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Productivity and biomass of *Thalassia testudinum* as related to water column nutrient availability and epiphyte levels: field observations and experimental studies

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ABSTRACT: *Thalassia testudinum* meadows from 0.5 m and 2.0 m (MLW) depths were studied at 9 sites in the Florida Keys and western Caribbean. Two meadows, one offshore of a populated island with over 2000 septic tanks, and one offshore of a large bird rookery, were similar in having elevated levels of water column nutrients (DIN and SRP), greater epiphyte levels, low shoot densities, low leaf area indices, and low biomass. Increased blade turnover time was partially responsible for increased epiphyte levels offshore of the populated island, but epiphyte communities developed faster on seagrass blades there than at a paired site offshore of an uninhabited island. Results of aquarium experiments approximated the observed phenomena from the field studies: elevated water column nutrients produced increased epiphyte levels and decreased blade turnover rates. Reduced irradiance moderated the effect of nutrient enrichment on epiphyte levels. Elevated levels of water column nutrients, by stimulating epiphyte growth, reduced rhizome growth rates. This could be related to the observed lower shoot density of *T. testudinum* meadows near sources of water column nutrient enrichment.

INTRODUCTION

Studies in Denmark (Borum 1985), Australia (Silberstein et al. 1986), Mexico (Flores-Verdugo et al. 1988), Chesapeake Bay, USA (Kemp et al. 1983), Florida, USA (Jensen & Gibson 1986), and Texas, USA (Dunton 1990) indicate that increased water column nutrient availability typically results in greater epiphyte levels on seagrass blades. Nutrient-induced increases in epiphyte coverage decrease the amount of light that seagrass blade tissue receives (Sand-Jensen 1977, Twilley et al. 1985, Silberstein et al. 1986). As a result, nutrient enrichment of nearshore marine waters is thought to be the major reason for degradation of seagrass meadows worldwide (e.g. Larkum 1976, Kemp et al. 1983, Cambridge & McComb 1984, Orth & Moore 1984, Bourcier 1986, Silberstein et al. 1986, Valiela et al. 1990).

A problem with determining the water column nutrient status of seagrass-containing areas, and the potential for epiphyte problems, is the rapid rate of uptake of soluble nutrients. Soluble reactive phosphorus in freshwater lakes can turn over in less than 10 min (Suttle & Harrison 1988), and ammonium levels in Long Island Sound, USA, were found to have turnover times of less than an hour during summer (Suttle et al. 1990). Related to this phenomenon, Smith et al. (1981) and Valiela et al. (1990) found that water column chlorophyll levels and benthic algal biomass were far better indicators of system-wide nutrient status than soluble nutrient levels. Borum (1985), studying *Zostera marina* along a nutrient gradient, found epiphyte standing stocks were even better indicators of nutrient availability than water column chlorophyll levels. Despite this, soluble nutrient levels alone are still used in monitoring studies designed to discern anthropogenic impacts on nearshore ecosystems.

In the Florida Keys, on-site sewage disposal systems (OSDS's) are used by the majority of people living

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outside of Key West (which has a secondary treatment sewage plant). OSDS's are known to increase the concentrations of dissolved inorganic and organic phosphorus and nitrogen species in both the groundwater and nearshore marine waters of the Florida Keys (Lapointe et al. 1990), and could be associated with increased epiphyte coverage in seagrass meadows near populated and perhaps even uninhabited islands. If epiphyte levels increase above an unknown threshold value, it is possible that adverse effects on seagrasses could result.

At high or low nutrient levels, low irradiance levels can directly limit seagrass growth. At high nutrient levels, high irradiance levels can indirectly limit growth by stimulating epiphyte growth to a greater extent than seagrass growth (Moore et al. 1989). As such, nutrient availability may interact with water depth, and thus irradiance, to produce different epiphyte levels with different combinations of proximity to water column nutrient sources and water depth.

The goals of this study were to survey *Thalassia testudinum* meadows from 2 water depths (0.5 m and 2.0 m, MLW) at various locations throughout the Florida Keys and western Caribbean. Density, biomass, and epiphyte levels were measured at 9 separate geographic locations, and productivity determined at 4 separate locations. In addition, a factorial experiment using 2 irradiance treatments (ambient and 33 % of ambient) and 2 nutrient treatments (ambient and enriched) was performed to further elucidate the mechanisms involved in structuring epiphyte levels in the seagrass *T. testudinum*.

