971). Grain size data was log(x+1) transformed as variances were proportional to the means. Sediment composition and *T. testudinum* tissue CNP data represent percentages and nutrient ratios such that parameters within each of these data groups are dependent on each other. As a result, a Bonferroni correction was applied to the significance value for analyses on these parameters ($\alpha/3$ i.e., significance determined as $p < 0.0167$).

RESULTS

Water quality, phytoplankton, and epiphytes

Water quality was generally higher in Bahía Almirante than in Laguna Chiriquí, while the outer lagoon was generally intermediate or highly variable for all parameters. Surface salinity (35.3‰ BA; 30.7‰ LC), temperature (29.5°C BA; 29.0 LC), pH (8.01 BA; 7.85 LC), Secchi depth (5.93 m BA; 3.14 LC), NH_4^+ (0.25 µM BA; 0.20 LC) and NO_3^- (0.19 µM BA; 0.14 LC) were all higher in Bahía Almirante than Laguna de Chiriquí (Table 1). However, total suspended solids (17.0 mg L^{-1} BA; 19.8 LC) and chlorophyll *a* (0.72 µg L^{-1} BA; 1.92 LC) were greater in Laguna de Chiriquí than Bahía Almirante. While mean total suspended solids and chlorophyll *a* were greatest in the outer lagoon (24.1 mg L^{-1} and 2.55 µg L^{-1}, respectively), this water body was highly variable between sites (e.g., minimum of 13.8 mg L^{-1} and 0.62 µg L^{-1}, respectively). No differences in water column phosphate, nitrite or dissolved oxygen were detected between water bodies (Table 1).

Based on the combined water quality axes, Bahía Almirante was different from Laguna Chiriquí, while the outer lagoon could not be differentiated from either of the other two water bodies (Fig. 3A). ANOSIM analysis confirmed that Bahía

TABLE 1. Comparison of water quality parameters between the three major water bodies of the Bocas del Toro archipelago (± standard errors); correlation coefficient values indicate correlation of each original variable to the MDS summary variables in ordination space (Fig. 3).

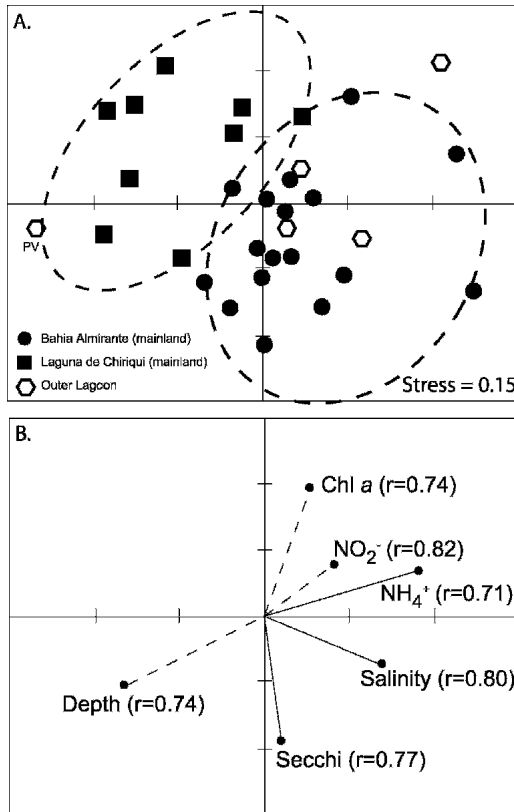| Parameter	Bahía Almirante	Laguna de Chiriquí	Outer Lagoon	Correlation coefficient
NH_4^+ µM	0.25 (0.02)	0.20 (0.01)	0.26 (0.02)	0.709
NO_3^- µM	0.19 (0.03)	0.14 (0.02)	0.21 (0.01)	0.654
Salinity ‰	35.3 (0.05)	30.7 (1.63)	34.9 (1.13)	0.803
Temp (°C)	29.5 (0.23)	29.0 (0.05)	28.8 (0.38)	0.572
pH	8.01 (0.03)	7.85 (0.06)	7.93 (0.13)	0.566
Secchi (m)	5.93 (0.72)	3.14 (0.61)	4.14 (1.41)	0.769
TSS mg L^{-1}	17.0 (1.04)	19.8 (1.15)	24.1 (6.85)	0.686
Chl *a* µg L^{-1}	0.72 (0.14)	1.92 (0.30)	2.55 (1.40)	0.739
PO_4^{3-} µM	0.13 (0.02)	0.14 (0.06)	0.10 (0.01)	0.584
NO_2^- µM	0.06 (0.00)	0.06 (0.02)	0.07 (0.01)	0.817
Depth (m)	1.82 (0.16)	1.78 (0.15)	1.84 (0.37)	0.735
DO mg L^{-1}	7.76 (0.42)	8.36 (0.26)	7.83 (0.50)	0.673
n	18	9	5	

