Seagrass epiphyte loads along a nutrient availability gradient, Florida Bay, USA

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ABSTRACT: Total epiphyte load, epiphyte chlorophyll load, epiphyte autotrophic index, and seagrass short shoot size are compared with water column nutrient concentrations and the elemental composition of seagrass leaf tissue. The spatial patterns in these parameters are described across a nutrient availability gradient in Florida Bay, Florida, USA. Multivariate and univariate statistical analyses were performed on these parameters to test for correlations with various measures of nutrient availability. Most of the variation in *Thalassia testudinum* short shoot size could be described by phosphorus availability, dissolved organic matter in the water column, and water column inorganic nitrogen concentrations. Total epiphyte and epiphyte chlorophyll loads were significantly, but weakly, correlated with phosphorus availability. The measurement of total epiphyte loads and observations of epiphytic species composition along a transect adjacent to a point source of nutrients revealed that the effect of nutrient enrichment on epiphyte levels is pronounced but very localized. Epiphyte levels may not be as sensitive to moderate nutrient enrichment as other seagrass parameters (e.g. leaf tissue nutrient content).

KEY WORDS: Epiphytes · Water quality · Nutrient availability · Seagrass · *Thalassia testudinum* · Florida Bay

INTRODUCTION

Seagrass meadows rank among the most productive ecosystems in nature, rivaling those of tropical rain forests and tidal marshes (Odum 1957, McRoy & McMillan 1977, Zieman & Wetzel 1980). Seagrass epiphytes are an important component of these highly productive ecosystems, often contributing greater than one-third to the total above ground biomass (Penhale 1977, Heijs 1984, Tomasko & Lapointe 1991) and as much as 30% to combined seagrass/epiphyte productivity (Penhale 1977, Morgan & Kitting 1984, Heijs 1984, 1985, 1987). Though most seagrass biomass must enter the detrital food web before it is available to higher trophic levels (Odum & de la Cruz 1963, Fenchel 1970, Fry & Parker 1979), epiphyte production can be a direct source of carbon available to higher trophic levels through grazing (Fry & Parker 1979,

Kitting et al. 1984). Epiphytes may also provide a more assimilable detrital carbon source than their seagrass hosts due to the large amount of refractory structural tissue and phenolic compounds in seagrasses (Harrison 1989).

In addition to being an important component of the seagrass community, epiphytes can also be detrimental to seagrasses. Seagrasses form extensive beds in many coastal embayments worldwide, and seagrass-dominated ecosystems have fared poorly in anthropogenically-influenced coastal regions because of the sensitivity of seagrasses to changes in water quality (e.g. Orth & Moore 1983, Giesen et al. 1990, Larkum & West 1990). The general pattern of changes in benthic vegetation accompanying eutrophication is from rooted macrophytes at low nutrient availability to domination by epiphytic and water column algae at higher levels of nutrient availability and eventually to seagrass loss during the latter stages of eutrophication (see Duarte 1995 for review). One mechanism for losses of submerged aquatic vegetation is overgrowth by epiphytes (Phillips et al. 1978, Kemp et al. 1983, Cambridge et

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al. 1986). Epiphyte loads reduce the productivity of macrophytes by shading and reducing nutrient availability (Bulthuis & Woelkerling 1983, Twilley et al. 1985, Wetzel & Neckles 1986, Tomasko & Lapointe 1991, Neckles et al. 1993, 1994, Neundorfer & Kemp 1993).

Various factors affect the distribution of epiphyte loads across both seasonal and regional scales. Structural factors, such as seagrass leaf area and seagrass leaf turnover rate, affect the space and time for epiphyte colonization and growth. Physico-chemical factors affecting epiphyte loads include nutrient availability, temperature, salinity, depth, current, and light availability and quality. Decreased seagrass leaf turnover rates and elevated nutrient availability have been implicated as causal factors for increased epiphyte loads in seagrass beds (Borum 1985, Twilley et al. 1985, Tomasko & Lapointe 1991). Epiphyte abundance has been experimentally demonstrated to be a function of nutrient availability (Tomasko & Lapointe 1991, Neckles et al. 1993, 1994; but see Bulthuis et al. 1992). Seagrass epiphyte density and biomass have also shown increases along nutrient availability gradients (Cambridge & McComb 1984, Borum 1985, Silberstein et al. 1986). Due to relatively small regional variation in leaf productivity rates, seagrass leaf turnover rate will affect epiphyte dynamics more in the temporal domain than the spatial domain (Humm 1964, Borum 1985, Zieman et al. 1989, Tomasko & Lapointe 1991, Frankovich 1996). Spatial differences in nutrient availability are believed to be major controls on regional variation in epiphyte loads.

Seagrass epiphytes are sessile plants and animals that grow attached to their seagrass host (Harlin 1980, Frankovich & Zieman 1994). Epiphyte carbonate often accounts for as much as 70 to 80% of epiphyte standing stock (Heijs 1984, Frankovich & Zieman 1994). This large amount of non-autotrophic mass in the epiphyte community may complicate the relationship between nutrient availability and epiphyte loads of seagrasses. Because autotrophs are the primary component of a community that responds to nutrient availability, some measure of autotrophic epiphyte biomass (e.g. epiphyte chlorophyll) should be more sensitive to nutrient availability than total (plant + animal) epiphyte load.

In this paper, we compare epiphyte loads, seagrass short shoot size, nutrient availability to seagrasses, and water column nutrient concentrations across a large tropical embayment. Large gradients in benthic and water column nutrient availability have been documented for this ecosystem (Zieman et al. 1989, Fourqurean et al. 1992a, 1993); nutrient availability ranged from limiting to seagrass and phytoplankton growth to adequate for dense seagrass growth (Powell et al. 1991, Fourqurean et al. 1992a, b, 1993). We document

the spatial patterns in epiphyte abundance across the ecosystem, and test the hypothesis that epiphyte biomass (total epiphyte load and epiphyte chlorophyll load) would be correlated with the gradient in nutrient availability.

METHODS

Study site. This work was done in a shallow subtropical embayment, Florida Bay, Florida, USA (Fig. 1). Seagrasses, predominantly *Thalassia testudinum*, carpet ca 2000 km^2 of Florida Bay. There is a strong gradient in seagrass density across the bay, with seagrass density in the western bay an order of magnitude higher than the eastern parts of the bay (Zieman et al. 1989). This gradient is the result of a strong gradient in benthic phosphorus availability; seagrass biomass in the eastern parts of Florida Bay is P-limited (Fourqurean et al. 1992a, b). In addition to the gradient in benthic nutrient availability, there is a corresponding gradient in water column nutrient availability, which leads to P-limitation of phytoplankton biomass (Fourqurean et al. 1993). We sampled seagrasses, epiphytes, and water column nutrients from 24 stations distributed across the seagrass and nutrient availability gradient. A bird colony island in eastern Florida Bay, Porjoe Key (Fig. 1), was also sampled for seagrasses and epiphytes; this bird colony is a local point source of nutrients in an otherwise oligotrophic portion of Florida Bay (Powell et al. 1991, Fourqurean et al. 1992a).

Seagrass and epiphyte sampling. On March 26–27, 1994, 6 arbitrary short shoots of *Thalassia testudinum* were collected from 24 long-term water quality monitoring sites within Florida Bay (Fig. 1). During August of 1991 and 1992, 10 short shoots of *T. testudinum* were collected at each of 3 equally-spaced points located along a 45 m transect perpendicular to the shoreline of the bird colony island (Fig. 1). Macroscopic epiphytic organisms occurring on the leaves of the sampled short shoots were recorded. Organisms were identified to the lowest taxon practical, and a qualitative estimate was made of the relative abundance of each organism. Epiphytes were separated from the seagrass leaves by gentle scraping of lyophilized seagrass leaves (Frankovich & Zieman 1995). The dry weight of the leaves of each short shoot and the dry weight of the epiphytes removed from each short shoot were recorded. Total epiphyte load (mg dry wt of epiphytes g^{-1} dry wt of seagrass leaf) was determined from the dry weight of the separated epiphyte material and the dry weight of scraped seagrass leaves.