MATERIALS AND METHODS

Field studies. The field studies were conducted in seagrass meadows at 2 depths (0.5 m and 2.0 m, MLW) at 9 locations in the Florida Keys and western Caribbean (Fig. 1). All field studies were completed within 30 d of each other, from mid-May to early June 1990. Two of the sites in the Florida Keys were offshore of Big Pine Key and Cutoe Key. Big Pine Key was chosen as a potential 'impacted' site, as the island contains over 2000 OSDS's, and the eastern side of the island (where the study site was located) contains many high density trailer parks and campgrounds, all of them utilizing OSDS's. Cutoe Key was chosen as a 'control' site, as it is uninhabited and potentially isolated from anthropogenic nutrient sources. The meadows from both these

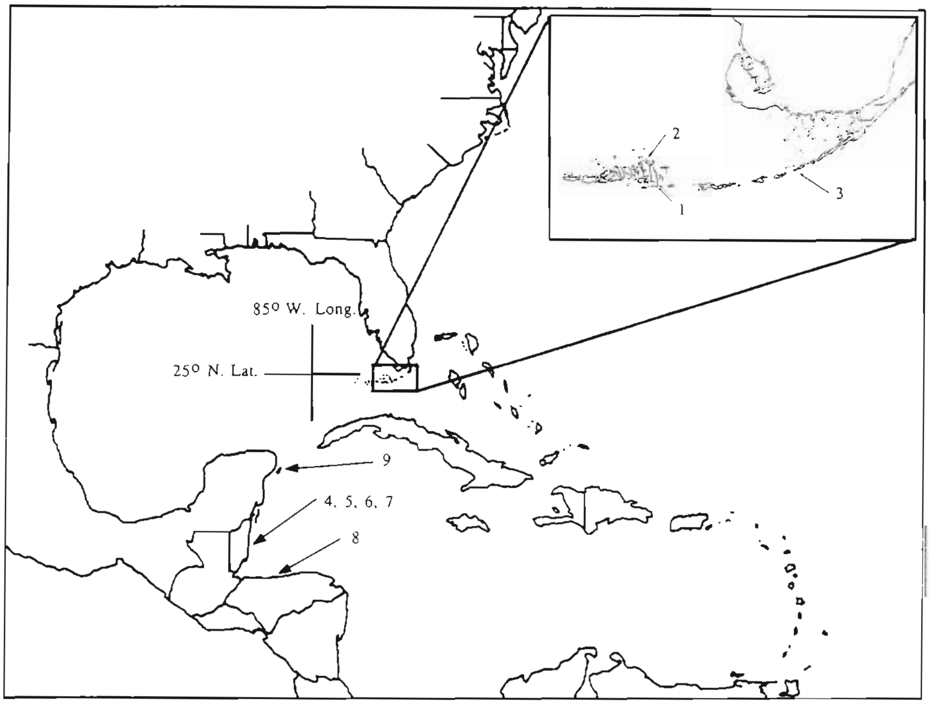

Fig. 1. The Caribbean region showing location of study sites. Sites are numbered as follows: 1, Big Pine Key; 2, Cutoe Key; 3, Alligator Reef (USA); 4, Carrie Bow Cay; 5, Twin Cays; 6, Glovers Reef Lagoon; 7, Man of War Cay (Belize); 8, Roatan (Honduras); 9, Isla Cozumel (Mexico)

sites were similar in sediment depth, alignment to prevailing winds, proximity to flushing channels, and exposure to wave energy as related to fetch. A third site in the Florida Keys, Alligator Reef, was located just behind the reef tract, ca 5 km from land. The seagrass meadow at Alligator Reef had no shallow zone (0.5 m) to study.