FIG. 3. Non-metric MDS of 31 sites throughout Bocas del Toro archipelago, based on water quality characteristics. A: MDS plot, dotted lines indicate approximate Bahía Almirante and Laguna de Chiriquí groupings (PV indicates the site on the tip of Peninsula Valiente; Fig. 1). B: vector plot of Principal Axis Correlations for highly correlated variables in MDS (correlation coefficients presented in brackets). Solid lines indicate variables with greatest influence on separating the two lagoons in the MDS.

of the outer lagoon sites grouped with Bahía Almirante while one grouped with Laguna de Chiriquí (Fig. 3A). The site grouping with Laguna de Chiriquí was on the tip of the Valiente Peninsula (Fig. 3A.—PV, 1). High correlation values for principal axis correlation suggest that Secchi depth, salinity and water column NH_4^+ resulted in the distinct groupings between the two water bodies, and values for all variables were generally higher in Bahía Almirante than in Laguna de Chiriquí (Fig. 3B, Table 1). While site depth, chlorophyll a and NO_2^- were highly correlated to spread in the ordination plot, this was attributed to variation between sites within the water bodies, as the direction of these vectors was generally perpendicular (top right to bottom left) to the axis of separation between the water bodies (top left to bottom right) (Fig. 3A, B).

Epiphytic algae

Mean epiphyte cover was consistently 5-20% in all water bodies (Table 2), although there was high variability between sites, with cover ranging from 0-5% along much of the mainland to 35-50% on the south of Cayo Agua (Fig. 4). The percentage of shoots with filamentous epiphytes was lowest in the outer lagoon (2%) and significantly greater in Laguna de Chiriquí (54.4%, Table 2). In Bahía Almirante, the percentage of shoots with filamentous epiphyte cover was intermediate (30.9%) and not significantly different to the other two water bodies (Table 2). Benthic microalgae ranged from 28 to 233 mg m^{-2}, with high variation between sites within all water bodies (Table 2). Grazing on *Thalassia testudinum* leaf blades was observed at six sites, five of which were in Bahía Almirante and one on the western shore of Laguna de Chiriquí (Fig. 4).

Almirante and Laguna de Chiriquí were significantly different (p = 0.001), while the outer lagoon was not significantly different to Bahia Almirante or Laguna de Chiriqui (p = 0.159 and p = 0.245 respectively). Four

TABLE 2. Comparison of epiphytes and benthic microalgae between lagoons, means (± standard errors); significance indicates results of 1-way ANOVAs and letters indicate results of Tukeys post-hoc analysis.