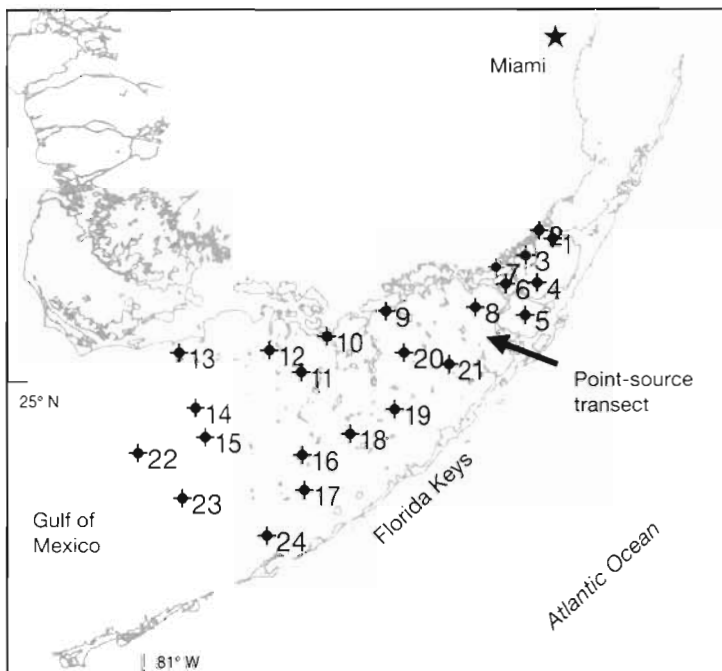For each of the 24 sites sampled in March 1994, autotrophic epiphytes were quantified by extracting

Fig. 1. Florida Bay, USA, showing sampling locations for seagrasses, epiphytes, and water quality data. The location of the Porjoe Key bird colony point source of nutrients transect is also shown

longer-term record (March 1991 to March 1994) of surface salinities was used to describe the salinity variability at each site. Water quality parameters collected for comparison to epiphyte loads were: concentrations of total organic nitrogen (TON), ammonium (NH_4^+), nitrate (NO_3^-), nitrite (NO_2^-), total phosphorus (TP), soluble reactive phosphorus (SRP), total organic carbon (TOC), and water column chl a, as well as salinity and turbidity. Methods for these water quality measurements are described elsewhere (Fourqurean et al. 1993).

Statistical methods. Before statistical analyses, all data were checked for normality, and were ln-transformed where appropriate. Statistical treatment of the total epiphyte loads measured at the 3 sites located along the nutrient point source transect was performed utilizing a 2-way ANOVA to detect significant differences in mean total epiphyte loads between sites and times. In the absence of a statistically significant time effect, a 1-way ANOVA with Scheffé's multiple comparison procedure (0.05 level of significance) was performed to detect significant differences between the time-averaged transect point means. Univariate relationships between water quality, seagrass, and epiphyte variables were checked using Pearson correlation. To define the independent underlying patterns in the nutrient availability data, a Principal Components Analysis, using the correlation matrix, was done on the nutrient availability data. The final solution was rotated to allow for interpretation of the principal components using a VARIMAX rotation. Stepwise multiple regression was used to determine which of the nutrient availability principal components explained significant portions of the variability in the epiphyte loads and seagrass morphology. We deemed significant only independent variables with partial F significant at $p \leq 0.05$.

RESULTS

Seagrass distribution

There was a strong gradient in the amount of green leaf material per short shoot of Thalassia testudinum across Florida Bay (Fig. 2). Short shoot (ss) size ranged from a low of 34 mg green leaf ss^{-1} at Stn 19 to a high of 525 mg green leaf ss^{-1} at Stn 13. There were relatively few stations with large short shoots; the median for the whole bay was 80 mg green leaf ss^{-1}. In general, short shoot size was smallest in eastern and central

chlorophyll a (chl a) from the lyophilized epiphytes. The separated epiphyte material from each shoot was steeped in either 5.0 or 20.0 ml (depending on total epiphyte weight) of 90% spectrophotometric grade acetone, and held in the dark below 0°C for a minimum of 36 h (Frankovich 1996). Chl a content of the acetone extracts was determined fluorometrically (Strickland & Parsons 1972). Epiphyte chlorophyll load (μg chl a mg^{-1} seagrass leaves) was determined from the chl a content of the acetone extracts and the dry weight of scraped Thalassia testudinum leaves. In order to detect differences in the amount of algal epiphytism relative to faunal epiphytism, an autotrophic index (AI = μg chl a mg^{-1} epiphyte) was determined.

The availability of nutrients to the seagrasses was assessed by analyzing the carbon, nitrogen, and phosphorus content of the seagrass leaves at each site (Fourqurean et al. 1992a, b). C and N content was determined by analyzing triplicate samples of the scraped seagrass leaves using a Carlo Erba CN analyzer. Phosphorus content of the same material was determined following a dry oxidation/acid hydrolysis procedure (Fourqurean et al. 1992a). Ratios of C, N, and P were calculated on a molar basis.

Water quality sampling. Mean values of monthly water quality data were determined for the 2 mo period prior to sampling (the seagrass/epiphyte turnover period for Florida Bay; Zieman et al. 1989). A
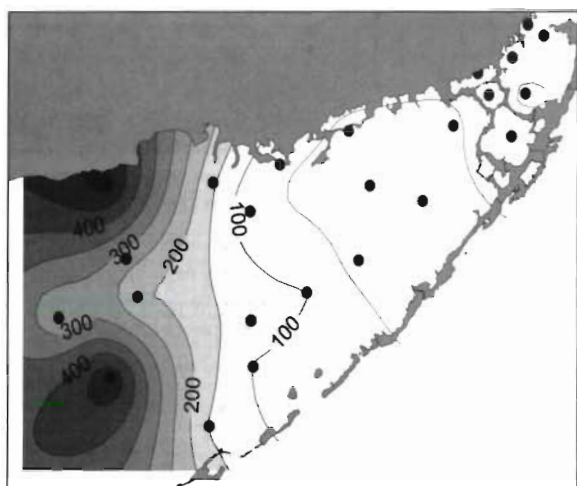
Fig. 2. *Thalassia testudinum*. Spatial distribution of the amount of green leaf material per seagrass short shoot (mg ss^{-1})

Florida Bay, and largest along the western boundary of the bay (Fig. 2). This gradient in short shoot size was mirrored by a gradient in P, but not N, content of the leaves. C:P of *T. testudinum* leaves generally increased from a minimum of 486 in the northwest part of Florida Bay to a maximum of 1807 at Stn 8 in eastern Florida Bay (Fig. 3b). The pattern in C:N of *T. testudinum* leaves was quite different, with a minimum of 11 at Stn 11 in the center of the bay. C:N increased in all directions from the center of the bay; the maximum C:N was 21 at Stn 7 (Fig. 3a). C:P was strongly correlated with short shoot size (Fig. 4), but C:N was not ($r^2 = 0.00$, $p = 0.807$). The one point that deviated strongly from the relationship between C:P and shoot size was Stn 11, where the shoot size was much smaller than predicted by the P content of the leaves (Fig. 4).

