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TOTAL EPIPHYTE AND EPIPHYTIC CARBONATE PRODUCTION ON *THALASSIA TESTUDINUM* ACROSS FLORIDA BAY

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ABSTRACT

Previous investigations of epiphytic carbonate production have suggested that seagrass epiphytes are significant producers of calcium carbonate and may be a primary source of lime muds in Florida Bay. This study determined total epiphyte and epiphytic carbonate standing stocks and calculated minimum estimates of yearly production at seven sites within Florida Bay and one site oceanside of the northern Florida Keys. These sites span a larger geographical area of increased environmental variability than those of previous Florida Bay epiphyte studies which were conducted in areas where conditions are considered favorable for epiphyte production. Total epiphyte and epiphytic carbonate loads along with seagrass shoot density and productivity were measured during four periods between August 1991 and August 1992. Epiphyte composition, standing stock, and production all exhibited marked variation across Florida Bay. Calcifying epiphytes were dominant in Florida Bay, and their distribution and the distribution of epiphyte production appear to reflect differences in the physical characteristics of salinity and the variability thereof. Minimum estimates of annual epiphytic carbonate production range from 1.9 g $CaCO_3 \cdot m^{-2} \cdot yr^{-1}$ to 282.7 g $CaCO_3 \cdot m^{-2} \cdot yr^{-1}$, a range lower than previous estimates. The differences between these estimates and previous ones are attributed to differences in environments and, to a lesser extent, differences in methodology.

Many investigators have constructed carbonate budgets to attempt to explain the origin of carbonate sediments (see Bosence, 1989 for review). Lowenstam (1955) was the first to hypothesize that the lime muds could be of biogenic origin as opposed to other studies which suggested that the physical precipitation of aragonite was the dominant calcifying process (Cloud, 1962; Broecker and Takahashi, 1966). Stockman et al. (1967) estimated calcium carbonate production by the green algae of the genus *Penicillus* and concluded that this production could account for all of the aragonitic mud in the inner Florida Reef Tract and one-third of the aragonite mud in northeastern Florida Bay. Later studies indicated that carbonate production by seagrass epiphytes can far exceed that of other biogenic carbonate producers (Table 1), especially in semi-restricted lagoonal environments.

Land (1970) produced the first estimate of epiphytic carbonate production. The coralline red algae *Melobesia membranacea* and *Fosliella farinosa* (Humm, 1964), which produce high magnesium calcite, and an unidentified serpulid worm, which produces aragonite, were identified as common epiphytes of the seagrass *Thalassia testudinum* in Discovery Bay, Jamaica. These epiphytes were estimated to produce as much as 180 g $CaCO_3 \cdot m^{-2} \cdot yr^{-1}$. This estimate was based on epiphyte standing crop data and on a qualitative estimate of epiphyte productivity (Land, 1970).

Patriquin (1972) refined the methodology for obtaining epiphytic carbonate production estimates by measuring leaf growth rates of *Thalassia testudinum.* He estimated carbonate mud production at Barbados as 2,800 $g \cdot m^{-2} \cdot yr^{-1}$. The first extensive field study of epiphytic calcium carbonate production, which also addressed seasonal and aerial variations in the standing crop of calcareous epiphytes, was performed by Nelson and Ginsburg (1986) in southeastern Florida Bay. They

Table 1. Calcium carbonate production by seagrass epiphytes compared with production of other calcifying organisms

Seagrass/organism, location	Production (g $CaCO_3 \cdot m^{-2} \cdot yr^{-1}$)	Reference
Epiphytes		
Thalassia testudinum, Jamaica	40–180	Land, 1970
T. testudinum, Barbados	2,800	Patriquin, 1972
T. testudinum, Florida Bay, USA	30–303	Nelsen and Ginsburg, 1986
Amphibolis antarctica, Shark Bay, Australia	50–526	Walker and Woelkerling, 1988
T. testudinum, Florida Bay, USA	81–482	Bosence, 1989
Other organisms		
Foraminifera, Florida Bay, USA	0.1–1.8	Bosence, 1989
Molluscs		
Biscayne Bay, USA	3.74–309	Moore, 1972
Florida Bay, USA	7–64	Bosence, 1989
Penicillus		
Florida Bay, USA	3.2	Stockman et al., 1967
	1–41	Bosence, 1989
Halimeda		
Card Sound, USA	0.1–10.4	Bach, 1979
Tavernier Mound, USA	23–103	Bosence et al., 1985
Florida Bay, USA	5–30	Bosence, 1989
Porites		
Tavernier Mound, USA	1,475	Bosence et al., 1985
Florida Bay, USA	14–1,170	Bosence, 1989

estimated an annual production of epiphyte carbonate of 118 $g \cdot m^{-2} \cdot yr^{-1}$, and concluded that this production could account for all of the mud-sized high magnesium calcite and aragonite within the study area.

Walker and Woelkerling (1988) estimated that production decreased from 526 $g \cdot m^{-2} \cdot yr^{-1}$ to 50 $g \cdot m^{-2} \cdot yr^{-1}$ along a hypersalinity gradient in Shark Bay, Western Australia. Bosence (1989) determined epiphytic carbonate production in two areas of Florida Bay: a semi-restricted lagoonal area and a well-flushed outer lagoonal area. Epiphytic carbonate production estimates were related to production estimates for other calcifying organisms found within the bay. Epiphytes of *Thalassia testudinum* produced more carbonate than other calcareous organisms with differences between epiphytes and other organisms being much smaller at the well-flushed site due to the presence of the coral *Porites* (Bosence, 1989).

The importance of the organic portion of epiphyte production has been largely ignored by those who have been estimating epiphyte inorganic (carbonate) production. Besides their importance as major sediment producers, seagrass epiphytes are also significant primary producers in seagrass ecosystems (Penhale, 1977; Heijs, 1984, 1985b, 1987; Morgan and Kitting, 1984; Kitting et al., 1984). Epiphytes may provide a primary source of organic carbon to higher trophic levels (Fry and Parker, 1979; Kitting et al., 1984), either through direct grazing by herbivores or via the microbial food web. Epiphyte detritus may have more trophic importance than seagrass detritus because of the large amount of structural tissue and phenolic compounds in seagrasses (Harrison, 1989).

In Papua New Guinea, the organic portion of epiphytes, estimated as ash-free dry weight (AFDW), comprised 20–29% of the total epiphyte standing stock (Heijs, 1984). The rest of the standing stock was assumed to be calcium carbonate. This organic portion of coralline epiphytes may be preserved in sediments, and through the use of modern technology such as GC-MS or GC-IRMS (Gas Chromatography-Isotope Ratio Mass Spectrometry), it may be possible to infer the source of the associated inorganic carbonate (S. A. Macko, pers. comm.).