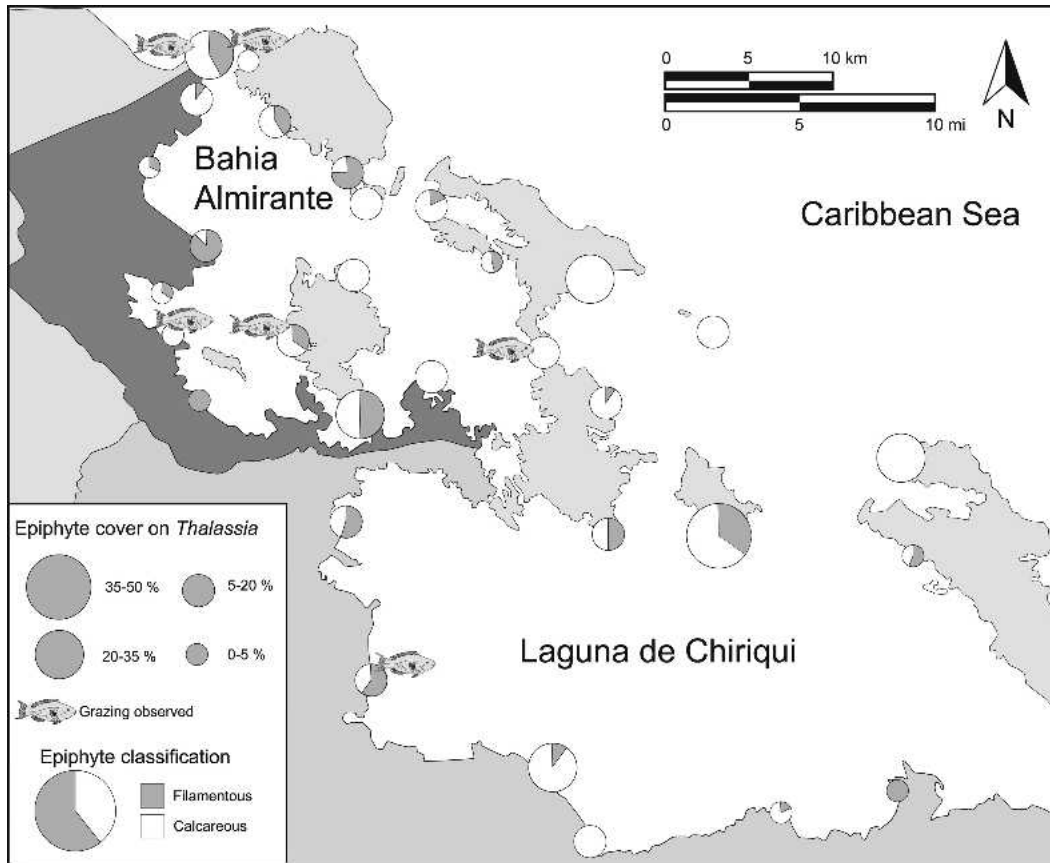| Parameter	Bahía Almirante	Laguna de Chiriquí	Outer Lagoon	Significance
Mean epipyte cover (%)	5-20	5-20	5-20	
Filamentous epiphytes (%)	30.9 (7.5)[ab]	54.4 (13.1)[a]	2.0 (2.0)[b]	$p < 0.05$
Calcareous epiphytes (%)	69.7 (9.3)	71.1 (11.6)	98.0 (2.0)	ns
Benthic microalgae (mg m^{-2})	74 (13)	89 (14)	84 (15)	ns
Range of BMA (mg m^{-2})	28-233	31-128	44-128	

FIG. 4. Epiphyte abundance and composition on *Thalassia testudinum* leaves throughout the Bocas del Toro archipelago; sites with evidence of fish grazing also indicated.

Sediment type and porewater nutrients

Porewater PO_4^{3-} levels were not significantly different between the three water bodies, with mean (± standard errors) ranging from 0.37 (± 0.04) µM to 0.62 (± 0.09) µM (Table 3). Mean porewater NH_4^+ concentrations ranged from 1.38 (± 0.30) µM to 3.50 (± 0.80) µM. Porewater NH_4^+ was significantly higher in Laguna de Chiriquí

TABLE 3. Sediment structure and porewater nutrients by water body in Bocas del Toro archipelago, means (± standard errors). Significance values indicate results of 1-way ANOVAs and letters indicate results of post-hoc Tukeys tests.

		Bahía Almirante	Laguna de Chiriquí	Outer Lagoon	Significance
Porewater	PO_4 µM	0.62 (0.09)	0.60 (0.11)	0.37 (0.04)	ns
	NH_4^+ µM	1.38 (0.30)[a]	3.50 (0.80)[b]	1.53 (0.28)[ab]	$p < 0.05$
Sediment structure	% carbonate	74.4 (6.30)[b]	28.4 (10.3)[a]	92.6 (2.90)[b]	$p < 0.01$
	% silicate	21.6 (5.90)[b]	68.9 (10.3)[a]	5.5 (2.70)[b]	$p < 0.01$
	% organic	4.2 (1.60)	2.8 (0.60)	1.9 (0.04)	ns
Sediment size	Geometric mean (mm)	0.57 (0.09)	0.27 (0.06)	0.60 (0.14)	$p < 0.05$
Sediment type		Coarse sand	Medium sand	Coarse sand	

than in Bahía Almirante, while in the outer lagoon it was not significantly different from either of the other two bays. In terms of sediment composition, percentage carbonate was significantly lower in Laguna de Chiriquí than either Bahía Almirante or the outer lagoon; sediment percentage carbonate in the latter two water bodies was not significantly different (Table 3).