Sites in the western Caribbean included Carrie Bow Cay, Twin Cays, Glovers Reef Lagoon, and Man of War Cay (all in Belize), as well as Roatan (Honduras) and Isla Cozumel (Mexico). The sites at Carrie Bow Cay and Roatan had coarse-grained sand with isolated corals (mainly *Porites* sp.). Carrie Bow Cay is flat, whereas Roatan is quite mountainous, with evidence of slash and burn clearing of the forested slopes just inland of the study site. Twin Cays and Man of War Cay both had lush mangrove fringes (*Rhizophora mangle*). Man of War Cay had a colony of magnificent frigate birds (*Fregata magnificens*) consisting of ca 75 nesting pairs (Sandy Sprunt pers. comm.). Glovers Reef Lagoon was within the atoll of Glovers Reef, and contained scattered coral colonies (mainly *Montastrea annularis*) and coarse carbonate sediments. The site at Isla Cozumel was offshore of a sandy beach, with a high-energy environment at the shallow site (with much scouring away of the grass beds) and a deep site similar to those at Carrie Bow Cay and Roatan.

During the experimental duration, water temperatures at all sites ranged between 28.5 and 30.5 °C, and salinities at all sites ranged between 35 and 38 ppt. Sediment depths were less than 10 cm at Carrie Bow Cay, Glovers Reef Lagoon and Roatan, and exceeded 50 cm at all other sites.

Water samples were collected at each location for determination of ammonium, nitrate plus nitrite, and soluble reactive phosphate (SRP). Water samples from Isla Cozumel were inadvertently discarded. Samples were placed in acid-washed Nalgene bottles, spiked with $HgCl_2$ (10 mg l^{-1}), and frozen until analysis. Ammonium concentrations, as well as nitrate plus nitrite, were determined on an Autoanalyzer II according to methods of Slawyk & MacIssac (1972) and Technicon (1973), respectively. Concentrations of SRP were determined by the molybdenum-blue method (Murphy & Riley 1962) using a Bausch and Lomb Spectronic 88 fitted with a 10 cm cell.

Blade productivity was determined at Big Pine Key, Cutoe Key, Carrie Bow Cay, and Twin Cays. Procedures were as described in Tomasko & Dawes (1989, 1990). Density was determined at all 9 sites by placing a 30 × 30 cm quadrat at random locations within the grass beds. Leaf area was determined for 20 randomly chosen individual shoots by multiplying blade lengths by the width of the second youngest blade. Epiphytes were scraped from the blades using a razor blade, and the few remaining calcareous types (mainly *Fosliella* sp.) were brushed from the blades after they had dried for at least 24 h at 65 °C. Epiphyte levels are expressed as a percent of the weight of the total blade-epiphyte complex.

Leaf area index was determined by multiplying leaf area per shoot by shoot density normalized to 1 m^2. Productivity and biomass per m^2 were determined by multiplying average shoot productivity and biomass by shoot density normalized to 1 m^2. Turnover time was calculated as biomass per m^2 divided by productivity per m^2.

Blade turnover rates and epiphyte levels were compared for both water depths at the paired sites in the Florida Keys, and for the paired sites in Belize. Statistical analysis used a 2 × 2 factorial ANOVA to determine the effects of site, water depth, and any interactions on blade turnover and epiphytes. Data were tested for assumptions of normality and homoscedasticity.

Aquarium studies. The aquarium studies were based on a 2 × 2 factorial design, utilizing 2 irradiance levels (ambient and 33 % of ambient), and 2 nutrient levels (ambient and enriched). This required a total of 8 outdoor aquaria, each of which received continuous flowing seawater (2 replicate aquaria for each of 4 treatments). Light reduction was achieved by covering the 30 gal aquaria with 2 layers of neutral density shade cloth.

The aquarium studies started May 16 and ended June 21, 1990. Plants were gathered from 2.0 m of water offshore of Vaca Key, Florida, and were brought back to the laboratory in coolers. Only units with intact rhizome apices and at least 3 short shoots were subsequently used. Plants were tagged just in front of their second youngest short shoot, and the distance between the tag and the end of the rhizome apex was recorded. Three plants were placed in each of 2 aquaria per treatment. A coarse sediment was supplied using dried material from offshore sandbars ('*Halimeda* hash'). Blades were marked for productivity measurements on June 16, 1990.