The seagrass meadows of Florida Bay, which are dominated by the seagrass *Thalassia testudinum* (Zieman et al., 1989), are ideal areas in which to conduct investigations of total epiphyte and epiphytic carbonate production. One striking feature of Florida Bay is the difference in the size and extent of the carbonate mudbanks between the western and eastern portions of the bay (Wanless and Tagett, 1989). The mineralogy of the mud fraction of these banks consists of predominantely aragonite with smaller amounts of high-magnesium calcite (Bosence et al., 1985). Coralline red algae may be the sole contributors to the high-Mg calcite mud fraction. Benthic foraminifera also produce high-Mg calcite, but their estimated annual production amounts to less than 2 g $CaCO_3 \cdot m^{-2} \cdot yr^{-1}$ (Bosence, 1989). The tests of these benthic foraminifera are also believed to breakdown to larger non-mud size fractions (R. N. Ginsburg, pers. comm. 1992). Thus epiphyte production may contribute significantly to the accumulation of carbonate sediments within Florida Bay, and may produce sediments which can be transported downstream of Florida Bay. The following questions may be postulated: Is it possible that epiphyte production is greater in western Florida Bay?, and if so, could this difference explain the differences in bank morphology?

We estimate total epiphyte and epiphytic carbonate production on *Thalassia testudinum* using a new methodology which, in addition to measuring the total amount of epiphytic material, is believed to more accurately determine epiphytic carbonate loads and standing stocks. This new methodology combines previously published techniques (Patriquin, 1972; Penhale, 1977) with direct measurements of seagrass productivity (Zieman, 1974; 1975; Zieman et al., 1989) to produce minimum estimates of annual epiphyte production. Estimates are produced for seven sites within Florida Bay and at one site oceanside of the northern Florida Keys (Fig. 1). These sites span a larger geographical area and have greater environmental variability than the sites of the previous epiphyte studies conducted within Florida Bay (Nelson and Ginsburg, 1986; Bosence, 1989). Previous investigations were conducted in the southeastern and southwestern edges of the bay, in areas characterized by conditions (tidal flushing, near-normal seawater salinities) believed to be favorable for increased epiphytic carbonate production (Johansen, 1981; Harlin et al., 1985; Walker and Woelkerling, 1988). The restricted circulation and high evaporation within the interior of the bay cause water conditions to vary spatially and temporally from brackish to hypersaline (Robblee et al., 1989), resulting in physical and biological gradients along a northeast to southwest transect (Schomer and Drew, 1982; Robblee et al., 1989; Tilmant, 1989). The biomass and productivity of *Thalassia* also show large but predictable variability across these gradients (Zieman et al., 1989). Therefore, the biomass and productivity of the associated epiphytes would similarly be expected to exhibit marked variation, with lower epiphyte production expected towards the more-restricted interior of Florida Bay.

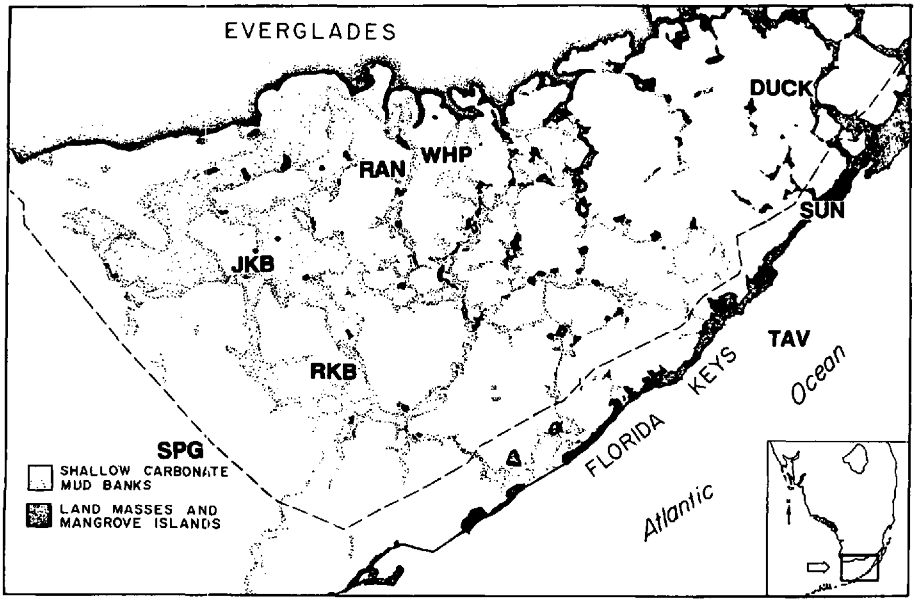

Figure 1. Location map of Florida Bay. Epiphyte production stations are indicated by abbreviations: DUCK = Duck Key, SUN = Sunset Cove, WHP = Whipray Basin, RAN = Rankin Lake, JKB = Johnson Key, RKB = Rabbit Key, SPG = Sprigger Bank, TAV = Tavernier Key.

Methods and Materials

Minimum annual epiphyte productions in terms of carbonate and total epiphyte mass, were determined by multiplying mean epiphyte standing stocks by the estimated number of seagrass crops per year (Fig. 2). The majority of production by seagrass epiphytes was assumed to occur on attached seagrass blades. Some production is believed to occur on detrital leaves detached from their corresponding short shoots, thus the epiphyte production estimates should be considered minimum. To determine the variability of these parameters across Florida Bay, measurements of epiphyte load (the amount of epiphytic material per shoot), seagrass shoot density and seagrass productivity were made at each of seven sites within Florida Bay and at one site oceanside of the northern Florida Keys (Fig. 1). These sites are representative of the various habitat types within Florida Bay and were chosen because of ongoing monitoring of seagrass productivity during the study period at these sites.

Epiphyte Load.—The following definition applies to all the epiphytes sampled in this investigation and is a modification of that of Harlin (1980). An epiphyte is any organism that lives upon a plant and completes its production while it is attached to that plant. This definition includes the coralline red algae as well as the mollusc *Pinctada,* but excludes mobile gastropods and benthic foraminifera which are able to move between leaves, and thus are likely to produce for longer periods of time.

At each site, 10 random *Thalassia* shoots were collected during August of 1991 and the months of January, March, and June of 1992. These shoots were brought back to the laboratory where the leaves were separated from each short shoot, rinsed in fresh water to remove salt and any adhered sediment, and frozen in separate zipper-lock freezer bags for each *Thalassia* shoot. The frozen leaves were lyophilized (freeze-dried) enabling the easy separation of calcareous epiphytes from the leaves by scraping with a spatula (Penhale, 1977). Total epiphyte load (g dw·shoot^{-1}) was measured by weighing the separated freeze-dried epiphytes in tared scintillation vials.