Epiphyte abundance

We identified 7 macroscopic algal and 11 faunal taxa that were epiphytic on the leaves of the sampled short shoots during the March 1994 sampling period (Table 1). All identified macroscopic algae were red algae (Rhodophyta). The epiphytic faunal composition was more diverse than the algal composition. Five phyla (Annelida, Bryozoa, Chordata, Hydrozoa, and Mollusca) were represented. Epiphyte occurrence and abundance were dominated by the coralline red algae *Melobesia membranacea* and *Fosliella farinosa* and the polychaete *Spirorbis* sp. *Spirorbis* sp. was the most ubiquitous epiphyte taxon, occurring at 75% of the sites, and was the most abundant epiphyte at 58% of the sites. The coralline red algae were the most abundant and ubiquitous of the algal species, occurring at
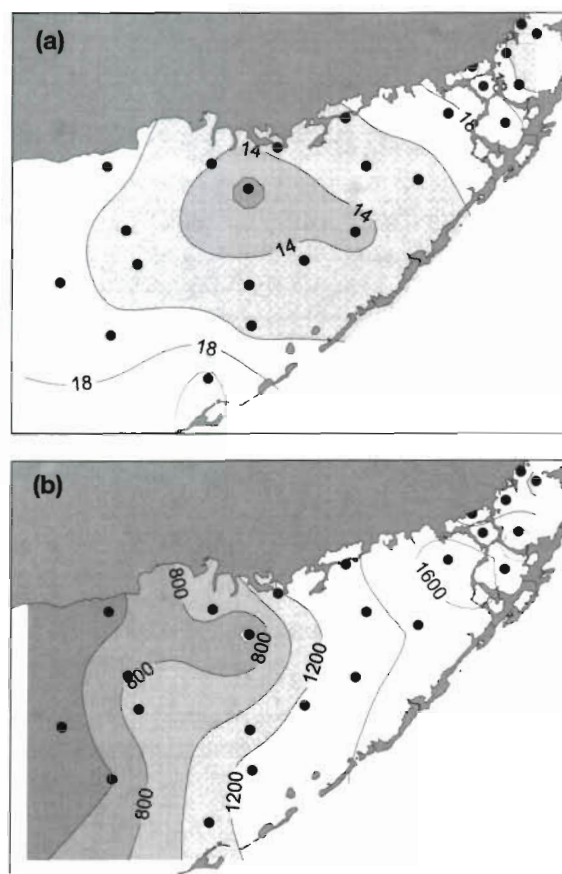

Fig. 3. *Thalassia testudinum*. Spatial distribution of (a) C:N ratio of green seagrass leaves, and (b) C:P of green seagrass leaves
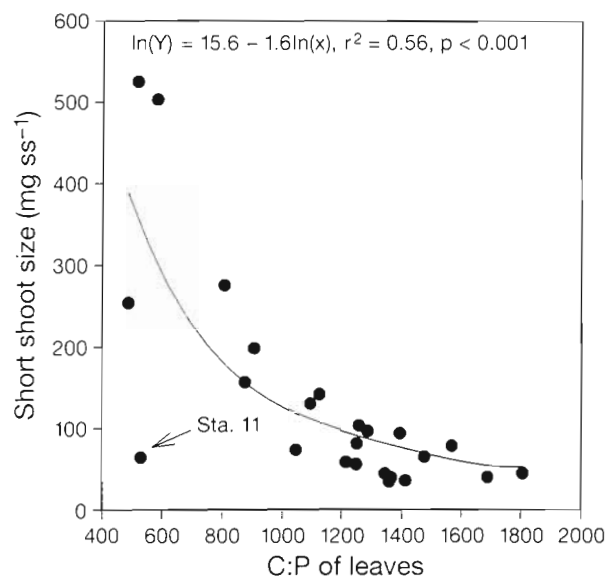

Fig. 4. *Thalassia testudinum*. Seagrass short shoot size (mass of green leaves per short shoot) as a function of P content of the leaves. Solid line represents the linear regression; regression statistics are shown on the figure

Table 1. Macroscopic algal and faunal epiphytes occurring on leaves of sampled short shoots of *Thalassia testudinum* from each of the individual sites located in Fig. 1 Epiphytes are listed in order of abundance. Numerals and capital letters correspond to algal and faunal epiphytes, respectively. Algal epiphytes: 1, Coralline algae (*Melobesia membranacea, Fosliella farinosa*); 2, *Ceramium* spp.; 3, *Spyridia* spp.; 4, *Hypnea* sp.; 5, *Laurencia* spp.; 6, *Amphiroa fragilissima* sp. Faunal epiphytes: A, polychaete (*Spirorbis* sp.); B, mollusc (*Pinctada imbricata*); C, mollusc (*Brachidontes exustus*); D, encrusting tunicates (*Botryllus planus, Botrylloides nigrum*); E, colonial tunicate (*Perophora* sp.); F, unidentified bryozoan; G, unidentified chiton; H, hydrozoan (*Sertularia* sp.); I, unidentified tube-forming polychaete; J, *Soritid foraminifera*; K, unidentified hydrozoan

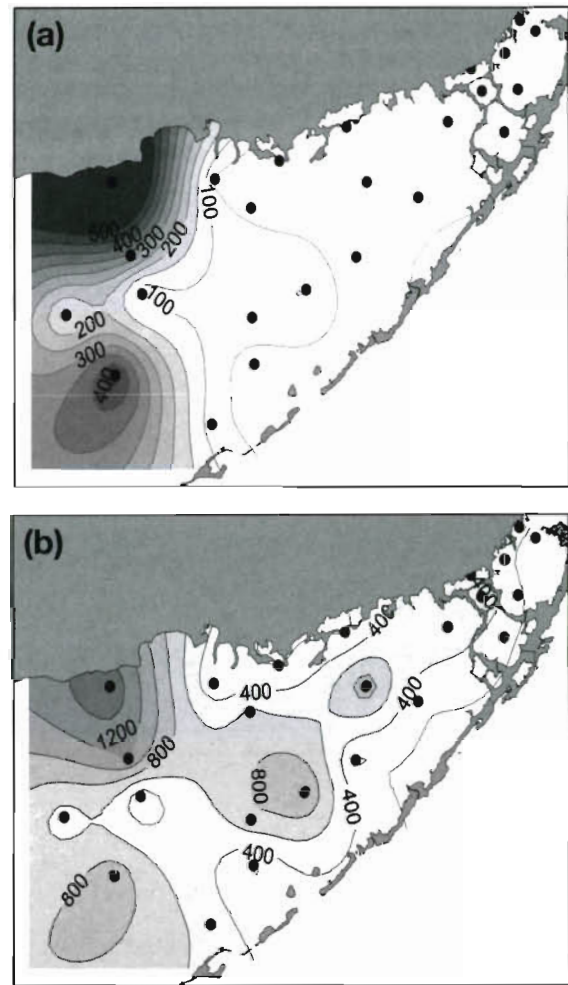| Site no.	Algal epiphytes	Faunal epiphytes
1	•	•
2	1, 3	A
3	1, 3	•
4	2, 1	A
5	3, 1	G
6	1	C, I
7	•	C
8	1, 2	A, B, G
9	1, 3	A
10	•	A
11	•	F, A, J
12	•	F, H, A, E, C, G
13	4	F, A
14	1	A
15	1	A
16	•	A
17	•	A
18	•	A, C
19	•	A
20	4	A
21	•	A
22	1, 4	•
23	1, 5, 6	D, A, K
24	1	A, F

• No epiphytes identified

Fig. 5. *Thalassia testudinum*. Spatial distribution of (a) total epiphyte abundance per short shoot of seagrass and (b) total epiphyte load as mass of epiphytes per g of seagrass leaves (mg g^{-1})

50% of the sites and being most abundant at 42% of the sites. Heavy carbonate encrustations were formed by these species at those sites in western Florida Bay where water is exchanged more freely with the Gulf of Mexico and the Atlantic Ocean.

The abundance of epiphytes, when measured on a per short shoot basis, was greatest in western Florida Bay and decreased eastward (Fig. 5a). There was a broad range (1.7 to 824 mg ss^{-1}) in epiphyte abundance across the bay, with a median abundance of 79.7 mg ss^{-1}. Given the spatial gradient in short shoot size, short-shoot-based measures of epiphyte abundance do not accurately reflect the effect of epiphytes on seagrasses, however. Normalizing this measure by the size of the short shoots gives a better estimate of the epiphyte load on the seagrasses. Total epiphyte load ranged from 23 to 1569 mg epiphyte g^{-1} seagrass, with

a median load of 376 mg g^{-1}. The spatial pattern in total epiphyte load was not as clear as the pattern in epiphyte abundance (Fig. 5b). In general, epiphyte load was highest in western Florida Bay, but there were also peaks in epiphyte load at Stns 18 and 20 in central Florida Bay.