Both Bahía Almirante and the outer lagoon sediments have high carbonate content, with mean percentages of 74.4 (± 6.3) and 92.6 (± 2.9), respectively. Results of analyses on the siliclastic content of the sediments revealed that while percent mineral was low and not significantly different in Bahía Almirante (21.6 ± 5.9) and the outer lagoon (5.5 ± 2.7), Laguna de Chiriquí sediments (68.9 ± 10.3) were significantly higher than either Bahía Almirante or the outer lagoon (Table 3). There was no significant difference in sediment organic content. Mean sediment grain size was smaller in Laguna de Chiriquí than either of the other two water bodies. Significant differences in mean grain size between bays were detected by ANOVA, but not by the less powerful Tukey's test (Table 3).

Thalassia testudinum meadows

Mean shoot densities in the three water bodies range from 277 (± 29) m^{-2} to 305 (± 23) m^{-2} and ANOVAs revealed no significant differences between Bahía Almirante, Laguna Chiriquí or the outer lagoon (Table 4). Similarly, seagrass tissue δ^{15}N levels, ranging from 2.45‰ (± 0.44) to 3.58‰ (± 0.24) showed no statistically significant differences between the three water bodies (Table 4). Seagrass maximum depth limit was higher in Bahía Almirante and the

outer lagoon than in Laguna de Chiriquí, although it was not possible to compare these statistically due to the small number of sites appropriate for measuring maximum depth limit (Table 4).

In each of the water bodies, mean values of seagrass leaf carbon (%C) and nitrogen (%N) ranged from 31.5 (± 0.54) to 33.4 (± 0.90) for %C and 2.38 (± 0.13) to 2.46 (± 0.13) for %N (Table 5). ANOVAs revealed no statistically significant differences in tissue %C or %N for seagrasses from the three water bodies. Percent phosphorus (%P) in seagrass leaf tissue from the three water bodies ranged from 0.21 (± 0.01) to 0.27 (± 0.02). Percent P in seagrass leaf tissue from Laguna Chiriquí was significantly lower than %P in seagrasses from Bahía Almirante or from the outer lagoon; %P in seagrass leaf tissue from the latter two water bodies was not significantly different (Table 5). These results are reflected in the tissue nutrient ratios, with C:N ratios showing little variation between the three water bodies (Table 5), while C:P and N:P ratios showed the same significant differences as the %P data. Both C:P and N:P ratios were significantly higher for seagrass tissues from Laguna Chiriquí than those from either Bahía Almirante or the outer lagoon. The seagrass tissue N:P ratios from the latter two water bodies were not significantly different (Table 5).

DISCUSSION

The Bocas del Toro archipelago shows clear differences between the carbonate-based, moderate freshwater input Bahía Almirante and the siliclastic-based, high freshwater input Laguna de Chiriquí. How-

TABLE 4. δ^{15}N and shoot density of *Thalassia testudinum* (shoots m^{-2}) as well as maximum depth limit (MDL) of *T. testudinum*.

| | Density | | | | |
	Mean (SE)	Max	Min	MDL (SE)	δ^{15}N ‰ (SE)
Bahía Almirante	277 (29)	450	30	4.32 (1.46)	3.19 (0.25)
Laguna de Chiriquí	292 (54)	490	45	2.13 (0.63)	2.45 (0.44)
Outer Lagoon	305 (23)	355	255	3.70 (−)	3.58 (0.24)
significance	ns				ns

TABLE 5. *Thalassia testudinum* leaf tissue nutrient concentrations by water body. Significance indicates results of 1-way ANOVAs and letters indicate results of Tukeys post-hoc analysis.

	C (%)	N (%)	P (%)	C:N	C:P	N:P
BA	31.5 (0.54)	2.46 (0.07)	0.26 (0.01)[a]	15.1 (0.39)	313.9 (7.1)[a]	20.9 (0.47)[a]
LC	32.6 (0.76)	2.38 (0.13)	0.21 (0.01)[b]	16.4 (0.96)	419.1 (23.5)[b]	25.7 (0.76)[b]
OL	33.4 (0.90)	2.45 (0.14)	0.27 (0.02)[a]	16.0 (0.69)	326.8 (28.6)[a]	20.3 (0.87)[a]
sig	ns	ns	$p < 0.001$	ns	$p < 0.001$	$p < 0.001$