To determine epiphyte load in terms of grams of $CaCO_3$ per shoot, the lyophilized epiphytes were acidified with 5% HCl (V/V). The acid solution was then titrated for calcium and magnesium utilizing the EDTA titrimetric method for hardness (APHA et al., 1989; Patriquin, 1972). Total carbonate as grams of $CaCO_3$ was then determined stoichiometrically.

Seagrass Shoot Density.—At each of the eight sites *Thalassia testudinum* shoot density was measured during each of the previously stated time periods. *Thalassia* shoots were counted within six replicate quadrats which were randomly placed on the bottom at each sampling site during each of the sampling periods. Quadrats were 10·20 cm in dimension.

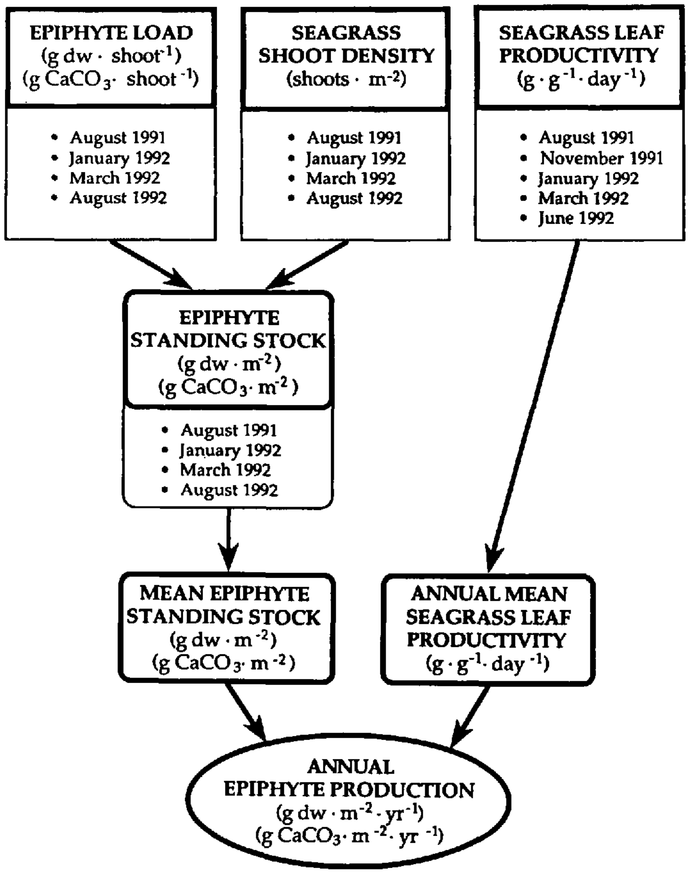

Figure 2. A flowchart illustrating how the three measured parameters (Epiphyte Load, Seagrass Shoot Density, and Seagrass Leaf Productivity) result in estimates of Annual Epiphyte Production. Bold squared boxes indicate measured parameters while bold rounded boxes indicate calculated quantities. Months given inside unbolded boxes are the sampling periods. The units of measured and calculated quantities are given in parentheses.

Seagrass Leaf Productivity.—*Thalassia testudinum* leaf productivity was measured during August and November of 1991 and January, March, and June of 1992 with the leaf marking method (Zieman, 1974, 1975; Zieman et al., 1989).

At each site, each *Thalassia* short shoot within six replicate 10·20 cm quadrats was perforated at the sediment-water interface with a syringe needle. Current practice has shown that punching with an appropriately sized needle is superior to stapling. The marked leaves were allowed to grow for approximately 2 weeks, after which all the short shoots within the quadrants were harvested at the sediment-water interface. Unperforated blades and portions of the blades below the perforation, considered to be new growth, were separated from the rest of the leaf material. All leaf material was washed in 5% HCl (V/V) and oven-dried at 85°C. Specific leaf production or the leaf turnover rate ($g \cdot g^{-1} \cdot day^{-1}$) is the ratio of the dry weight of new growth to the total dry weight of attached leaves (above-ground standing crop) divided over the time of the growth period measured. The number of seagrass/epiphyte crops per year was estimated by multiplying the annual mean specific growth rate by 365 days.

RESULTS

Epiphyte Community Composition.—The coralline red algae *Melobesia membranacea* and *Fosliella farinosa* and the serpulid worm *Spirorbis* sp. were the most

Table 2. Mean total epiphyte load and mean epiphytic carbonate load of ten random *Thalassia* shoots from each site located in Figure 1 at each sampling period. Epiphyte loads are given as mean and coefficient of variation (sample standard deviation/sample mean).

Site	Sampling period			
	August 1991	January 1992	March 1992	August 1992
	Total epiphyte load (mg dw·shoot^{-1})			
Duck Key	1.17 (±97%)	10.77 (±263%)	23.84 (±201%)	2.20 (±110%)
Sunset Cove	6.77 (±81%)	64.08 (±156%)	256.19 (±120%)	101.41 (±215%)
Whipray Basin	25.10 (±53%)	9.19 (±71%)	1.67 (±101%)	9.93 (±64%)
Rankin Lake	—	37.10 (±81%)	93.93 (±93%)	18.72 (±69%)
Johnson Key	11.94 (±53%)	55.00 (±62%)	322.87 (±36%)	7.72 (±54%)
Rabbit Key	7.48 (±88%)	40.17 (±39%)	17.46 (±116%)	23.63 (±126%)
Sprigger Bank	202.41 (±56%)	146.40 (±49%)	340.77 (±61%)	592.80 (±15%)
Tavernier Key	37.71 (±114%)	17.04 (±74%)	27.11 (±58%)	38.34 (±45%)
	Epiphytic carbonate load (mg $CaCO_3$·shoot^{-1})			
Duck Key	0.29 (±149%)	5.12 (±233%)	12.36 (±159%)	0.91 (±133%)
Sunset Cove	0.79 (±83%)	29.07 (±160%)	190.93 (±131%)	69.07 (±259%)
Whipray Basin	4.16 (±56%)	2.30 (±46%)	0.32 (±84%)	4.28 (±72%)
Rankin Lake	—	18.17 (±61%)	48.91 (±88%)	4.88 (±75%)
Johnson Key	1.69 (±64%)	35.67 (±68%)	205.09 (±52%)	0.86 (±61%)
Rabbit Key	4.62 (±110%)	26.90 (±43%)	14.31 (±120%)	16.77 (±129%)
Sprigger Bank	150.64 (±56%)	111.96 (±48%)	252.31 (±56%)	421.84 (±16%)
Tavernier Key	21.83 (±69%)	14.39 (±77%)	21.21 (±58%)	32.83 (±47%)

common epiphytes present on the sampled leaves of *Thalassia testudinum.* Coralline red algae were most abundant at Sprigger Bank and at Tavernier Key and also during the March 1992 sampling period at Johnson Key. *Spirorbis* occurred at every site but was most common at Rabbit Key. Other common calcifying epiphytes samples include the bivalve *Pinctada imbricata,* which was most common in Sunset Cove, and the bivalve *Brachidontes exustus,* which was most common at Rankin Lake. Distribution of these two molluscs was patchy, but due to their large size relative to other epiphytes, *Pinctada* and *Brachidontes* contributed significantly to total epiphyte and epiphytic carbonate production at these two sites. Non-calcareous algae were not as common as the calcareous epiphytes at the study sites but those which were observed include the red algae *Laurencia* spp., *Ceramium* spp., and *Chondria* spp., and the winter-occurring brown algae *Cladosiphon occidentalis,* which occurred at Sprigger Bank during the January 1992 sampling period. A green tunicate *Perophora* sp. was present at the Johnson Key site during all sampling periods. Uncommon epiphytes sampled include the chicken liver sponge *Chondrilla nucula,* the variable encrusting tunicate *Botryllus planus,* the flat tunicate *Botrylloides nigrum,* and the mollusc *Crepidula* sp.

