



An Experimental Test of the Capacity of Food Web Interactions (Fish–Epiphytes–Seagrasses) to Offset the Negative Consequences of Eutrophication on Seagrass Communities

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A mechanism of competition between epiphytes and seagrasses potentially modulated by grazers was studied in a high-nutrient *Thalassia testudinum* meadow in the Indian River Lagoon (Florida, U.S.A.). The effects of fish grazing on epiphytes, and likely enhancing *T. testudinum* growth, was tested through an exclusion experiment. Twelve (2 × 2 m) independent experimental plots were selected within a shallow monospecific bed to which three randomized treatments (exclusion fences, open fences and controls) with four replicates each were assigned. The epiphyte load was monitored on *T. testudinum* leaves inside the plots from January 1995 to March 1996. Treatment effects occurred during a chlorophyte bloom in March 1995, when the epiphyte biomass was significantly higher inside the exclusion cages than in either of the controls. The composition of the epiphytic community in March 1995 was dominated by sheet-like *Enteromorpha* and filamentous algae such as *Cladophora*, which are less resistant to herbivory than the coarsely-branched forms of red algae (e.g. *Hypnea*, *Chondria* and *Acanthophora*) that bloomed subsequently. These results suggest that herbivory change seasonally depending on the availability of different prey species to fish-grazers, which preferentially utilize the fleshy green algae typical of bloom conditions over the thicker coarsely-branched red algae. In the nutrient-rich lagoon the role of top-down interactions in enhancing *T. testudinum* growth is limited to the reduction of shading by green macroalgae.

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Introduction

Plant communities are regulated by a combination of bottom-up factors, involving a dependence on resource availability, and top-down factors, involving the activities of higher trophic levels (McQueen, 1989). Changes in trophic levels above plant communities can cascade down through the food web (Carpenter *et al.*, 1985), triggering complex interactions whose outcome will depend on the quantity (Threlkeld, 1988) and quality (Levitan, 1987) of the processes involved.

In seagrass systems, an increase in nutrient supply to the water column leads to increased epiphyte loads on seagrass blades (Sand-Jensen, 1977; Cambridge &

McComb, 1984; Twilley *et al.*, 1985; Silberstein *et al.*, 1986; Tomasko & Lapointe, 1991) causing a shift in the primary production of the community. Overgrowth of epiphytes reduces nutrient and gaseous exchange as well as light supply to the seagrass leaves, suppressing seagrass growth (Kiorbøe, 1980; Kemp *et al.*, 1983; Short & Short, 1984) and reproduction (Orth & Van Montfrans, 1984). Grazing by invertebrate mesofauna can regulate epiphyte biomass and, therefore, seagrass productivity (Orth & Van Montfrans, 1984; Klumpp *et al.*, 1992). Consequently, grazing activity may act to buffer the negative consequences of the enhanced nutrient load on seagrass communities associated with epiphyte overgrowth. However, the importance of these interactions have not been thoroughly tested, partially because of the complexity of the interactions triggered by changes in food webs (Hunter & Price, 1992).

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The interactions between groups of producers (seagrasses and epiphytes) in a nutrient-rich estuarine system and the potential alleviating effect of macroherbivores were investigated here. The hypothesis that herbivorous fish can regulate epiphytic algal overgrowth thereby enhancing primary production and growth of the dominant seagrass (*Thalassia testudinum* Banks *ex* König) was also tested. To do this an enclosure experiment was carried out within a monospecific *T. testudinum* meadow in the Indian River Lagoon, Florida, U.S.A. The study involved a series of multifaceted approaches including: (1) characterization of environmental parameters in the study area, particularly those that may be conducive to enhanced epiphytic algal growth; (2) experimental tests of the direct effects of fish grazing on epiphyte biomass, species composition and relative abundance (exclusion treatments); (3) assessment of the indirect role of grazers on seagrass primary production and biomass accumulation; (4) documentation of the high abundances of the two predominant herbivorous fish species; and (5) evaluation of the possible consequences of fish exclusion on populations of mesograzers.