ever, using the widely distributed seagrass *Thalassia testudinum* as a bioindicator of integrated nutrient status, no evidence was measured of a mainland to offshore (Cayos Zapatillos) gradient in nutrient status. Small differences were measured in nutrient status of *T. testudinum* between Bahía Almirante and Laguna de Chiriquí, but in a regional context, leaf tissue nitrogen and phosporus content were very high throughout the whole archipelago. Relatively high chlorophyll *a* concentrations and seagrass leaf tissue nutrient content suggest that this system has higher nutrient availability than many other tropical, seagrass-dominated ecosystems of the Caribbean. It seems likely that the high nutrient availability is partly a consequence of large volumes of runoff from the mountainous, volcanic watershed. Whether the recent history of agriculture and land clearing has increased nutrient availability in this system to the detriment of seagrass communities in Bocas del Toro archipelago has yet to be explicitly demonstrated. However, it is known that the coral community of the archipelago has undergone a major shift from *Porites* spp. to *Agaricia tenuifolia* in recent decades and this shift was hypothesized to be related to a reduction in water quality (Aronson et al. 2004).

Water quality and epiphyte patterns in the Bocas del Toro archipelago

Water quality measurements in shallow seagrass habitats in Bocas del Toro archipelago demonstrated that Laguna de Chiriquí and Bahía Almirante were significantly different from each other. Laguna de Chiriquí had lower salinity, lower pH and Secchi depths, with higher total suspended sediments, all consistent with higher over-all river flow into this lagoon. While water column dissolved inorganic nitrogen in Laguna de Chiriquí was lower than Bahía Almirante, high chlorophyll *a* suggests that water column nutrients in Laguna de Chiriquí are rapidly taken up by phytoplankton populations. O'dea and Jackson (2002) report estimates of chlorophyll concentrations in Bocas del Toro being lower (around 1 µg l^{-1}) during February to April and higher (around 3 µg l^{-1}) the rest of the year. It is likely, therefore, that with the low flow conditions experienced during the current study, chlorophyll *a* measurements were at their annual minimum.

Phytoplankton concentrations measured in Bahía Almirante were similar to sites in Jamaica classified as mesotrophic (0.57 ± 0.02 µg l^{-1}), while Laguna de Chiriquí and the outer lagoon were closer to mean values from sites classified as eutrophic (>2 µg l^{-1}) (Green and Webber 2003), and approach concentrations measured during February/March in Florida Bay (2.5 µg l^{-1}; Frankovich and Fourqurean 1997).

Sediment type and porewater nutrient patterns in the Bocas del Toro archipelago

Sediment in Laguna de Chiriquí was predominantly medium grain silicate sand, while sediments in Bahía Almirante and the outer lagoon were predominantly coarse carbonate sand. These observed differences in sediment structure within seagrass meadows throughout the archipelago are likely a result of the underlying geomorphology in combination with both greater terrestrial input of sediment to seagrass habitats in Laguna de Chiriquí (through river flow) and greater production of carbonate sands (by coral and calcifying macroalgae such as *Halimeda*) in

Bahía Almirante. For recently formed sediments, high terrigenous sediment input is inversely related to production of carbonate sediment as differences in river flow between the lagoons influence patterns in coral abundance. Coral reefs are common in Bahía Almirante down to 23 m while there is only one reef in Laguna de Chiriquí at a maximum depth of only 3 m (Guzmán and Guevara 1998a).

While porewater soluble reactive phosphorus (SRP) concentrations were comparable or slightly higher than values reported from similar habitats in the Caribbean, porewater NH_4^+ concentrations were one to two orders of magnitude lower than most reports for seagrass meadows. SRP concentrations in sediment porewater from *T. testudinum* meadows in the outer lagoon were comparable to those reported for Florida Bay (0.49 ± 0.10 μM) (Fourqurean et al. 1992a). However, porewater SRP concentrations in Bahía Almirante and Laguna de Chiriquí sites were an average of 1.5 times greater those reported for Florida Bay, but still similar to concentrations reported for the Bahamas and Bermuda (Table 3, McGlathery et al. 2001; Short et al. 1985). In contrast, porewater NH_4^+ concentrations measured in Bocas del Toro (Table 3) were almost two orders of magnitude lower than concentrations reported for *T. testudinum* meadows in Florida Bay (98.0 ± 29.5 μM, Fourqurean et al. 1992a) and *Syringodium filiforme* meadows in the Bahamas (100 μM, Short et al. 1985) and also only one-third to one-half concentrations measured at 5 cm depth into the sediment in Bermuda (6-8 μM, McGlathery et al. 2001). These differences in NH_4^+ concentrations may in part be a function of sediment grain size. Florida Bay is characterized by very fine carbonate mud, while the Bermuda sites had a grain size similar to Bocas del Toro (50-60% of sediment grains 0.2-0.7 mm, McGlathery et al. 1994). However, regardless of the mechanism and even recognizing that the measurements taken in the current study were during an extended dry period, porewater concentrations of NH_4^+ throughout the archipelago were extremely low.