Similar to total epiphyte abundance, autotrophic epiphyte abundance also was highest in northwestern Florida Bay (Fig. 6a). The median epiphyte chl *a* abundance was 2.7 µg ss^{-1}, with a range of 0.1 to 106 µg ss^{-1}. Epiphyte chlorophyll loads ranged from 1.5 µg g^{-1} at Stn 1 in the east to 298.7 µg g^{-1} at Stn 14 in northwestern Florida Bay (Fig. 6b). The median epiphyte chlorophyll load was 34.8 µg g^{-1}. Almost two-thirds (62.5%) of the sites had mean epiphyte chlorophyll loads less than 50 µg g^{-1}. Aside from the high epiphyte chlorophyll loads measured at Stns 18
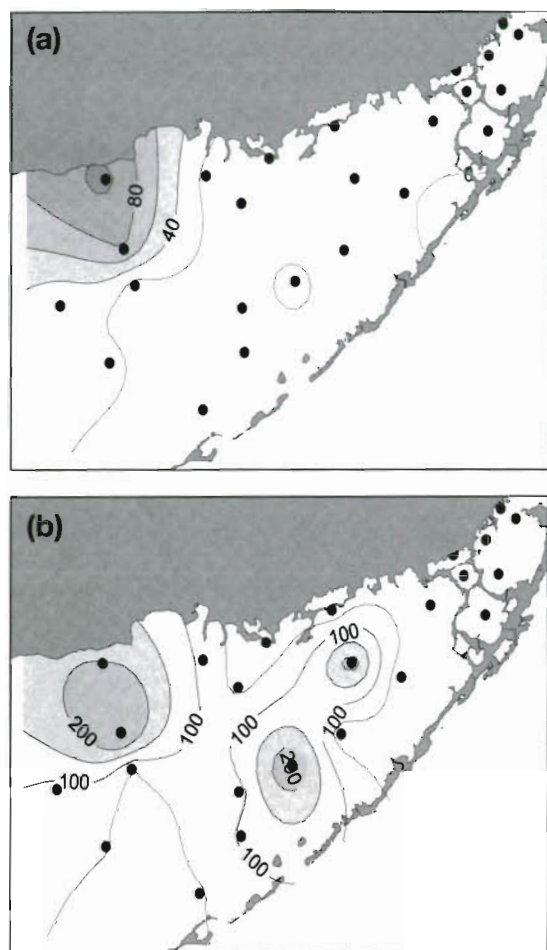
Fig. 6. *Thalassia testudinum*. Spatial distribution of (a) epiphyte chl *a* abundance per short shoot of seagrass (mg ss⁻¹); and (b) epiphyte chl *a* load as mass of epiphytes per g of seagrass leaves (mg g⁻¹)

ern Florida Bay while the occurrence of the polychaete *Spirorbis* sp. and the molluscs *Brachidontes exustus* and *Pinctada imbricata* increased towards the more restricted eastern Florida Bay. Total epiphyte loads were anomalously high near Porjoe Key, the point source of nutrients in eastern Florida Bay. Mean total epiphyte loads measured along the transect near the point source ranged from 10.6 to 399.0 mg g⁻¹ (Fig. 8). The results of the 2-way ANOVA indicate significant differences only between transect points. As a result of the lack of a significant difference between sampling times, Scheffé's multiple comparison procedure was performed on the time-averaged transect point means. Time-averaged mean epiphyte loads were significantly higher ($F = 13.2$, $p < 0.001$) at the transect point located in closest proximity to the bird island. Mean epiphyte loads were 3 to 36 times higher at the transect point located closest to the island than at those located further away. Significant differences in the time-averaged mean epiphyte loads were only evident between the closest point to the nutrient source and the 2 more distally located points (Scheffé's, $p < 0.05$).

Water quality sampling

In February and March 1994, Florida Bay was a polyhaline estuary, with salinities from 18.3 psu in the northeast to 35.4 psu in the center of the bay (Table 2, Fig. 9a). Fully two-thirds of the bay was characterized by water approximating marine salinity (~34 psu). This is in contrast to the historic salinity characteristics of the bay. Salinity can vary widely in this system, from freshwater in the northeast reaches of the bay to over 60 psu over much of the central and eastern portions of the bay. The southwest margin has the lowest vari-

and 20, mean epiphyte chlorophyll loads generally decreased from higher values in northwest Florida Bay to lower values in extreme northeastern Florida Bay (Fig. 6b).

There was not a constant assemblage of autotrophs and heterotrophs making up the total epiphyte load. The autotrophic index (AI) ranged from 0.02 µg mg⁻¹ at Stn 8 in northeastern Florida Bay to 0.68 µg mg⁻¹ at Stn 17 in southwestern Florida Bay. More than half of the sites (54.2%) had AIs less than 0.1 µg µg⁻¹. AIs tended to be lower in northeastern Florida Bay, with higher values towards the southwestern and northwestern areas of Florida Bay (Fig. 7).

At the 24 water quality monitoring sites, all measures of epiphyte abundance and load were low in eastern Florida Bay relative to western Florida Bay, owing to the general oligotrophic nature of eastern Florida Bay. The coralline red algae were most abundant in west-
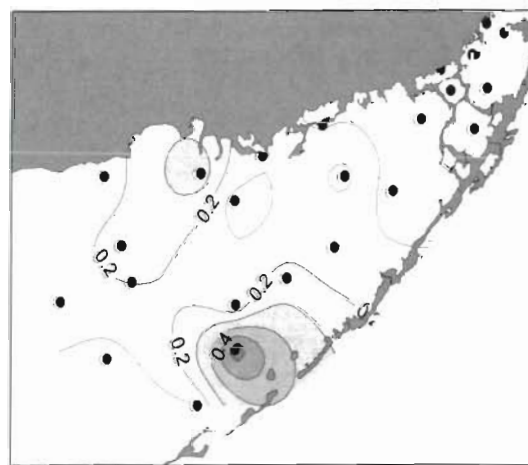

Fig. 7. *Thalassia testudinum*. Spatial distribution of epiphyte community autotrophic index (µg chl mg⁻¹ epiphyte)
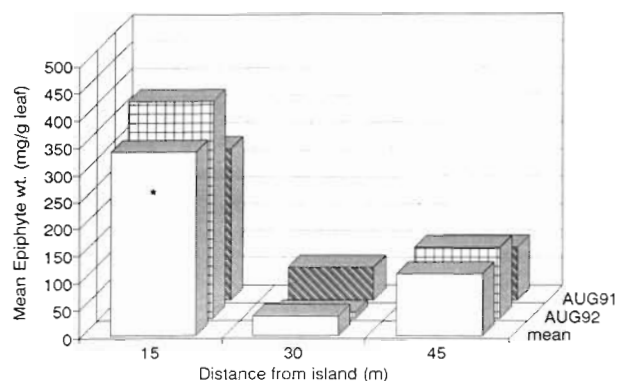
Fig. 8. *Thalassia testudinum*. Total epiphyte load as a function of distance from a point source of nutrients at the Porjoe Key bird colony. * denotes significant differences between the time-averaged transect point mean at 15 m and the 2 more distally located transect points (Scheffé, p < 0.05)

ability in salinity, with a range of 10 psu over the period 1990 to 1994, while salinity in waters adjacent to the mainland have varied over 48 psu (Fig. 9b).