Methods

Environmental monitoring

The study was conducted in a *T. testudinum* bed 1.2 m deep (± 0.15 m tidal range) in the Indian River Lagoon, north of the Link Port Jetty (27°32'N, 80°21'W; Figure 1). All field work was conducted from a small boat using snorkel equipment. To characterize the environmental features and trophic state of this system and document any catastrophic events, temperature, salinity and macronutrients were measured 0.5 m above the seagrass bed at monthly intervals from January 1995 to March 1996. Water samples for the determination of dissolved inorganic nitrogen and phosphorus were collected at the same depth (0.5 m) in acid-washed Nalgene bottles and kept frozen until analysis. Temperature was measured with a Fisher-brand thermometer and salinity with an Aquatic Eco-systems refractometer. All nutrient analyses were performed with automatic colorimetric techniques (D'Elia *et al.*, 1995). Ammonium concentrations were determined by the phenol hypochlorite method with a Bran Luebbe Traacs-800 Analyzer. Nitrate and nitrite were measured by the cadmium reduction method, and soluble reactive phosphorus (SRP) by the ammonium molybdate ascorbic acid method on a Technicon Autoanalyzer II.

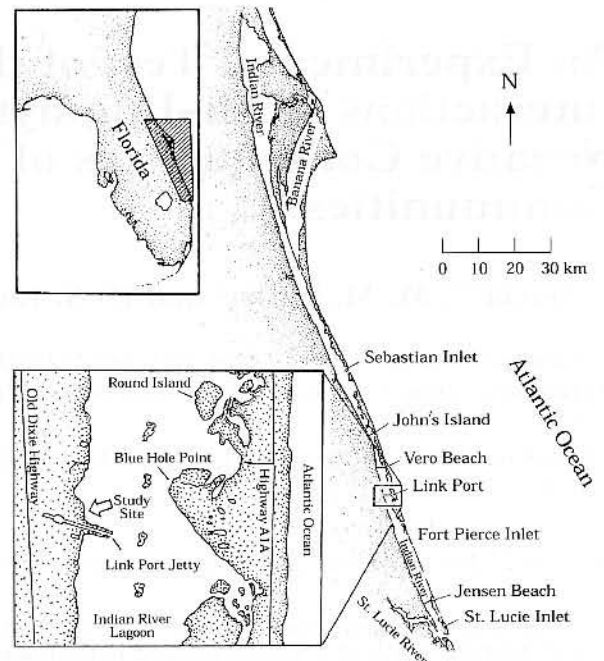


FIGURE 1. Location of the Indian River Lagoon, Central Florida, and the sampling site north of Link Port Jetty.

Fish exclusion experiment

To test the central hypothesis that herbivorous fish potentially play a role in regulating the overgrowth of competing epiphytes, thereby enhancing seagrass development, 12 independent experimental plots (4 m² each) were selected within a large seagrass bed and treatments randomly assigned to these. Three treatments with four replicates each were established in January 1995 as follows:

- (1) cages (topless fences, 2 × 2 m × 1.5 m high) constructed of plastic-coated 2 × 4 cm wire mesh to exclude medium to large herbivorous fish and to allow other predators to access the enclosure [K];
- (2) cage controls of the same mesh, but with only two 2 m long × 1.5 m high sides orientated perpendicular to the dominant current to ascertain artifactual cage effects (e.g. changes in water circulation and fouling) [KC];
- (3) control plots of the same size without mesh, allowing natural fish populations to graze on epiphytes [C].

The composition and biomass of the macroalgal epiphytic assemblage were recorded when changes in the biomass, structure or composition of the epiphyte community (i.e. a conspicuous bloom) were visually observed in the study site; 13 March, 25 September and 30 November 1995, and 17 January, 20 February and 25 March 1996. Eight *T. testudinum* shoots per

plot were selected randomly by placing four $1 \times 1 \text{ m}^2$ frames using a grid system that selected eight randomized positions within the $2 \times 2 \text{ m}^2$ area of each plot. The nearest shoots to the designated position were removed to determine epiphyte biomass when this was significant (scraping method; McGlathery, 1995), and seagrass standing crop (organic dry mass). Epiphytic biomass data were standardized to shoot biomass. Species composition and the relative abundance of the epiphytic community were determined under optical microscopy and reported on the basis of decreasing relative abundance of the different species identified for the various algal phyla (e.g. Rhodophyta, Phaeophyta, Chlorophyta, and Cyanophyta), using a routine phytosociological scale (Braun Blanquet, 1946) from rare (1) to very abundant (5). The category rare (1) was used for species observed in less than 20% of the fields of view explored, present (2) when observed at low frequency (20–40%), present at high frequency (3) observed between 40–60% of the occurrences, abundant (4) for commonly observed (40–60%), and very abundant (5) for those species that dominated the samples (80–100%).