At the end of each day, nutrient-enriched aquaria were pulsed by supplying sufficient ammonium, nitrate, and phosphate to produce initial nutrient concentrations of: 10 µM ammonium, 10 µM nitrate, and 1 µM phosphate. Preliminary experiments showed that initial nutrient concentrations in pulsed aquaria would decrease to ambient levels (which were highly variable) within 3 h. During the nutrient pulse, water flow was turned off in all 8 aquaria, and aeration was supplied for the period 16:00 to 08:00 h. At 08:00 h, all aquaria were returned to flow-through status. Grazing organisms were added to all aquaria by sieving 4 m^2 of a heavily epiphytized grass bed with a fine mesh net and dividing the acquired organisms between all aquaria.

Blade turnover time, epiphyte levels, and belowground growth rates were analyzed with a 2 × 2 factorial ANOVA to determine the effects of irradiance, nutrient enrichment, and any interactions. Data were tested for assumptions of normality and homoscedasticity.

RESULTS

Field studies

Water column dissolved inorganic nitrogen levels were nearly 8 times higher offshore of Big Pine Key vs Cutoe Key (Table 1). Highest DIN values were at Big Pine Key and Man of War Cay, as were highest SRP values. Lowest DIN values were at Glovers Reef Lagoon and Roatan. Lowest SRP values were at Alligator Reef and Roatan. Ratios of N:P varied from low values at Cutoe Key and Glovers Reef (2.6 and 2.8, respectively) to high values at Big Pine Key and Twin Cays (14.7 and 18.3, respectively).

Blade turnover rates for the paired sites in the Florida Keys (Big Pine Key and Cutoe Key) had significant effects of site ($p \leq 0.001$, 1 df) and water depth ($p \leq 0.001$, 1 df), but no significant interaction. At both water depths, blade turnover rates were higher at Cutoe Key vs Big Pine Key (Table 2). At both Cutoe Key and Big Pine Key, blade turnover rates were higher at 2.0 m vs 0.5 m (Table 2).

Blade turnover rates for the paired sites in Belize (Carrie Bow Cay and Twin Cays) had no significant effects of site, water depth, or any interactions. Turnover rates were similar at all combinations of site and water depth (Table 2). It should be noted that blade turnover rates can be similar even though values for blade production per shoot differ dramatically. Thus, seagrasses from Carrie Bow Cay have dissimilar rates of blade production per shoot vs seagrasses from Twin Cays, but due to different leaf area per shoot values (Table 3), turnover rates are not significantly different.

Epiphyte levels for the paired sites in the Florida Keys (Big Pine Key and Cutoe Key) had significant

Table 1. Concentrations (μM) of dissolved ammonium, nitrite plus nitrate, total DIN, soluble reactive phosphorus, and the N:P ratio of seawater at study sites. Data are means (n = 2, ± SD) for Big Pine Key and Cutoe Key, and single values for all other sites. ud: undetectable, –: unable to calculate

Location	NH_4	$NO_2 + NO_3$	DIN	SRP	N:P
Big Pine Key	1.64 (0.08)	2.32 (1.28)	3.96	0.27 (0.23)	14.7
Cutoe Key	0.15 (0.09)	0.35 (0.13)	0.50	0.19 (0.11)	2.6
Alligator Reef	ud	0.26	0.26	ud	–
Carrie Bow	0.28	0.09	0.37	0.04	9.3
Twin Cays	1.05	0.05	1.10	0.06	18.3
Glovers Reef	ud	0.14	0.14	0.05	2.8
Man of War	3.20	0.60	3.80	0.43	8.8
Roatan	ud	0.15	0.15	0.03	5.0

Table 2. *Thalassia testudinum*. Blade turnover rate (% d^{-1}), and blade production (mg dwt $shoot^{-1}$ d^{-1}); values are means (n = 20; ± SE). Plastochrone interval (d), areal production (g dwt m^{-2} d^{-1}), areal biomass (g dwt m^{-2}) and turnover time (d) are calculated as described in the text. Data are for seagrass from 0.5 and 2.0 m at 4 sites