Thalassia testudinum in relation to water quality and sediment characteristics of the Bocas del Toro archipelago

At the time of sampling, sediment porewater and water column PO_4^{3-} concentrations were consistent between Bahía Almirante and Laguna de Chiriquí but *T. testudinum* leaf %P was significantly higher in Bahía Almirante. As carbonate sediments have a higher potential for binding phosphorus (Hemminga and Duarte 2000), this is the opposite trend to what might be expected. The higher seagrass %P in Bahía Almirante suggests that overall annual supply of phosphorus through freshwater inputs is likely to be higher into this Lagoon. While shoot density did not show any lagoonal scale patterns, the maximum depth limit of seagrass was greater in Bahía Almirante (Table 4), which is consistent with the lower TSS and chlorophyll *a* measured within this lagoon (Figure 4).

Previous studies have suggested that in areas with porewater SRP <2 μM, *T. testudinum* will tend to be phosphorus limited (Fourqurean et al. 1992b) and in areas with ammonium concentration <100 μM, *T. testudinum* will potentially be nitrogen limited (Lee and Dunton 2000). All seagrass samples in the current study were taken at approximately 1.5 m depth which was at least 0.5 m shallower than the maximum depth limit of seagrass in any of these meadows, suggesting that the sampled seagrasses were not light limited, and leaf tissue nitrogen and phosphorus concentrations suggest that *T. testudinum* was, also, not nutrient limited. So the question arises as to the source of this high nutrient content. Seagrass uptake of nutrients through leaf tissue is well recognized as an important mechanism (Hemminga and Duarte 2000) and the current results suggest, considering the low porewater nutrient concentrations, it is possible that a high supply of nutrients through freshwater inputs are supporting the high seagrass nutrient concentrations.

Bocas del Toro in a Caribbean context

Shoot density of *Thalassia testudinum* in the Caribbean varies from 150 shoots m^{-2} in Curaçao up to 1000 shoots m^{-2} in Belize (CARICOMP 1997). In the current study,

mean shoot densities for all water bodies were near the lower end of this range, with densities ranging from 277 to 305 shoots m^{-2}. *Thalassia testudinum* has been shown to be susceptible to increases in water column nutrients; for example, Tomasko et al. (1996) reported greatest shoot density (500-600 shoots m^{-2}) in areas of Sarasota Bay, Florida, with the lowest nitrogen inputs (mean annual TN approximately 42 μM). Meadows had lower densities and higher shoot turnover in areas with higher nitrogen input (Tomasko et al. 1996). In Jamaica, shoot densities of approximately 900 shoots m^{-2} were measured at oligotrophic sites, while densities at eutrophic sites were only 450-600 shoots m^{-2} (Green and Webber 2003). Long term (8 yr) fertilization experiments (by addition of bird feces) in Florida Bay resulted in an initial increase in production followed by a reduction in density of *T. testudinum* until this species was completely replaced by *Halodule wrightii* (Fourqurean et al. 1995). In all these studies, *T. testudinum* thrived in low nutrient, oligotrophic conditions and show decline (evidenced by reduction in density) with continued nutrient increase. Although no time series of shoot density is available for Bocas del Toro archipelago, shoot density at many sites is relatively low. It would be valuable to monitor these areas to assess if shoot density is stable or undergoing a broad scale decline.

The nutrient content (both N and P) of the *Thalassia testudinum* leaf blades from the archipelago are very high compared to most other literature values reported for this species (Table 5, 6), or any other seagrass species (Atkinson and Smith 1983; Duarte 1990), indicating very high nutrient availability for seagrasses in the region. The Bermuda and Yucatan data in Table 6 come from sites with known anthropogenic nutrient additions and while the %N values in Bocas lagoons are high, the %P is much greater than these other locations and equivalent to mean values from the Gulf of Mexico. In Laguna de Chiriquí, the N:P ratio is very close to the proposed 'Redfield' ratio for seagrass (24-30, Duarte 1990; Fourqurean and Rutten 2003) and similar to the Bermuda and east Gulf of Mexico sites, but much lower than ratios reported from the Bahamas or south Florida (Table 6). Although the N:P ratios in Bahía Almirante and the outer lagoon were lower (Table 5), suggesting that these carbonate sites may tend towards potential nitrogen limitation, the difference in ratios is driven not by change in tissue nitrogen (these were not significant, Table 5), but rather by higher tissue phosphorus in these carbonate lagoons (Table 5). By comparing the leaf tissue C:N and C:P ratios in all the Bocas del Toro lagoons (Table 5) with the global median values (Table 6), the relative enrichment in all three lagoons is apparent – especially considering that the global median values include the known eutrophic temperate estuaries of north America and Europe. The high N and P content is likely due to the high riverine inputs into this system, resulting from high rainfall into a steep watershed with a long history of agriculture. This high nutrient availability also supports high phytoplankton concentrations compared to many tropical seagrass ecosystems, and shallow maximum depth limits for *T. testudinum* meadows in this system.