In addition to the exclusion of fish-grazers, cages might also protect benthic invertebrates from predation. Such potential increases in the density of mesograzers could have an important effect on the biomass of epiphytes. To rule out such an effect, densities of crustacean-grazers living in the seagrass bed under the three different treatments were measured during June 1996. All seagrass shoots in three randomly assigned 900 cm^2 areas per plot were rapidly collected and stored in polyethylene bags. Samples were rinsed in fresh water in the laboratory to dislodge animals and the water filtered through two sieve sizes (1 mm^2 and 2 mm^2 pore area). Filtered material was preserved in 70% methanol and the crustaceans counted under a dissection microscope using a multiple counter and calibrated-grid Petri dishes. The crustaceans were grouped as amphipods, isopod and tanaidaceans. Their densities were standardized to plant biomass.

Production of new leaves and seagrass biomass was determined using a modification of the marking method developed by Zieman (1974) (see also Tomasko & Dawes, 1989). Within each plot, eight plants were randomly selected, identified with a labelled wooden stake and the number of leaves per shoot counted and marked by small pin holes. From January 1995 to March 1996, and after a maximum time interval of 2 months, the marked shoots were recovered and the leaves counted and sorted as either newly produced (without pin-hole scars) or old (with holes in the blades). In the laboratory, blades were

cleaned of epiphytes and the mass of the new growth (newly produced leaves plus the old leaves from the base of the blade to the nearest hole) and the remaining tissue determined. Leaf tissues of both groups were placed separately in aluminium trays and dried at 60°C for 24 h. Biomass data were expressed as grams of organic dry mass (g ODM) by subtracting the ash weight from the total dry mass obtained following ashing at 500°C for 6 h in a Fisher Scientific muffle oven.

Survey of density and size distribution of fish-grazers

The study focused on the pinfish *Lagodon rhomboides* (L.) and black mullet *Mugil cephalus* (L.), the dominant omnivorous species in the lagoon seagrass beds (Gilmore, 1988). Throughout the year large schools of black mullet were routinely observed agitating the surface layer and frequently jumping in the study area. Pinfish were not wary and were always observed by the divers. Pinfish switch from a carnivorous to a more herbivorous diet at size classes greater than 70 mm (Stoner & Livingston, 1984), while black mullet larger than 30 cm mainly feed on delicate algae (Odum, 1973). Since visibility was consistently poor in the study area, direct counts of fish were not possible. Because of their dissimilar behaviour two different sampling techniques were used to document the high pinfish and mullet densities (Gilmore, 1988). *Lagodon rhomboides* was sampled with a $30 \text{ m} \times 1.3 \text{ m}$ nylon net seine of $0.9 \times 0.6 \text{ cm}$ mesh size hauled over a standardized area of 150 m^2 during August and September 1996. Black mullet abundances near the study area were obtained from professional fishermen catch records during July and August 1996. Fishermen used at 4.2-m diameter cast net that was thrown when schools of *M. cephalus* were detected. Only individuals of commercial fisheries interest ($>20 \text{ cm}$ total length) were included in the data set. The potential for considerable consumption of epiphytes by pinfish and mullet was demonstrated by combining relative abundances per unit area (m^2) with published estimates of feeding rate (Odum, 1973; Darcy, 1985).

Statistical analyses

Differences in epiphyte loads on *T. testudinum* leaves, seagrass production and crustacean densities were tested using a nested ANOVA analysis (Zar, 1984) for the different periods sampled. Because time-course phenomena were not a central consideration, ANOVA was appropriate for comparing among

treatments at discrete times. The model used in the ANOVA was:

$$X_{ijk} = \mu + \text{time}_i + \text{treatment}_j + \text{time} \times \text{treatment}_{ij} \\ + \text{replicate (treatment)}_{k(j)} + \text{time} \\ \times \text{replicate (treatment)}_{ik(j)} \times e_{e(ijk)}$$

where time had six levels (sampling events) for epiphyte biomass, and eight levels for *T. testudinum* new biomass and new leaves; treatment had three levels (controls, cage controls and exclosures); and replicate had four levels (replicates) per treatment. *Post hoc* comparisons of treatment means were done with Tukey's multiple comparison test (Sokal & Rohlf, 1995). Prior to statistical analysis, the data were tested for normality and homoscedasticity. When necessary, the data were log transformed to fulfil the assumptions of ANOVA.