Site/depth	Blade turnover rate	Blade production	Plastochrone interval	Areal production	Areal biomass	Turnover time
Big Pine Key						
0.5 m	1.11 (0.14)	2.2 (0.3)	46.7	0.306	27.57	90.1
2.0 m	1.58 (0.15)	4.9 (0.7)	20.0	1.083	69.18	63.9
Cutoe Key						
0.5 m	1.90 (0.12)	3.2 (0.5)	20.0	0.768	40.37	52.6
2.0 m	2.77 (0.11)	8.4 (1.1)	26.7	1.372	49.98	36.4
Carrie Bow						
0.5 m	2.42 (0.15)	1.6 (0.1)	26.7	0.665	27.86	41.9
2.0 m	2.34 (0.16)	1.9 (0.2)	20.0	0.498	22.26	42.7
Twin Cays						
0.5 m	2.68 (0.21)	6.1 (0.8)	26.7	1.327	49.21	37.1
2.0 m	2.83 (0.29)	6.1 (0.7)	26.7	0.901	31.81	35.3

Table 3. *Thalassia testudinum*. Density (no. per 30 cm × 30 cm), leaf area per shoot (cm^2 $shoot^{-1}$), and epiphyte load (percent of total blade-epiphyte biomass); values are means (n = 20; ± SE). Leaf area index (m^2/m^2) and biomass (g dwt m^{-2}) are calculated as described in the text

Site/depth		Density	Leaf area	Epiphytes	Leaf area index	Biomass
Big Pine Key	0.5 m	12.5 (1.0)	38.1 (3.1)	43.9 (3.8)	0.53	27.6
	2.0 m	19.9 (1.1)	60.1 (5.9)	30.1 (2.3)	1.33	69.2
Cutoe Key	0.5 m	21.6 (1.2)	32.8 (4.0)	16.5 (1.9)	0.79	40.4
	2.0 m	14.7 (1.3)	49.6 (5.4)	14.6 (2.4)	0.81	50.0
Alligator Reef	2.0 m	21.1 (1.4)	47.6 (0.9)	20.9 (1.0)	1.11	105.8
Carrie Bow	0.5 m	36.4 (1.7)	16.2 (1.1)	14.6 (1.2)	0.66	27.9
	2.0 m	23.4 (0.8)	17.3 (1.1)	16.7 (1.5)	0.45	22.3
Twin Cays	0.5 m	19.6 (1.0)	48.0 (4.2)	16.2 (1.5)	1.05	49.2
	2.0 m	13.2 (0.8)	53.9 (4.8)	12.4 (1.5)	0.79	31.2
Glovers Reef	0.5 m	13.5 (1.1)	48.4 (3.5)	15.6 (1.5)	0.73	37.2
	2.0 m	9.5 (1.1)	41.6 (2.5)	23.1 (1.6)	0.44	22.5
Man of War	0.5 m	10.5 (1.2)	32.1 (2.1)	30.0 (3.1)	0.37	17.3
	2.0 m	22.6 (0.7)	40.3 (3.4)	6.5 (0.9)	1.01	48.6
Roatan	0.5 m	33.5 (1.7)	20.6 (1.6)	24.0 (1.7)	0.77	42.1
	2.0 m	29.2 (0.4)	24.4 (2.7)	19.7 (1.6)	0.79	40.9
Isla Cozumel	0.5 m	76.8 (2.9)	37.8 (2.6)	5.3 (0.7)	3.23	150.0
	2.0 m	16.1 (1.4)	22.3 (2.2)	24.7 (1.8)	0.40	20.5

effects of site ($p \leq 0.001$, 1 df), water depth ($p \leq 0.005$, 1 df), and a significant site by water depth interaction ($p \leq 0.04$, 1 df). Epiphyte levels were higher at Big Pine Key vs Cutoe Key at both water depths (Table 3), and were higher at 0.5 m than at 2.0 m depth at both sites. However, shallow blades at Cutoe Key had a very slight increase in epiphyte levels vs deep blades, while shallow blades at Big Pine Key had 50 % higher levels vs deep blades (Table 3). Epiphyte levels for the paired sites in Belize (Carrie Bow Cay and Twin Cays) had no effects of site, water depth, or any interactions.

The areal production of the shallow grass bed at Big Pine Key was the lowest found, only 40 % that of its paired shallow site at Cutoe Key (Table 2). Turnover times of the grass beds at both depths at Big Pine Key were higher than at Cutoe Key or either of the sites in Belize (Table 2).