Epiphyte Load.—Epiphyte loads (the amount of epiphytic material on seagrass shoots) in terms of both total epiphyte weight and epiphytic carbonate weight varied greatly across Florida Bay. Total epiphyte load ranged from 0.00 to 750.24 mg per shoot, while epiphytic carbonate load ranged from 0.00 to 512.62 mg per shoot. The maximum values were obtained from one *Thalassia testudinum* shoot sampled from Sprigger Bank during the August 1992 sampling period. Epiphytic carbonate consisted of approximately 70% of the total epiphyte dry weight for all *Thalassia* shoots sampled, and the majority of the *Thalassia* shoots had total epiphyte loads less than 100 mg per shoot.

Inter-site variation in mean total epiphyte loads and mean epiphytic carbonate loads (Table 2) spanned two orders of magnitude and was greater than intra-site

Table 3. Mean *Thalassia* shoot density for each of the sampling periods at each of the sites located in Figure 1. Shoot densities are given as mean and coefficient of variation (sample standard deviation/sample mean).

Site	Sampling period			
	August 1991	January 1992	March 1992	August 1992
	Thalassia shoot density (shoots·m^{-2})			
Duck Key	833 (±33%)	825 (±27%)*	800 (±31%)	367 (±56%)
Sunset Cove	725 (±36%)	925 (±27%)	958 (±21%)	692 (±32%)
Whipray Basin	47 (±53%)	283 (±55%)	392 (±26%)	250 (±54%)
Rankin Lake	883 (±30%)	958 (±30%)	700 (±26%)	900 (±26%)
Johnson Key	908 (±39%)	725 (±36%)	708 (±32%)	492 (±47%)
Rabbit Key	1,442 (±14%)	975 (±66%)	1,475 (±13%)	1,233 (±24%)
Sprigger Bank	430 (±21%)	325 (±44%)	240 (±27%)	150 (±42%)
Tavernier Key	625 (±32%)	825 (±24%)	608 (±33%)	492 (±39%)

* Estimated from density measurements taken in January and June of 1992.

variation. Inter-site variation for both mean total epiphyte loads and mean epiphytic carbonate loads was also greater than the intra-site seasonal differences. Mean total epiphyte load ranged from 1.17 mg dw·shoot^{-1} at Duck Key during the August 1991 sampling period to 592.80 mg dw·shoot^{-1} at Sprigger Bank during the August 1992 sampling period. The mean epiphytic carbonate load ranged from 0.29 mg $CaCO_3$·shoot^{-1} at Duck Key during the August 1991 sampling period to 421.84 mg $CaCO_3$·shoot^{-1} at Sprigger Bank during the August 1992 sampling period. Sprigger Bank had the highest mean total epiphyte loads and mean epiphytic carbonate loads at all times measured, while Duck Key had the lowest mean total epiphyte loads at 50% of all times measured and Whipray Basin had the lowest mean epiphytic carbonate loads at 50% of all times measured.

Seagrass Shoot Density.—Mean *Thalassia testudinum* shoot density varied considerably between sites, ranging from 47 shoots·m^{-2} in Whipray Basin to 1,475 shoots·m^{-2} at Rabbit Key (Table 3). The highest shoot densities were at Rabbit Key at all times measured, while the lowest shoot densities were at Sprigger Bank and Whipray Basin. In Rankin Lake and Whipray Basin, which were severely affected by seagrass die-off (Robblee et al, 1991), *Thalassia* distribution was very patchy. The high shoot densities measured at the Rankin Lake site are representative of the remaining dense "islands" of grass within surrounding bare areas of former seagrass die-off. The anomalously low shoot density at the Whipray Basin site during August of 1991 may be the result of recent seagrass die-off or more likely it is the result of patchiness. The sampling design was not sensitive enough to detect actual seasonal changes in shoot density, but the inter-site variation in shoot density appeared greater than intra-site seasonal variation.

Epiphyte Standing Stock.—Epiphyte standing stocks (g dw·m^{-2} or g $CaCO_3$·m^{-2}) were calculated from epiphyte load (g dw·shoot^{-1} or g $CaCO_3$·shoot^{-1}) estimates and seagrass shoot density estimates. Total epiphyte standing stocks ranged from 0.7 g dw·m^{-2} in Whipray Basin to 245.4 g dw·m^{-2} in Sunset Cove (Table 4); both of which were form the March 1992 sampling period. Epiphytic carbonate standing stocks ranged from 0.1 g dw·m^{-2} in Whipray Basin to 182.9 g dw·m^{-2} in Sunset Cove (Table 4); both of which were also from the March 1992 sampling period.

The mean total epiphyte standing stocks for the four sampling periods were also lowest for Whipray Basin (1.7 g $CaCO_3$·m^{-2}) and highest for Sunset Cove

Table 4. Total epiphyte standing stocks and epiphytic carbonate standing stocks for each of the sampling periods at each of the sites located in Figure 1. Coefficients of variation of monthly standing stocks obtained from the variance of the product of epiphyte load and seagrass shoot density $\sigma^2(X) = \bar{X}^2\sigma^2(x_1)\bar{x}_1^{-2} + \bar{X}^2\sigma^2(x_2)\bar{x}_2^{-2}$ (Volk, 1958).