Water column nutrient concentrations varied across Florida Bay for the 2 mo preceding the March 1994 seagrass and epiphyte sampling (Table 2). Total organic carbon (TOC) ranged from 220 to 1410 μM with the higher values from sites in central Florida Bay. Organic forms of nitrogen and phosphorus dominated the nutrient pool, constituting approximately 90% of respective total concentrations of these nutrients. Concentrations of both DIP (range 0.01 to 0.33 μM, median = 0.03 μM) and TP (range 0.2 to 1.7 μM, median = 0.4 μM) were quite low baywide (Fig. 10). Maximum DIP was found in the center of Florida Bay, while
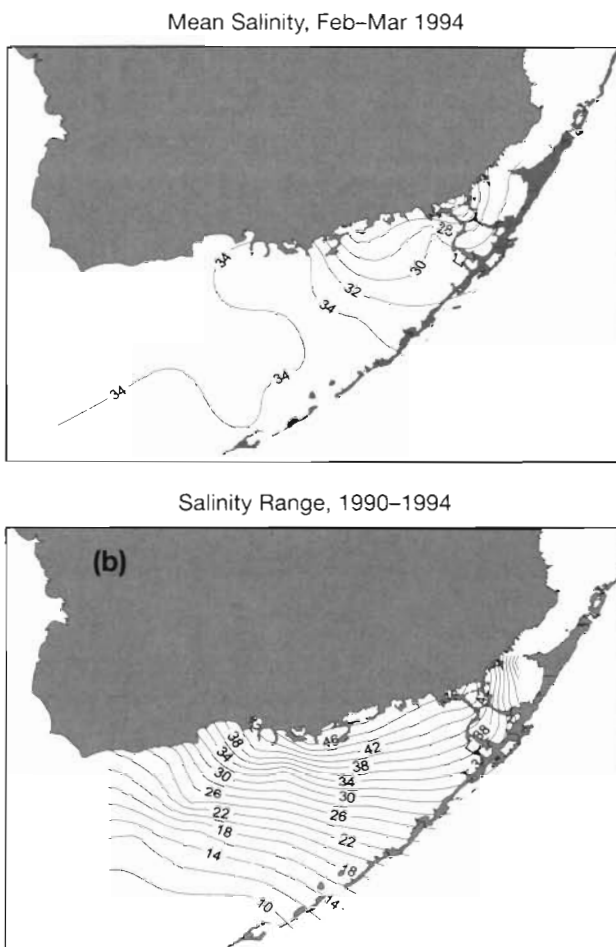

Fig. 9. Distribution of surface salinity in Florida Bay. (a) Mean of data collected in February–March 1994; and (b) range in salinity values over the period 1991 to 1994

maximum TP was found in northwest Florida Bay. In contrast to P, concentrations of TN (range 19.6 to 142.1 μM) and DIN (1.2 to 22.0 μM) were relatively high (Fig. 10). Peak DIN (22.0 μM) was found in eastern Florida Bay; TN was maximum in the north-central part of the bay. Water column chl *a* concentrations were low across the bay (range 0.6 to 6.9 μg l^{-1}, median = 1.6 μg l^{-1}).

Many of the indicators of nutrient availability, seagrass biomass, and epiphyte abundance were correlated (Table 3; for example, compare the distribution of C:P of *Thalassia testudinum* leaves, Fig. 3b, with the distribution of water column TP, Fig. 10a). In order to define independent underlying patterns in the nutrient availability data, a Principal Components Analysis was done on the ln-transformed nutrient availability data. Four Principal Components (PC1 through PC4) were extracted from the data that described 86% of the variation in the original data set (Table 4). PC1 was highly correlated with measures of inorganic nitrogen con-

Table 2. Summary statistics for baywide water quality at 24 stations for February–March 1994, Florida Bay, USA. DO: dissolved oxygen; TOC: total organic carbon; DIN: dissolved inorganic nitrogen; TON: total organic nitrogen; TN: total nitrogen; DIP: dissolved inorganic phosphorus; TP: total phosphorus

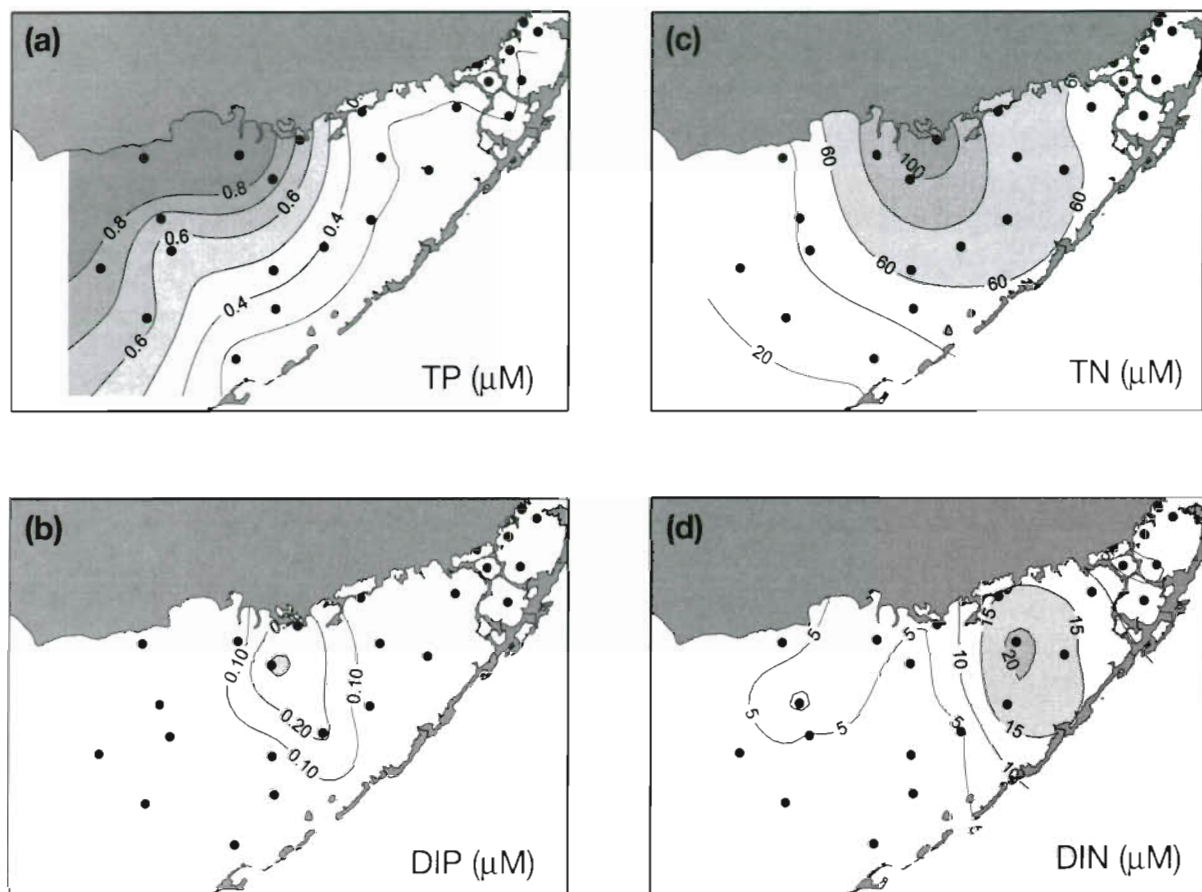|	Min.	Max.	Median	Mean	SD
Salinity (psu)	18.3	35.4	32.9	30.9	4.3
Temp. (°C)	21.0	23.9	22.6	22.5	0.9
DO (mg l^{-1})	6.2	7.6	7.0	7.0	0.4
Turbidity (NTU)	0.9	188.1	26.8	38.4	44.6
TOC (μM)	220	1410	744	815	312
NO$_3^-$ (μM)	0.08	6.47	0.97	1.66	1.74
NO$_2^-$ (μM)	0.11	0.80	0.31	0.34	0.18
NH$_4^+$ (μM)	1.02	18.25	3.26	5.37	4.89
DIN (μM)	1.21	21.96	4.89	7.38	5.95
TON (μM)	17.6	136.8	46.2	52.9	29.7
TN (μM)	19.6	142.1	51.3	60.3	30.4
DIP (μM)	0.01	0.33	0.03	0.07	0.09
TP (μM)	0.21	1.67	0.37	0.57	0.41
Chl *a* (μg l^{-1})	0.6	6.9	1.6	2.5	2.1