Man of War Cay was the only site (out of 8) which had lower shoot densities at its shallow edge than Big Pine Key (Table 3). At both depths, seagrasses from Big Pine Key had the highest epiphyte levels of all sites, with epiphyte levels at Man of War Cay being second highest at the shallow depth (Table 3). The lowest leaf area index and biomass values for shallow depths were found at Man of War Cay, with the second lowest values coming from Big Pine Key (Table 3).

Leaf area index was highest at the shallow edge of Isla Cozumel, followed by the seagrasses from 2.0 m at Big Pine Key (Table 3). The high leaf area index from Isla Cozumel is due mostly to the very high shoot densities, while the high leaf area index from 2.0 m at Big Pine Key is due mainly to the shoots being the 'leafiest' (highest leaf area per shoot) of any of the surveyed grass beds (Table 3).

Aquarium studies

Nutrient levels, but not light levels, affected blade turnover rates ($p \leq 0.03$, 1 df). Turnover rates were similar in both ambient light and shaded aquaria without nutrient enrichment, but were lower in aquaria with nutrient additions (Fig. 2).

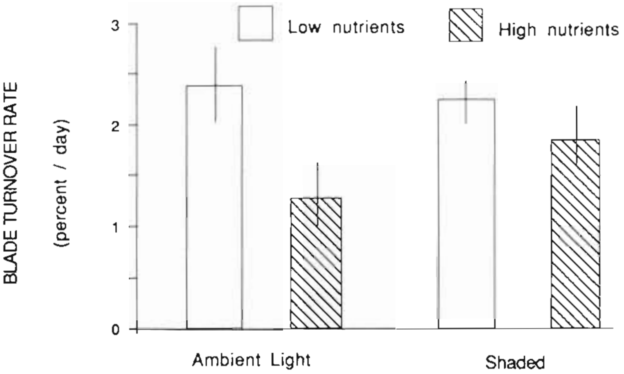

Fig. 2. *Thalassia testudinum*. Blade turnover rates for seagrass grown in aquaria under conditions of ambient and 33 % ambient light, and ambient and enriched water column nutrients. Values are means of n = 6, ± SE

Light significantly affected epiphyte levels ($p \leq 0.003$, 1 df), as did nutrients ($p \leq 0.001$, 1 df), and a light by nutrient interaction ($p \leq 0.02$, 1 df). Both nutrient regimes had highest epiphyte levels at ambient light levels, and for both ambient light and shaded treatments, epiphyte levels were highest in enriched aquaria (Fig. 3). The interaction effect is due to the magnitude of the increase in epiphyte levels with nutrient enrichment in ambient light aquaria being much greater than the increase in epiphyte levels of nutrient-enriched shaded aquaria.

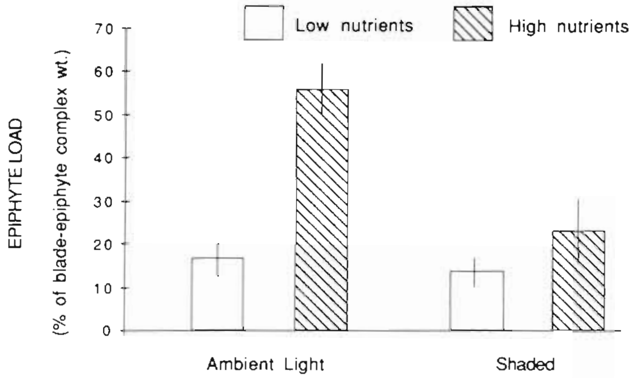

Fig. 3. *Thalassia testudinum.* Epiphyte levels for seagrass grown in aquaria under conditions of ambient and 33 % of ambient light, and ambient and enriched water column nutrients. Values are means of n = 6, ± SE

Nutrient levels, but not light levels, had a significant effect on rhizome growth rates ($p \leq 0.02$, 1 df). For both ambient light and shaded aquaria, rhizome growth rates were lower in aquaria with nutrient enrichment (Fig. 4).