CONCLUSIONS

Throughout the Bocas del Toro archipelago, no distinct onshore to offshore gra-

TABLE 6. Comparative table of seagrass leaf tissue nutrient contents.

Location	C(%)	N(%)	P(%)	C:N	C:P	N:P	Genus	Reference
Bahamas	32.8	1.29	0.061	30	1390	47	*Syringodium*	Short et al. 1985
South Florida	36.9	1.82	0.113	25	937	40	*Thalassia*	Fourqurean and Zieman 2002
Bermuda	33.4	2.11	0.187	19	464	25	*Thalassia*	McGlathery et al. 1994
Yucatan	32.8	2.72	0.139	14	669	47	*Thalassia*	Gallegos et al. 1993
E Gulf Mexico	—	2.27	0.230	—	—	22	*Thalassia*	Fourqurean and Cai 2001
Global median	33.5	1.9	0.24	22	435	20	all	Duarte 1992

dient in the nutrient status of *Thalassia testudinum* meadows was measured. In contrast, distinct differences were measured between Bahía Almirante and the Laguna de Chiriquí, with the northern region of the outer lagoon being most similar to Bahía Almirante and the southern region more similar to Laguna de Chiriquí (Fig. 3). As a result, we propose the following conceptual synthesis of broad scale nutrient processes within the Bocas del Toro archipelago (Fig. 5).

Bahía Almirante and northern outer lagoon (Fig. 5A)

The underlying sediment is marine sedimentary rock with overlying coarse carbonate sand. The watershed is approximately the same size as the Bahía Almirante, bounded by the volcanic rock central mountains in the west. The watershed is predominantly cleared as a result of forestry, subsistence agriculture, banana and cacao plantations, but wetlands and man-
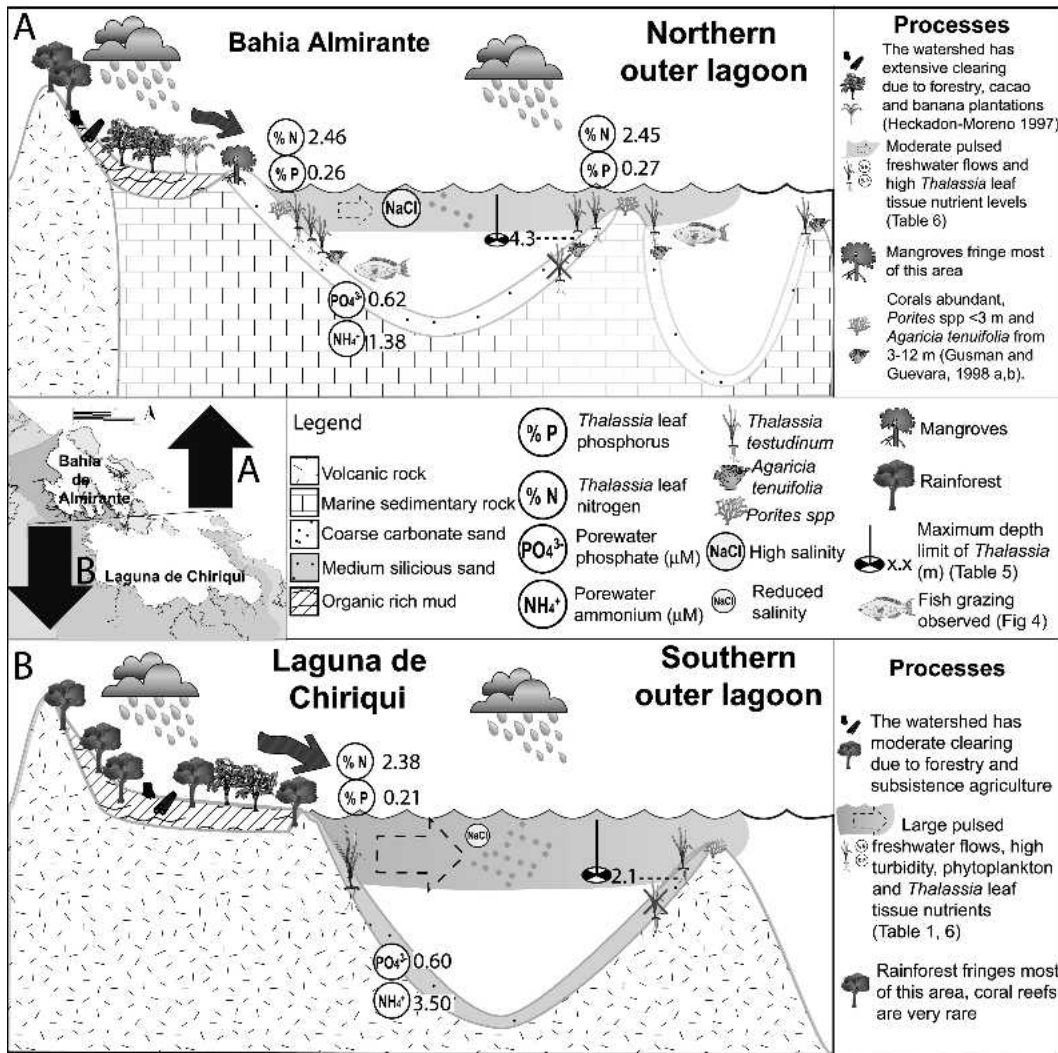