Fig. 10. Distribution of concentrations of (a) TP (b) DIP (c) TN and (d) DIN in the water column during February–March 1994

centration in the water column, and accounted for 27.9% of the variance in the original data set. PC2 was positively correlated with TN, TON, TOC, and DIP concentrations in the water column. We interpreted this factor, which explained 25.5% of the variation, to be an indicator of dissolved organic matter in the water column. A further 21.7% of the variation in the nutrient availability data set was explained by PC3, which was positively correlated with TP, turbidity, and chl a concentrations in the water column and negatively correlated with C:P of *T. testudinum* leaves. This factor represented P availability in both the water column and the seagrass bed. A fourth principal component (PC4) was significantly correlated with salinity and N content of *T. testudinum* leaves; PC4 explained an additional 11.2% of the variation in the nutrient availability data set.

Since the aim of this paper was to describe how epiphyte loads on seagrass were determined by various measures of nutrient availability, we used the factor scores of the principal components extracted from the nutrient availability data set as independent variables in stepwise regression to describe the shoot size, total

epiphyte load, epiphyte chlorophyll load and AI for each station. The mass of short shoots of *Thalassia testudinum* in Florida Bay was positively related to P availability (PC3), but negatively related to dissolved inorganic N concentration (PC1) and dissolved organic matter (PC2) in the water column. The equation ln(short shoot size) = 4.5 + 0.5(PC3) − 0.4(PC2) − 0.3(PC1) had an adjusted multiple r^2 of 0.745, with partial F for all factors >15, p for all factors ≤0.001. Total epiphyte load on *T. testudinum* from Florida Bay was significantly, albeit weakly, related to only P availability [ln(total epiphyte load) = 5.9 + 0.4(PC3), r^2 = 0.14, p = 0.04]. Similarly, epiphyte chlorophyll load was significantly, but weakly, related to P availability. An example of the raw data indicates the pattern of the relationship between P availability and epiphyte chlorophyll load (Fig. 11a); the generalized relationship between epiphyte chlorophyll load and P availability, as represented by PC3, is significant (Fig. 11b), although P availability explains only 17.4% of the variation. None of the principal components was significantly correlated with the AI of the epiphyte community, however.

Table 3. Pearson correlation coefficient matrix for water quality, seagrass and epiphyte variables. Below the diagonal are the correlation coefficients (r) for the correlation between the ln-transformed variables. Above the diagonal is the statistical significance of the correlations (p). **Boldface** type indicate correlations significant at $p \leq 0.05$

	TIN	NH4+	NO3	NO2	TON	TN	TOC	DIP	TP	Chl a	Turbidity	Salinity mean	Salinity variability	Thalassia leaf C:P	Thalassia leaf C:N	Thalassia shoot mass	Total epiphyte abundance	Autotrophic epiphyte abundance	Total epiphyte load	Autotrophic epiphyte load	Autotrophic index
TIN		0.000	0.000	0.000	0.399	0.086	0.244	0.207	0.071	0.057	0.627	0.426	0.017	0.040	0.325	0.010	0.031	0.036	0.222	0.162	0.458
NH4+	0.961		0.001	0.000	0.187	0.028	0.125	0.253	0.104	0.133	0.476	0.529	0.013	0.033	0.181	0.005	0.019	0.049	0.191	0.274	0.851
NO3	0.822	0.646		0.000	0.563	0.905	0.961	0.117	0.077	0.017	0.866	0.183	0.093	0.228	0.866	0.250	0.276	0.114	0.462	0.121	0.120
NO2	0.765	0.687	0.739		0.284	0.086	0.436	0.567	0.028	0.022	0.595	0.453	0.008	0.039	0.390	0.011	0.062	0.024	0.418	0.106	0.118
TON	0.180	0.279	-0.124	0.228		0.000	0.000	0.003	0.608	0.212	0.974	0.908	0.007	0.148	0.011	0.005	0.032	0.135	0.302	0.643	0.633
TN	0.358	0.448	0.026	0.358	0.981		0.000	0.011	0.844	0.397	0.842	0.984	0.004	0.086	0.007	0.001	0.015	0.084	0.255	0.568	0.670
TOC	0.247	0.322	0.010	0.167	0.823	0.829		0.034	0.220	0.107	0.237	0.931	0.019	0.619	0.005	0.043	0.110	0.426	0.419	0.919	0.262
DIP	-0.267	-0.243	-0.329	-0.123	0.587	0.510	0.435		0.194	0.250	0.550	0.976	0.234	0.989	0.353	0.396	0.930	0.769	0.554	0.907	0.608
TP	-0.375	-0.340	-0.368	-0.448	0.110	0.042	0.260	0.275		0.000	0.000	0.002	0.028	0.000	0.043	0.001	0.003	0.001	0.064	0.012	0.102
Water column chl a	-0.393	-0.316	-0.036	-0.465	0.264	0.181	0.338	0.244	0.908		0.001	0.000	0.042	0.003	0.030	0.012	0.021	0.004	0.143	0.012	0.436
Turbidity	0.105	0.153	-0.281	-0.114	0.007	0.043	0.251	-0.128	0.710	0.631		0.038	0.339	0.012	0.006	0.083	0.023	0.027	0.038	0.039	0.436
Salinity mean	-0.171	-0.135	0.351	-0.161	0.025	0.004	0.019	-0.007	0.604	0.668	0.427		0.000	0.005	0.831	0.012	0.152	0.155	0.604	0.068	0.022
Salinity variability	0.482	0.502	0.256	0.529	0.575	0.624	0.462	0.234	-0.447	-0.419	-0.204	-0.709		0.255	0.229	0.046	0.479	0.605	0.463	0.089	0.073
Thalassia leaf C:P	0.423	0.436	0.036	0.424	0.304	0.358	0.107	-0.003	-0.758	-0.582	-0.502	-0.423	0.555		0.000	0.012	0.027	0.004	0.095	0.064	0.368
Thalassia leaf C:N	-0.210	-0.283	-0.244	-0.184	-0.507	-0.538	-0.553	-0.198	-0.416	-0.444	-0.344	-0.544	0.046	-0.762		0.152	0.605	0.002	0.497	0.681	0.138
Thalassia shoot mass	-0.512	-0.557	-0.232	-0.512	-0.553	-0.621	-0.417	-0.181	0.639	0.506	0.361	0.423	-0.715	-0.632	0.152		0.000	0.958	0.024	0.006	0.123
Total epiphyte abundance	-0.441	-0.476	-0.331	-0.387	-0.438	-0.489	-0.335	-0.019	0.588	0.468	0.463	0.300	-0.487	-0.601	-0.011	0.830		0.000	0.000	0.000	0.352
Autotrophic epiphyte abund.	-0.430	-0.407	-0.158	-0.459	-0.314	-0.360	-0.170	-0.063	0.630	0.570	0.451	0.447	-0.561	-0.349	-0.146	0.820	0.905		0.000	0.000	0.002
Total epiphyte load	-0.259	-0.276	-0.325	-0.173	-0.220	-0.242	-0.173	0.127	0.384	0.308	0.425	0.111	-0.157	-0.384	-0.157	0.458	0.876	0.733		0.000	0.864
Autotrophic epiphyte load	-0.295	-0.233	-0.326	-0.338	-0.100	-0.123	0.022	0.025	0.505	0.504	0.425	0.378	-0.355	-0.192	-0.089	0.548	0.783	0.928	0.773		0.000
Autotrophic index	-0.159	-0.040	-0.326	-0.328	0.103	0.092	0.239	-0.110	0.342	0.430	0.167	0.464	0.373	-0.192	-0.312	0.323	0.199	0.597	0.037	0.663	

DISCUSSION

We measured gradients in water column nutrients, benthic nutrient availability, short shoot size of the seagrass *Thalassia testudinum*, and the abundance of epiphytes per short shoot in Florida Bay. During the March 1994 sampling, a period of maximal epiphyte abundance on seagrass in South Florida (Frankovich 1996), total epiphyte load and epiphyte chlorophyll load were weakly correlated with measures of nutrient availability, specifically phosphorus availability (PC3). Over the course of a year, we also measured the strong influence of a point source of nutrients on total epiphyte loads in the oligotrophic eastern part of Florida Bay. Our results demonstrate that, at the time of sampling, both water column and benthic nutrient availability may play a role in structuring the epiphytic community in this subtropical seagrass bed, but that the relationship between nutrient availability and epiphyte load alone cannot accurately predict the epiphyte loads at any station in Florida Bay.