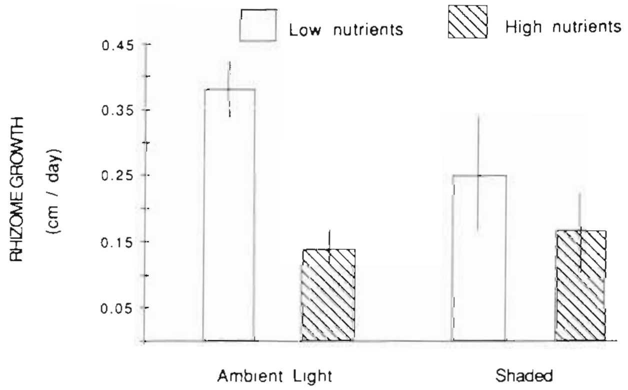

Fig. 4. *Thalassia testudinum.* Rhizome growth rates for seagrass grown in aquaria under conditions of ambient and 33 % of ambient light, and ambient and enriched water column nutrients. Values are means of n = 6, ± SE

DISCUSSION

Soluble nutrient levels in nearshore waters of Big Pine Key, the 'impacted' site, were lower than those found in canals directly receiving groundwater contaminated by OSDS's (Lapointe et al. 1990), but higher than values from all other sites except the bird roost island at Man of War Cay, Belize. Although values from these 2 sites are lower than values used in the aquaria studies, no effort was made to take ambient water samples after rainfall events, when nutrient pulses caused by groundwater flow would produce highest values in nearshore waters (Lapointe et al. 1990). Nonetheless, epiphyte levels in nutrient-enriched ambient light aquaria were similar to epiphyte levels at shallow depths of nutrient-enriched sites.

Although higher DIN and SRP levels at Big Pine Key and Man of War Cay indicate nutrient inputs into nearshore waters are elevated here, greater nutrient inputs would not necessarily result in higher levels of soluble nutrients. Suttle & Harrison (1988) and Suttle et al. (1990) both indicate that levels of soluble nutrients, due to their rapid turnover, reflect rates of recycling, rather than rates of input. Smith et al. (1981), in their study on the effects of sewage input into Kaneohe Bay, Hawaii, concluded '...measurement of the limiting nutrient concentration is a poor indicator of eutrophication. A more useful indicator would be (water column) chlorophyll or some other particulate material...'. As epiphyte biomass is a better indicator of system-wide nutrient availability than water column chlorophyll (Borum 1985), and water column chlorophyll is a better indicator of nutrient availability than soluble nutrient levels (Smith et al. 1981, Soulemane 1990, Valiela et al. 1990), we believe that epiphyte levels should be viewed as important variables to consider in future seagrass studies.

Giffordia mitchellae, Dictyota divaricata, and *Enteromorpha flexuosa* were abundant epiphytes at impacted sites. Frondose and filamentous macroalgae such as these are typically phosphorus limited in the Florida Keys (Lapointe 1987, Lapointe 1989). One of these species, *D. divaricata,* has elevated levels of alkaline phosphatase activity (Lapointe 1989). As dissolved organic phosphate (DOP) has greater mobility in carbonate substrata than soluble reactive phosphate (Lapointe et al. 1990), and DOP is often regenerated by marine organisms, this would indicate that inputs of dissolved organic phosphate from OSDS's, as well as phosphorus recycling, might be important in regulating epiphyte levels in nearshore seagrass meadows in the Florida Keys.

It appears that the shallow (0.5 m) portion of the *Thalassia testudinum* meadow at Big Pine Key is structurally similar to the shallow meadow off Man of War

Cay. Both sites had lower shoot densities, lower leaf area indices, lower biomass, and higher epiphyte levels than shallow meadows at 6 other locations. As Man of War Cay was the only site containing a bird colony, the data suggest that nutrient enrichment of nearshore waters due to bird feces has resulted in the high epiphyte levels and low biomass of its shallow water seagrass meadows.

The combination of higher epiphyte levels and reduced blade turnover rates for *Thalassia testudinum* from Big Pine Key complicates our understanding of the development of epiphyte communities in impacted sites. It would be possible for increased epiphyte levels to be related simply to increased time that seagrass blades are present as a substrate for attachment and growth. However, when comparing Big Pine Key vs Cutoe Key, epiphyte levels at Big Pine Key increase 70 % faster than turnover times, indicating epiphyte communities develop faster at Big Pine Key than at Cutoe Key.