Site	Sampling period: August 1991	January 1992	March 1992	August 1992	Mean
	Total epiphyte standing stock (g $dw \cdot m^{-2}$)				
Duck Key	1.0 (±102%)	8.9 (±228%)	19.2 (±158%)	0.8 (±123%)	7.5 (±100%)
Sunset Cove	5.0 (±89%)	59.3 (±157%)	245.4 (±82%)	70.2 (±83%)	95.0 (±95%)
Whipray Basin	1.2 (±75%)	2.6 (±90%)	0.7 (±104%)	2.5 (∓84%)	1.7 (±48%)
Rankin Lake	—	35.5 (±66%)	65.7 (±90%)	16.8 (±74%)	39.4 (±51%)
Johnson Key	11.3 (±66%)	39.9 (±72%)	228.6 (±48%)	3.8 (±72%)	70.9 (±130%)
Rabbit Key	11.3 (±89%)	39.2 (±77%)	25.8 (±117%)	29.1 (±128%)	26.3 (±38%)
Sprigger Bank	89.1 (±60%)	47.6 (±66%)	81.8 (±67%)	88.9 (±45%)	76.8 (±22%)
Tavernier Key	23.6 (±118%)	14.0 (±78%)	16.5 (±67%)	18.8 (±60%)	18.2 (±19%)
	Epiphytic carbonate standing stock (g $CaCO_3 \cdot m^{-2}$)				
Duck Key	0.3 (±153%)	4.2 (±79%)	10.0 (±83%)	0.3 (±144%)	3.7 (±107%)
Sunset Cove	0.6 (±90%)	26.9 (±231%)	182.9 (±112%)	47.8 (±105%)	64.5 (±109%)
Whipray Basin	0.2 (±77%)	0.7 (±72%)	0.1 (±88%)	1.1 (±90%)	0.5 (±75%)
Rankin Lake	—	17.4 (±68%)	34.2 (±80%)	4.4 (±79%)	14.0 (±95%)
Johnson Key	1.6 (±75%)	25.9 (±77%)	145.2 (±61%)	0.4 (±77%)	43.3 (±138%)
Rabbit Key	6.9 (±111%)	26.2 (±79%)	21.1 (±121%)	20.7 (±131%)	18.7 (±38%)
Sprigger Bank	66.3 (±60%)	36.4 (±65%)	54.1 (±63%)	63.3 (±45%)	55.0 (±21%)
Tavernier Key	13.6 (±76%)	11.9 (±81%)	12.9 (±67%)	16.2 (±61%)	13.6 (±12%)

(95.0 g $CaCO_3 \cdot m^{-2}$). These two sites also had the lowest and highest mean epiphytic carbonate standing stocks, 0.5 g $CaCO_3 \cdot m^{-2}$ and 64.5 g $CaCO_3 \cdot m^{-2}$, respectively.

Seagrass Leaf Productivity.—*Thalassia testudinum* leaf productivity measurements showed a predictable pattern with higher productivities measured during the summer months (August of 1991 and June of 1992) and the lowest measured productivities during the winter (January 1992) sampling period (Table 5). *Thalassia* leaf productivities ranged from 0.002 $g \cdot g^{-1} \cdot day^{-1}$ in Whipray Basin during the January 1992 sampling period to 0.022 $g \cdot g^{-1} \cdot day^{-1}$ on Sprigger Bank and at Tavernier Key, during the August 1991 sampling period.

Annual mean *Thalassia* leaf productivity was lowest at Whipray Basin, Rankin Lake, Johnson Key, and Rabbit Key (0.010 $g \cdot g^{-1} \cdot day^{-1}$) and highest at Tavernier Key (0.016 $g \cdot g^{-1} \cdot day^{-1}$). These low and high mean annual productivities correspond to 3.65 and 5.84 seagrass/epiphyte crops per year, respectively.

Annual Epiphyte Production.—Annual epiphyte productions were calculated from mean epiphyte standing stocks and annual mean seagrass leaf productivities. Total epiphyte productions ranged from 6.3 g $dw \cdot m^{-2} \cdot yr^{-1}$ in Whipray Basin to 416.0 g $dw \cdot m^{-2} \cdot yr^{-1}$ in Sunset Cove (Table 6). Epiphytic carbonate productions ranged from 1.9 g $CaCO_3 \cdot m^{-2} \cdot yr^{-1}$ to 282.7 g $CaCO_3 \cdot m^{-2} \cdot yr^{-1}$, also in Whipray Basin and Sunset Cove, respectively. Using the production figures from the seven sites within Florida Bay, total epiphyte and epiphytic carbonate production for Florida Bay as a whole was estimated as 188.4 g $dw \cdot m^{-2} \cdot yr^{-1}$ and 79.7 g $CaCO_3 \cdot m^{-2} \cdot yr^{-1}$, respectively.

Rates of Epiphytic Carbonate Accumulation.—Using the epiphytic carbonate production estimates, the density of solid carbonate (2.81 $g \cdot cm^{-3}$), and the average porosity of lime muds (50%) (Nelson and Ginsburg, 1986), rates of sediment

Table 5. Seagrass leaf productivities of *Thalassia testudinum* for each of the sampling periods at each of the sites located in Figure 1. Productivities are given as mean and coefficient of variation (sample standard deviation/sample mean).

Site	Sampling period					Annual mean	Crops·year^{-1}
	August 1991	November 1991	January 1992	March 1992	June 1992		
	Seagrass leaf productivity (g dw growth·g dw standing crop^{-1}·day^{-1})						
Duck Key	0.013 (±13%)	0.010 (±21%)	0.006 (±19%)	—	0.020 (±20%)	0.012 (±43%)	4.38
Sunset Cove	0.011 (±14%)	0.012 (±18%)	0.008 (±26%)	0.013 (±10%)	0.015 (±17%)	0.012 (±21%)	4.38
Whipray Basin	—	0.010 (±26%)	0.002 (±80%)	0.012 (±23%)	0.017 (±11%)	0.010 (±50%)	3.65
Rankin Lake	0.008 (±32%)	0.012 (±15%)	0.004 (±31%)	0.012 (±15%)	0.013 (±9%)	0.010 (±33%)	3.65
Johnson Key	0.016 (±24%)	0.009 (±16%)	0.004 (±20%)	0.009 (±12%)	0.012 (±13%)	0.010 (±41%)	3.65
Rabbit Key	0.015 (±11%)	0.007 (±8%)	0.004 (±34%)	0.009 (±14%)	0.015 (±12%)	0.010 (±46%)	3.65
Sprigger Bank	0.022 (±7%)	0.012 (±13%)	0.006 (±24%)	0.010 (±13%)	0.017 (±20%)	0.013 (±43%)	4.75
Tavernier Key	0.022 (±25%)	—	0.009 (±15%)	0.012 (±16%)	0.021 (±15%)	0.016 (±35%)	5.84

Table 6. Total epiphyte and epiphytic carbonate productions at each of the sites located in Figure 1. Carbonate mud accumulation rates are calculated for all sites except Sunset Cove and Rankin Lake which are dominated by molluscan epiphytes which break down into larger non-mud size fractions (Ginsburg, 1956). Productions are given as mean and coefficient of variation. Coefficients of variation obtained from the variance of the product of mean epiphyte standing stock and annual mean seagrass leaf productivity $\sigma^2(X) = \bar{X}^2\sigma^2(x_1)\bar{x}_1^{-2} + \bar{X}^2\sigma^2(x_2)\bar{x}_2^{-2}$ (Volk, 1958).