There are large gradients in nutrient availability across Florida Bay, and biomass of phytoplankton and the dominant seagrass *Thalassia testudinum* has been shown to be phosphorus limited (Fourqurean et al. 1992a, 1993). We measured a host of factors related to nutrient availability; Principal Components Analysis indicated that the various proxies for nutrient availability could be reduced to 4 factors: inorganic nitrogen concentration, dissolved organic matter in the water column, phosphorus availability, and a factor related to benthic N availability and water column salinity (Table 4). Due to high rates of *in situ* biogenic mud production (Nelsen & Ginsburg 1986, Bosence 1989, Frankovich & Zieman 1994), the water column is the ultimate source of nutrients for the benthos of Florida Bay over geologic time. This results in the strong correlation between water column measures of N and P concentration with the N and P content of the seagrass leaves (Tables 3 & 4). Because other primary producers are P limited in Florida Bay, it is reason-

Table 4. PCA results. Factor loadings for 4 principal components (PC1, inorganic N; PC2, dissolved organic matter; PC3, phosphorus availability; PC4, salinity and *Thalassia testudinum* leaf N). Loadings are the correlation between the natural-log transforms of the data with the principal components. Correlations greater than 0.5 are highlighted in **bold** type. In total, the 4 principal components explained 86.3% of the variation in the original data set

Original variable	PC1	PC2	PC3	PC4
TIN	**0.971**	0.118	−0.080	−0.014
NH$_4^+$	**0.915**	0.212	−0.064	0.038
NO$_3^-$	**0.858**	−0.158	−0.076	−0.185
NO$_2^-$	**0.805**	0.138	−0.307	0.096
TON	0.075	**0.965**	−0.061	0.137
TN	0.253	**0.939**	−0.064	0.141
TOC	0.195	**0.872**	0.247	0.012
DIP	−0.409	**0.714**	−0.031	−0.067
TP	−0.337	0.162	**0.903**	0.264
Turbidity	0.190	0.024	**0.860**	0.109
Chl *a*	−0.377	0.270	**0.733**	0.380
Thalassia leaf C:P	0.328	0.259	**−0.738**	−0.179
Thalassia leaf C:N	−0.207	−0.462	−0.287	**−0.695**
Mean salinity	−0.147	−0.060	0.374	**0.864**
Variance explained	27.9%	25.5%	21.7%	11.2%

Fig. 11. *Thalassia testudinum*. Relationship between P availability and epiphyte chl *a* load in Florida Bay

able to expect that epiphytic algae within this system may also be P limited. At the time of sampling, both total epiphyte load and epiphyte chlorophyll load were significantly correlated with P availability in Florida Bay, suggesting that the autotrophic component of the epiphyte community may also be P limited.

P availability explained only 14% of the variation in total epiphyte load and 17% of the epiphyte chlorophyll load, but the majority of the variability in water column chl *a* concentrations has been described by water quality nutrient variables, particularly those of phosphorus availability (Fourqurean et al. 1993). A stepwise multiple linear regression revealed that 83% of the variation in water column chl a can be explained by total phosphorus concentrations (r = 0.91, p < 0.001). This disparity suggests that the factors controlling epiphyte accumulation are different from those controlling phytoplankton levels.

Relative P availability is a primary factor determining the biomass of benthic plants in Florida Bay (Fourqurean et al. 1992a), but it is not the only factor. Since 1987, Florida Bay has experienced the rapid decline in seagrass biomass in areas that formerly supported dense *Thalassia testudinum* communities; over 40 000 ha have been affected by this die-off (Robblee et al. 1991, Durako 1994). While the causes of this phenomenon are not well understood, the changes in the ecosystem caused by the death of the dominant primary producer have been followed closely. Epi-
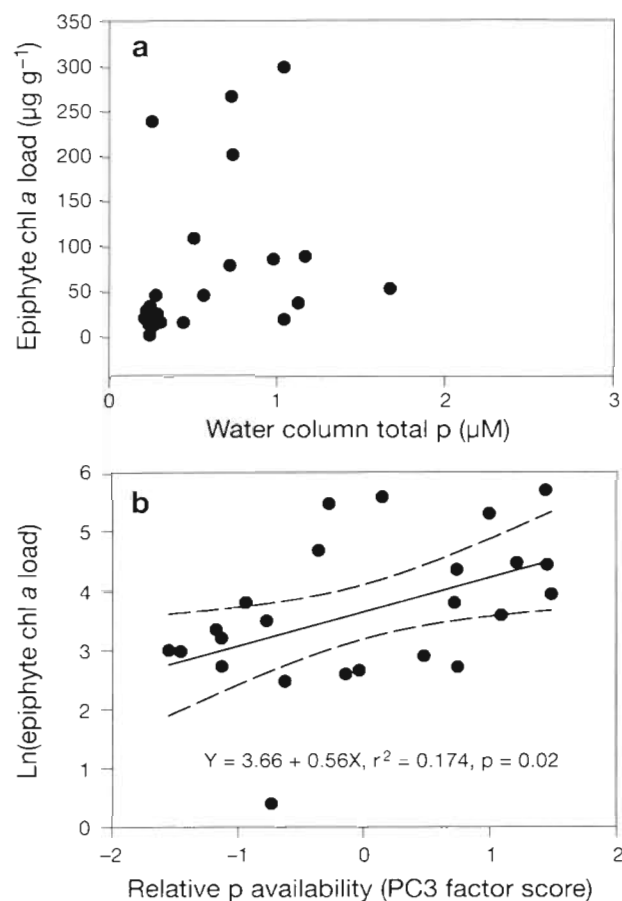
phytism did not play a role in the initial loss of seagrasses (Robblee et al. 1991, J.W.F. pers. obs.), but nutrient releases subsequent to the death of seagrasses led to increased phytoplankton concentrations in areas that had experienced seagrass mortality (Phlips & Badylak 1996). We also noted heavy accumulations of benthic diatoms on the leaves of surviving seagrasses in the months following the die-off; we believe that the increased microalgae in the water column and epiphytic on the seagrasses was stimulated by nutrients released by decaying seagrasses. Data on the N and P content of seagrass leaves from both before and after the die-off show that these nutrient releases did not appreciably change the regional pattern of relative N and P availability in Florida Bay. The spatial distributions of *T. testudinum* leaf C:P and C:N ratios measured in this study (Fig. 3) are identical to those observed prior to seagrass die-off (Fourqurean et al. 1992a). This indicates that the massive seagrass die-off that drastically decreased *T. testudinum* biomass and shoot density did not affect the wholesale distribution of nutrients within the ecosystem.