FIG. 5. Conceptual diagram of key nutrient features and hypothesized processes for A. Bahía Almirante and the northern outer lagoon and B. Laguna de Chiriquí and the southern outer lagoon.

groves still fringe most of the mainland coast of Bahía Almirante. Fresh, sediment-laden pulses of runoff occur following rainfall events and support phytoplankton populations which can be considered mesotrophic (Green and Webber 2003), however water clarity is still reasonably high, supporting seagrass to a depth greater than 4 m (Table 4). Evidence from coral communities suggests that water quality has declined significantly over the last few decades (Aronson et al. 2004). *Thalassia testudinum* is the dominant seagrass, often with high fish grazing and growing mixed with the dominant corals *Agaricia tenuifolia* (3-12 m depth) and *Porites* spp. (<3 m depth) (Guzmán and Guevara 1998 a, b). Porewater nutrient concentrations are low; however seagrass tissue nutrient concentrations are regionally high even at their most seaward extent – suggesting a continual delivery of nutrients from the inflowing rivers.

Laguna de Chiriquí and southern outer lagoon (Fig. 5B)

The underlying sediment is volcanic rock with overlying medium siliclastic sand. The watershed is many times the size of the Laguna de Chiriquí, bounded by the volcanic rock central mountains in the south and west. The watershed is partially cleared as a result of forestry, subsistence agriculture and cacao plantations, with rainforest and mangroves occurring along the mainland shoreline of Laguna de Chiriquí. Fresh, sediment-laden pulses of runoff occur following rainfall events (Carruthers and Barnes unpublished data) and may be supporting these large phytoplankton populations (at concentrations indicative of eutrophic conditions). As a result, water clarity is low and only supports seagrass to a depth of approximately 2 m (Table 4). *Thalassia testudinum* is the dominant seagrass, with evidence of fish grazing only rarely observed. Once again, low porewater nutrient concentrations and high seagrass tissue nutrient concentrations, throughout the lagoon, suggest a continual delivery of nutrients from the inflowing rivers.

The main water bodies of the Bocas del Toro archipelago show signs of high (presumably) river input of sediment and nutrients. Significant variations in sediment structure of seagrass meadows between Bahía Almirante and Laguna de Chiriquí may be due to a combination of geological differences in the watersheds of these bays, as well as the much larger watershed, with more abundant and larger rivers into Laguna de Chiriquí. However, the higher phosphorus availability in Bahía Almirante may reflect the higher land clearing and agriculture in this watershed. The very low water column nutrients, as well as high phytoplankton concentrations and high tissue nutrients in *Thalassia testudinum,* suggest that the marine biota may be effectively filtering the majority of incoming nutrients and retaining them within the archipelago.

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