Site	Total epiphyte production ($g\ dw{\cdot}m^{-2}{\cdot}yr^{-1}$)	Epiphytic carbonate production ($g\ CaCO_3{\cdot}m^{-2}{\cdot}yr^{-1}$)	*Carbonate mud accumulation rate ($cm{\cdot}1{,}000^{-1}{\cdot}yr^{-1}$)
Duck Key	32.8 (±109%)	16.2 (±115%)	1.2
Sunset Cove	416.0 (±97%)	282.7 (±111%)	not applicable
Whipray Basin	6.3 (±69%)	1.9 (±90%)	0.1
Rankin Lake	143.7 (±61%)	51.1 (±101%)	not applicable
Johnson Key	258.8 (±136%)	157.9 (±144%)	11.2
Rabbit Key	96.1 (±60%)	68.4 (±60%)	4.9
Sprigger Bank	365.0 (±48%)	261.3 (±48%)	18.6
†Florida Bay mean	188.4	119.9	7.2
Tavernier Key	106.4 (±40%)	79.7 (±37%)	5.6

* Determined using density of solid carbonate (2.81 $g{\cdot}cm^{-3}$) and the average porosity of modern lime muds (50%) (Nelsen and Ginsburg, 1986).
† Determined from epiphyte productions of the Duck Key, Whipray Basin, Johnson Key, Rabbit Key and Sprigger Bank sites.

accumulation were calculated for Duck Key, Whipray Basin, Johnson Key, Rabbit Key, Sprigger Bank, and Tavernier Key. These sites were dominated by calcareous epiphytes which disintegrate into mud-sized sediments (Nelson and Ginsburg, 1986). The five of these site located within Florida Bay were used to estimate the average mud-sized sediment accumulation rate for Florida Bay as a whole (Table 6). These rates of epiphytic carbonate accumulation can be compared with the estimated historical average carbonate mud accumulation rate for high-magnesium calcite and aragonite in Florida Bay of 7.5 $cm{\cdot}1{,}000^{-1}{\cdot}yr^{-1}$ (Nelson and Ginsburg, 1986). Estimated epiphytic carbonate accumulation rates for Sprigger Bank and Johnson Key exceed this estimate of historical lime mud accumulation, but the mean epiphytic carbonate accumulation rate calculated for Florida Bay as a whole (7.2 $cm{\cdot}1{,}000^{-1}{\cdot}yr^{-1}$) does not.

Discussion

Seagrass epiphytes are important primary producers and producers of carbonate sediments. No previously published studies have coupled epiphytic carbonate production with total epiphyte production. With the notable exception of Walker and Woelkerling (1988), most investigations of epiphytic carbonate production were conducted in areas of limited geographical scope and in areas where conditions are considered favorable for epiphyte production. Because the environments and the biomass and productivity of *Thalassia testudinum* vary greatly across Florida Bay (Zieman et al., 1989), it is not surprising that epiphyte loads, standing stocks, and productions also vary greatly across the bay and are due to the production of a variety of organisms.

The dominant carbonate producing epiphytes sampled in this investigation were the coralline red algae *Melobesia membranacea* and *Fosliella farinosa* which precipitate high-magnesium calcite and the bivalve *Pinctada imbricata,* which precipitates aragonite. Of these two sets of organisms only the coralline red algae produce calcium carbonate which breaks down to mud-sized sediments (Ginsburg, 1956). Therefore, the dominant mud-sized carbonate sediment being produced is high-magnesium calcite. This appears to contradict the dominance of aragonite within the mud-sized sediments of Florida Bay. One explanation for this may be the incongruent dissolution of high-magnesium calcite which precipitates aragonite within the pore fluids of the carbonate mud sediments (Winland, 1969). Walter and Burton (1990) found that the dissolution of red algal substrates ranged from 10 to 50%·yr^{-1} in the iron-poor, organic-rich, and actively bioturbated sediments of Florida Bay.

Evaluation of Results.—Due to the short 1-year time extent of this investigation and the limited number of sampling periods (4) within this time span, the analysis of temporal trends in the data is beyond the scope of this investigation. Thus, the discussion is limited to examining the spatial differences in epiphyte loads and productions.

Epiphyte productions were determined from the product of the mean measurements of epiphyte load, seagrass shoot density, and seagrass productivity. As such, the variances of epiphyte productions were estimated utilizing the square of the partial derivative of the product (epiphyte production) with respect to each variable (epiphyte load, seagrass shoot density, seagrass productivity) (Volk, 1958). Because the variances of the productions are estimated, statistically significant differences between sites cannot be tested for using routine analysis of variance; therefore, intersite differences in epiphyte productions should be interpreted with discretion. The most reliable figures are those for epiphyte load, seagrass shoot density, and seagrass productivity.

Epiphyte productions should be viewed as minimum estimates for the following reasons. Epiphyte standing stocks do not measure epiphyte production which occurs on younger leaves during the time of one seagrass turnover period. The measurement of the amount of epiphyte material present at one point in time may underestimate epiphyte accumulation which occurs during the latter stages of the growth of the leaves which are youngest initially (Bulthuis and Woelkerling, 1983). Also, evidence of epiphyte removal and/or premature leaf loss due to herbivorous grazing existed at Sprigger Bank and Whipray Basin, probably by parrotfish (*Scarus* spp. and *Sparisoma* sp.) at Sprigger Bank, and the gastropod *Cerithium muscarum* in Whipray Basin (T.A.F., personal observation). Also some epiphyte production may occur on seagrass leaves that have already died and been released from the short shoot.

Inferring past epiphyte production rates from those presently calculated is highly speculative; therefore comparing calculated present-day epiphytic carbonate production rates with historical sedimentation rates should be done with extreme caution. Long-term investigations of epiphyte production which would provide some idea of year-to-year variability are lacking, but greatly needed. Because seagrasses serve as a substratum for the attachment of epiphytes, epiphyte production is highly dependent upon seagrass abundance. The distribution and abundance of *Thalassia testudinum* in Florida Bay is known to vary greatly over both long and short-term periods (Zieman et al., 1989; Robblee et al., 1991). The recent and continuing seagrass die-off in Florida Bay (Robblee et al., 1991) is drastically altering the present abundance and distribution of seagrasses. The comparison of epiphyte production rates with carbonate accumulation rates is tenuous also because the magnitude of carbonate dissolution losses from the sediments is largely unknown. The results of substrate incubation experiments suggest that dissolution of high-magnesium calcite may be significant, ranging between 10 to 50%·yr^{-1} (Walter and Burton, 1990).