The amount of *Thalassia testudinum* leaf biomass determines the amount of space available for colonization and growth of epiphytic biomass because the leaf biomass to leaf area ratio is constant (T.A.F. unpubl. data). The trend of increasing *T. testudinum* short shoot size from eastern towards western Florida Bay (Fig. 2) was similar to the gradient in seagrass standing crop in the ecosystem (Zieman et al. 1989). The regional distribution of *T. testudinum* leaf biomass per short shoot (Fig. 2) and epiphyte abundance per short shoot (Fig. 5) showed a similar pattern. In Florida Bay, approximately 35% of the variation in epiphyte material on *T. testudinum* short shoots can be accounted for by leaf biomass alone (Frankovich 1996). The increase in epiphyte abundance (on a per short shoot basis) along this gradient was likely due to the increase in seagrass leaf substratum. In addition to epiphyte abundance on a per short shoot basis, total epiphyte loads were also greatest in western Florida Bay and were lowest within the tidally-restricted areas within central and northeastern Florida Bay.

The large differences in mean total epiphyte loads along the bird island transect were likely due to nutrient enrichment from bird defecation on Porjoe Key, a bird colony island. Eutrophication of the seagrass community causes biomass and species composition changes close to bird colonies in Florida Bay (Powell et al. 1991). The highest mean total epiphyte loads were always located at the transect point closest to the island (distance = 15 m). Epiphyte loads decreased drastically between the closest point and the 2 more distally located points (Fig. 8). Differences in epiphytic species composition were also observed along this transect. Various 'fleshy' rhodophytes and chlorophytes (*Chondria* sp., *Ceramium* spp., *Laurencia* spp., and *Derbesia* sp.) were abundant close to the island (15 m). Lesser amounts of *Chondria* sp. were observed at the middle transect point (distance = 30 m), while epiphyte composition furthest from the island (45 m) was dominated by animal epiphytes (especially the epiphytic bivalves *Pinctada imbricata* and *Brachidontes exustus*). Along a similar transect at Porjoe Key, Powell et al. (1991) documented an increase in seagrass biomass and a change in seagrass species composition from *Thalassia testudinum* to *Halodule wrightii* as distance decreased from the bird island. These changes in seagrass biomass and species composition are coincident with the changes in epiphyte loads and species composition of the present study. The absence of significant differences in the total epiphyte loads at 30 and 45 m from the island and the observed change in epiphytic species composition along the transect suggest that the effect of bird colony nutrient enrichment on epiphyte levels is pronounced but very localized, not extending even 30 m from the island. In contrast, seagrass stand-

ing crop was enhanced up to 200 m from the bird island (Powell et al. 1991) and the nutrient content of the seagrass biomass showed elevated phosphorus as far as 90 m from the bird island (Fourqurean et al. 1992a). These findings suggest that seagrass biomass, species composition, and nutrient content are more sensitive indicators of nutrient availability than epiphyte load.

The trend of decreasing epiphyte chlorophyll loads from northwest to northeast Florida Bay and Barnes Sound was coincident with a gradual shift from algal epiphytes in western Florida Bay to animal epiphytes in the more tidally-restricted central and eastern areas of the bay (Table 1). The relative importance of algal epiphytes to the total epiphyte community, as measured by the AI, was minimum in the northeast parts of Florida Bay, and maximum in the southwest part of the bay (Fig. 7). Even though, at the time of sampling, no relationship was observed between epiphyte load and salinity or the variability thereof (p > 0.05), the salinity and the range in salinity that an individual site experiences may be a prominent factor in the epiphytic species composition at that site. The paucity of epiphytic coralline red algae and the occurrence of the epiphytic bivalves *Pinctada imbricata* and *Brachidontes exustus* in the eastern and central areas of Florida Bay is coincident with high and very often variable salinities experienced in those areas (Fig. 9; Schomer & Drew 1982, Robblee et al. 1989, Fourqurean et al. 1993). Harlin et al. (1985) attributed the decrease in the density of epiphytic coralline red algae in the interior of Shark Bay, Western Australia, to increases in hypersalinity. In contrast, the relative abundance of the previously mentioned epiphytic molluscs in the interior of Florida Bay has been attributed to their ability to withstand 'large salinity fluctuations and other effects of poor circulation' (Turney & Perkins 1972). Along a hypersalinity gradient in Shark Bay, the diversity and density of epiphyte species decreased significantly as levels of hypersalinity increased (Harlin et al. 1985, Kendrick et al. 1988). The standing crop of epiphytic diatoms on *Halodule wrightii* also decreased significantly along a hypersalinity gradient in south Texas (Jewett-Smith 1991).

Traditionally, increased epiphyte levels and elevated water column nutrient concentrations were pointed to as evidence of nutrient enrichment (Cambridge & McComb 1984, Silberstein et al. 1986, Larkum & West 1990, Tomasko & Lapointe 1991), which subsequently led to declines in seagrass ecosystem health (see Duarte 1995 for review). Recent studies have shown that these traditional indicators do not fully describe nutrient availability within the ecosystem (Bulthuis et al. 1992, Neckles et al. 1993, 1994, Lin et al. 1996, Moore et al. 1996, Tomasko et al. 1996, Nelson & Waaland 1997). Active uptake of increased nutrient loading

Table 5. Total epiphyte loads, total dissolved inorganic nitrogen (DIN) and dissolved inorganic phosphorus (DIP) found for seagrasses at various locations. Epiphyte loads are expressed as percent of total seagrass blade + epiphyte biomass

Epiphyte load	DIN (µM)	DIP (µM)	Seagrass	Location	Source
5.3–43.9	0.14–3.96	0.03–0.43	*Thalassia testudinum*	Florida, USA Caribbean	Tomasko & Lapointe (1991)
9–77	43–52	–	*Thalassia testudinum*	Florida, USA	Tomasko et al. (1996)
11	22	1.73	*Zostera marina*	Washington, USA	Nelson & Waaland (1997)
6.5–87.5	3–22	0.3–1.5	*Zostera marina*	Virginia, USA	Moore et al. (1996)
2.2–61.1	1 2–22	0.01–0.33	*Thalassia testudinum*	Florida, USA	Present study
27.3[a]	4.9[a]	0.03[a]			

[a]Median of observed values

keeps water column nutrient concentrations low (Lin et al. 1996) and top-down grazer control of epiphyte or macroalgal biomass may mask any obvious effect of nutrient enrichment (Neckles et al. 1993, 1994, Williams & Ruckelshaus 1993). Grazing pressure was found to have stronger effects on epiphyte biomass than either increases in nutrient loading (Neckles et al. 1993) or changes in leaf turnover rate (Borum 1987). It can be hypothesized that, during the time of sampling, the nutrient concentration gradient in Florida Bay (particularly that of P availability), though pronounced, is under the threshold for epiphyte superabundance. TIN and DIP concentrations in Florida Bay are low relative to levels measured in other seagrass ecosystems (Table 5). Phosphorus, the limiting nutrient to primary production in Florida Bay (Fourqurean et al. 1992a) and other tropical carbonate environments (Short et al. 1990), is extremely low. At the time of sampling, median DIP concentration in Florida Bay was lower or equal to that measured in other environments (Table 5), yet the total epiphyte loads measured in Florida Bay (Frankovich & Zieman 1994, present study) span the entire range of those measured in other locations (Table 5). At the present level of epiphyte productivity, other unmeasured factors (grazing pressure, current regimes, etc.) may exert sufficient control over epiphyte accumulation. In Florida Bay, only in the immediate proximity to the bird island, a point source of nutrients, and along the northwestern boundary of Florida Bay was phosphorus availability high enough to cause increases in epiphyte levels. The uptake and storage of nutrients by seagrasses (Fourqurean et al. 1992a, b) and their resistance to grazing pressure (Harrison 1989) make them ideal bio-indicators of ecosystem health. This study has shown that epiphyte levels are not very sensitive to moderate nutrient enrichment. Elevated water column nutrient concentrations and increased epiphyte loads are obvious but, unfortunately, may be late indicators of nutrient enrichment, and these symptoms may only become evident when seagrass ecosystems are already in decline.

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