A comparison between the meadows at Carrie Bow Cay and Twin Cays provides further useful information. The seagrasses at Carrie Bow Cay grew in an area where sediment depth was less than 10 cm, while those at Twin Cays had sediment depths greater than 50 cm. The low values of blade production and leaf area per shoot at Carrie Bow Cay probably reflect this difference in sediment depth. Similar results were previously reported for *Thalassia testudinum* by Zieman (1972) and Zieman et al. (1989). Despite lower biomass per shoot values, and lower per shoot productivity rates, turnover times were similar at Carrie Bow Cay vs Twin Cays, indicating blade turnover rates remain at near-constant levels.

It appears that proximity to mangroves and mangrove detritus has little consequence as relates to epiphyte levels on *Thalassia testudinum*. Both Cutoe Key and Twin Cays had very lush mangrove fringes, yet epiphyte levels were similar to or lower than those from Carrie Bow Cay and Isla Cozumel, where mangroves were absent. Although Lapointe et al. (1987) showed a significant positive effect of mangrove detritus on the productivity of *Acanthophora spicifera* and *Dictyota divaricata*, it would seem that fewer soluble nutrients are available from decomposing mangrove leaves than from bird feces and sewage. Thus, greatly elevated epiphyte levels on seagrasses from various sites in the Florida Keys and Florida Bay (Tomasko pers. obs.) are probably not due to a possible closer proximity to mangroves or mangrove detritus, but proximity to some other nutrient source.

From the aquarium studies, it appears that the observed phenomena in the field can be approximated. Increased water column nutrient levels did not benefit *Thalassia testudinum*; rather, they seemed to result in decreased vigor. Reduced rhizome growth rates were evident upon nutrient enrichment of the water column, due probably to decreased available energy as a result of shading by denser epiphyte communities. A reduction in rhizome growth rates would decrease shoot formation rates, and perhaps contribute to the lower shoot densities found in shallow seagrass meadows near significant water column nutrient inputs. The combination of lower shoot densities and decreased blade turnover rates results in sharply reduced areal productivities.

The aquarium studies indicated that the increased epiphyte levels associated with nutrient enrichment were themselves modified by irradiance; high light and high nutrients supported more epiphytes than low light and high nutrients. Similar results were found by Moore et al. (1989) for *Zostera marina*, and suggest that the reduced epiphyte levels for seagrasses at 2.0 m vs 0.5 m at Big Pine Key may be due to reduced irradiance, and not necessarily due to their greater distance from island-based nutrient inputs. The increased 'leafiness' of shoots at 2.0 m off Big Pine Key vs all other sites may indicate a morphological response to light limitation similar to that found for *Thalassia testudinum* from deep vs shallow edges off Anclote Key, Florida (Dawes & Tomasko 1988).

A study by Powell et al. (1989) in eastern Florida Bay can be interpreted as showing species substitution of seagrasses (*Halodule wrightii* replacing *Thalassia testudinum*) after 3 yr of nutrient enrichment from birds utilizing specially designed perches. This seems to agree with Zieman et al. (1990), '. . . *Halodule* is a pioneering species which occurs under disturbance conditions not tolerated by *Thalassia* . . .'. It would appear that in their study, and in ours as well, nutrient enrichment of the water column via bird feces is such a disturbance. Our data suggest that heavily epiphytized meadows of *T. testudinum* off bird islands and islands with large numbers of OSDS's have reduced above and below ground productivity, and may be stressed to the point that continued persistence of this species would be dependent upon decreased availability of water column nutrients.

Nutrient enrichment of the water column due to cultural eutrophication has been implicated as the major reason for seagrass decline in Botany Bay, Australia (Larkum 1976), Cockburn Sound, Australia (Cambridge & McComb 1984, Silberstein et al. 1986), the French Mediterranean (Bourcier 1986), Chesapeake Bay, USA (Kemp et al. 1983, Orth & Moore 1984), and Waquoit Bay, Massachusetts, USA (Valiela et al. 1990). In the Florida Keys, some long-time residents have noticed a decline in seagrass coverage, or a replacement of *Thalassia testudinum* by *Halodule wrightii*, within residential canals. It would appear that nutrient enrichment of nearshore waters has altered the structure of seagrass beds in the Florida Keys both inside and outside of canals, and that continued reliance of residents of the Florida Keys on OSDS's will further degrade affected meadows.

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