Distribution of Epiphyte Production.—Epiphyte production was highest on Sprigger Bank and in Sunset Cove, but these productions were due to two separate sets of organisms. The epiphytes of *Thalassia testudinum* on Sprigger Bank, located on the western edge of Florida Bay, were almost entirely coralline red algae which completely encrusted the older leaves and the distal portions of the younger leaves. In contrast, the high epiphyte production in Sunset Cove, in the eastern part of the bay, was due primarily to the patchy occurrence of one relatively large epiphytic organism, the bivalve *Pinctada imbricata.* The conditions responsible for the success of one set of epiphytes are likely to be detrimental to the other. Most coralline red algae have a requirement for water motion (Johansen, 1981) and are most abundant in high energy areas (Humm, 1964; Willcocks, 1982; Heijs, 1985a). Sprigger Bank, which experiences strong tidal currents and the two ocean-facing sites of previous investigations (Land, 1970; Patriquin, 1972) are characterized by these conditions. *Pinctada,* on the other hand, is commonly found in lower energy areas (T.A.F., personal observation), and on windward bank margins (Bosence, 1989; T.A.F., personal observation). The higher energy at ocean-facing sites would likely remove these organisms from their seagrass host or cause premature leaf loss. *Pinctada* is also noted as being abundant in areas characterized by high and variable salinities (Turney and Perkins, 1972), while Harlin et al. (1985) found that the density of coralline red algae decreased markedly as salinity levels increased above that of normal seawater.

Sprigger Bank and Sunset Cove, the sites of highest epiphyte production, both lie within Ginsburg's (1956) zone of tidal exchange within Florida Bay. The Johnson Key and Rabbit Key sites lie along the boundary of this zone. Any effect of an increase in tidal exchange would likely be observed at these two sites. The high epiphyte production at Johnson Key was due to an anamolous "bloom" of coralline red algae during the March 1992 sampling period. The mean epiphyte load at Johnson Key was over 600% higher during this period than during any of the other sampling periods. Epiphyte production at the remaining sites within the more restricted areas of Florida Bay (Rankin Lake, Whipray Basin, and Duck Key) was substantially lower.

The lowest epiphyte production was at the Whipray Basin site. This site is presently characterized by very low *Thalassia testudinum* shoot densities, due to the massive seagrass die-off which began in the summer of 1987 (Robblee et al., 1991). This site is located in the shallow (≈1.0 m depth) northern part of that restricted basin, and is subject to large variations of temperature and salinity (Robblee et al., 1989). The combined effects of low *Thalassia* shoot density and extreme environmental conditions are most likely the factors severely limiting epiphyte production here.

Epiphyte production at Tavernier Key, the only site located outside Florida Bay, is due mainly to the light encrustation of the previously mentioned coralline red algae. This is the deepest of the sites (≈2.7 m MLW); all other sites are less than 2 m deep. Nelson and Ginsburg (1986) and Bosence (1989) both found that the standing stock of epiphytic carbonate decreased with depth. This increased depth and low leaf area index relative to the the other sites (J. C. Zieman, unpubl.) may provide some explanation for epiphyte production being lower than that expected for a site with significant tidal exchange.

The description of four sub-environments and a transition zone based upon water circulation, salinity characteristics, wind characteristics, and mollusc distribution in Florida Bay made by Turney and Perkins (1972) coincides with the distribution of epiphyte species and production. The seven Florida Bay sites of this study are located in three of the five areas described by Turney and Perkins (1972). The sites of Duck Key, Sunset Cove, Whipray Basin, and Rankin Lake are all located within the "Interior sub-environment," which was described as an area of restricted circulation and tidal exchange with large fluctuations in salinity

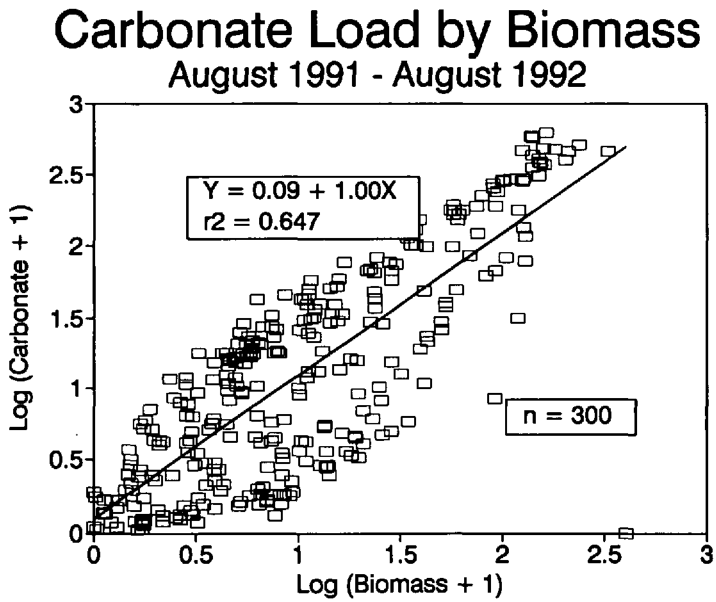

Figure 3. The relationship between epiphyte biomass (total epiphyte load-epiphytic carbonate load) and epiphytic carbonate load. The regression is highly significant ($P < 0.0005$), and explains 64.7% of the variation in epiphytic carbonate load.

due to seasonal variations in rainfall. This sub-environment was also characterized by long periods of turbidity. All of these conditions were also characteristic of this area during the present study. The molluscs *Brachidontes exustus* and *Pinctada imbricata* (formerly *P. radiata*) were "index species" (those species which were abundant in one sub-environment and absent in all others) of the "Interior sub-environment." The bivalves were also the dominant epiphytes at the Rankin Lake and Sunset Cove sites, respectively. Turney and Perkins (1972) attributed the relative abundance of these species to their ability to withstand large salinity fluctuations and other effects of poor circulation. The Rabbit Key and Johnson Key sites lie within the "Transition Zone" between the "Gulf" and "Interior" sub-environments. This is also coincident with the previously mentioned line of tidal influence (Ginsburg, 1956). The last Florida Bay site (Sprigger Bank) lies within the "Gulf sub-environment," which was characterized by "near normal" water temperatures and salinity. These conditions are also characteristic for those observed at Sprigger Bank during the duration of the study.

The great similarity in the "sub-environments" described by Turney and Perkins (1972) for molluscs and the patterns of epiphyte distribution and production of this study are likely due to a shared trait between molluscs and Florida Bay epiphytes. This shared trait is the process of calcification. The amount of calcium carbonate present on the shoots on *Thalassia* is remarkably consistent with epiphytic biomass present on those shoots (Fig. 3). This relationship is highly significant and reveals that Florida Bay epiphytes consist of predominately calcium carbonate. Except for the occurrence of *Cladosiphon occidentalis* at Sprigger Bank during the January 1991 sampling period, non-calcifying epiphytes were not abundant at the study sites. Non-calcifying epiphytes were abundant in high nutrient areas such as bird islands and the areas immediately surrounding recent die-off zones (T.A.F., personal observation). These observations and the relationship between epiphytic carbonate load and epiphytic biomass (Fig. 3) suggest that non-calcifying epiphytes are of limited localized importance in Florida Bay.

Comparison with Other Data.—A variety of methods have been employed in the measurement of epiphyte standing stocks and in the estimation of epiphyte productions; therefore direct comparisons between the results of this study and previous investigations may be tenuous.

The most intensive investigations of epiphyte biomass and production have been conducted in the ocean-facing seagrass meadows of Papua New Guinea (Brouns and Heijs, 1986; Heijs, 1984, 1985a, 1985b, 1987). The mean annual epiphyte standing crops were determined for five separate seagrass species including the most abundant species *Thalassia hemprichii* (Heijs, 1985a), the Pacific counterpart of *T. testudinum* (Tomlinson, 1974). Estimates ranged from 20.1 to 89.6 g dw·m^{-2} on *Thalassia hemprichii* (Heijs, 1984: table 1) and from 38.8 to 123.1 g dw·m^{-2} on the seagrass species *Cymodocea rotundata* and *C. serrulata* (Heijs, 1985b: table V), respectively. These standing stocks are similar to the total epiphyte standing stocks in Table 4. Total epiphyte standing stocks on *T. testudinum* for various sites in the Caribbean and lower Florida Keys were also computed from the epiphyte load and *Thalassia* standing crop data of Tomasko and Lapointe (1991). These estimates ranged form 3.4 to 29.8 g dw·m^{-2}, and also fall within the range of those of the present study.

Estimates of epiphytic carbonate standing stocks can be produced from the standing crop data of Heijs (1984, 1985b), assuming that the difference in epiphyte dry weight and ash-free dry weight is due mainly to calcium carbonate. Estimates of mean annual epiphytic carbonate standing stocks range from 14.2 to 71.6 g $CaCO_3$·m^{-2} on *T. hemprichii,* and from 27.0 to 93.5 g $CaCO_3$·m^{-2} on *C. rotundata* and *C. serrulata,* respectively. These ranges are slightly higher than that of the present study, possibly due to more favorable conditions at ocean-facing sites. Land (1970) also produced comparable estimates of epiphytic carbonate standing stocks on *T. testudinum,* which ranged from 7.2 to 48.0 g $CaCO_3$·m^{-2} for six shallow areas in Discovery Bay, Jamaica. These estimates fall within the range of those of the present study.

Estimates of annual epiphyte production are scarce, especially in the seagrass literature. Most of the earlier estimates of epiphyte productivity were based on ^{14}C-uptake measurements and were related to total seagrass/epiphyte productivity (Penhale, 1977; Morgan and Kitting; 1984). Heijs (1987: table VII) summarized annual mean epiphyte production estimates for the five previously mentioned seagrass species of Papua New Guinea. Epiphyte production was greatest on *T. hemprichii* (0.411 g AFDW·m^{-2} sediment·day^{-1}). Scaling this daily production estimate to yearly production results in an estimate of 150 g AFDW·m^{-2}·yr^{-1}. This production figure in terms of AFDW is comparable to the difference between the total epiphyte production estimates and the epiphytic carbonate production estimates in Table 6. These differences range from 4.4 to 103.7 g dw·m^{-2}·yr^{-1} and are 31–97% lower than the yearly production estimate for *T. hemprichii* in Papua New Guinea. This is to be expected given that the production estimates of the present study are minimum estimates and are for an area (Florida Bay) characterized by conditions considered sub-optimal for epiphyte production (Johansen, 1981; Nelsen and Ginsburg, 1986; Kendrick et al., 1988; Bosence 1989).

Estimates of annual epiphytic carbonate production vary greatly, and in each of the previously published investigations (Land, 1970; Patriquin, 1972; Nelsen and Ginsburg, 1986; Walker and Woelkerling, 1988; Bosence, 1989), a different technique was used in the determination of epiphytic carbonate production. Estimates for regions outside the study area range from 180 g $CaCO_3 \cdot m^{-2} \cdot yr^{-1}$ (Land, 1970) to 2,800 g $CaCO_3 \cdot m^{-2} \cdot yr^{-1}$ (Patriquin, 1972). Epiphytic carbonate production for two areas inside Florida Bay (the Cross Banks–Cross Bank and Upper Cross Bank, and Buchanan Banks) was recently estimated (Nelson and Ginsburg, 1986; Bosence, 1989). A similar technique involving the gravimetric measurement of carbonate material by leaf acidification and estimates of seagrass leaf productivity was used in each investigation. For the Cross Banks area, estimated epiphytic carbonate production in both investigations were very similar and ranged from 30–303 g $CaCO_3 \cdot m^{-2} \cdot yr^{-1}$ (Nelsen and Ginsburg, 1986) and from 55–264 g $CaCO_3 \cdot m^{-2} \cdot yr^{-1}$ (Bosence, 1989), while estimates for the Buchanan Banks area range from 448–1,042 g $CaCO_3 \cdot m^{-2} \cdot yr^{-1}$ (Bosence, 1989). These latter estimates are greater than those calculated for the eight sites of this study. Three factors are believed responsible for the lower epiphytic carbonate production estimates of this investigation. First, production figures obtained by the two previous Florida Bay investigations were determined by measuring the carbonate present on older portions of leaves (Bosence, 1989) or on the oldest leaves (Nelsen and Ginsburg, 1986). This present study measured carbonate on entire seagrass shoots. Thus, the figures produced by the two previous investigations should be considered maximum estimates and those of this study should be considered minimum estimates. Second, seagrass leaf productivity and shoot density, which are multipliers in the calculation of epiphyte production, has declined in Florida Bay since the time of the previous investigations. This is most likely due to the factors causing the ongoing seagrass die-off in the bay. Third, the "scrape and titrate" method of measuring epiphytic carbonate, as was used in the present study, results in a more accurate determination of epiphytic carbonate, but the results are 30–81% lower than estimates produced by the measurement of leaf/epiphyte weight loss after acidification (Frankovich and Zieman, in review) as was used by the previously mentioned studies.

Conclusions

The variability in epiphyte loads, standing stocks, and productions is great across Florida Bay, and regional variation of these factors exceeds the seasonal variation at most sites. Calcifying epiphytes are the dominant epiphytes in Florida Bay; their distribution and the distribution of epiphyte production in Florida Bay appear to reflect variability in salinity. Estimates of epiphytic carbonate production suggest that epiphytes are important sources of carbonate sediment. Although these estimates of epiphytic carbonate production are lower than previous ones for Florida Bay, they approximate the most recent estimates of sediment accumulation in Florida Bay (Nelsen and Ginsburg, 1986).

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