To explore the relationships between the density of crustaceans, total plant biomass, seagrass biomass and drift algal biomass, stepwise multiple linear regression analysis (forward model, Sokal & Rohlf, 1995) was used. All statistical analyses were performed using SYSTAT version 5.2.1. (Wilkinson, 1990).

Results

The lagoon is a warm-temperate system with a mean annual water temperature of $25.8^\circ\text{C} \pm 6.95$ SD [Figure 2(a)]. Salinity was highly variable in the system [Figure 2(a)] and tracked seasonal patterns of freshwater input. Dissolved nutrient concentrations in the water column did not correlate with either salinity or temperature, however relatively high values were seen at both the end of winter and summer seasons [Figure 2(b)]. Ammonium was the dominant form of dissolved inorganic nitrogen (DIN) with mean (\pm SD) annual concentrations of 7.2 ± 3.33 μM , 15 times higher than those of nitrate (mean 0.53 ± 0.31 μM). Mean annual concentration of soluble reactive phosphorus (SRP) values was 0.84 ± 0.27 μM and showed a pattern of variation similar to that of ammonium [Figure 2(b)].

The composition of the algal epiphytic assemblage fluctuated markedly in the exclosure experiment. Coarse red algae dominated the biomass throughout the sampling period, except during the late winter of 1995, when ephemeral green algae of the genera *Cladophora* and *Enteromorpha* were most abundant (Table 1). Epiphytic algal sudden increases in biomass (blooms) occurred, in general, following peaks in DIN and SRP [Figure 2(b)].

Maximum epiphyte biomass was recorded in March 1995 inside the fish-exclusion cages (mean

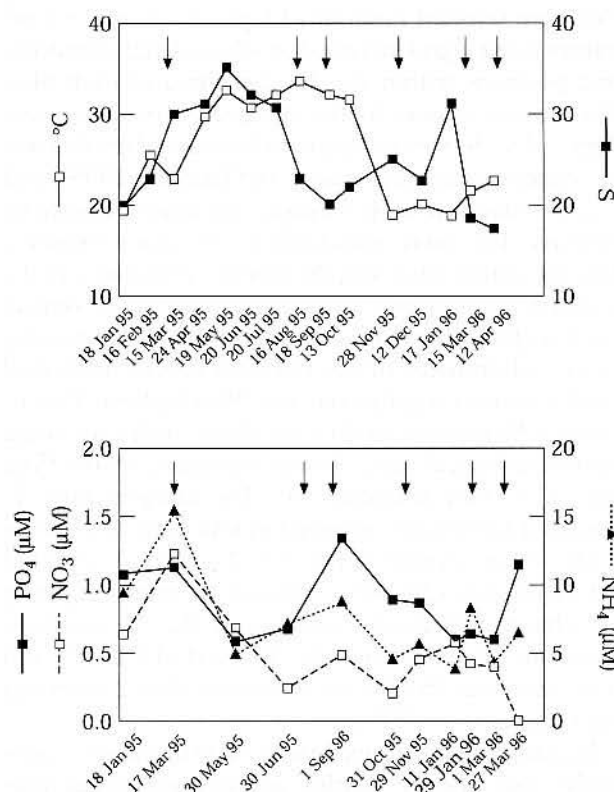


FIGURE 2. Physical-chemical characteristics of the water column in the *T. testudinum* bed from January 1995 to April 1996; (a) temperature and salinity, (b) dissolved inorganic nutrient concentrations (μM) of nitrogen (nitrate and ammonium) and soluble reactive phosphorous. Arrows indicate epiphyte blooms.

0.15 g ODM epiphytes shoot⁻¹; Figure 3), and minimum levels were present during November 1995 (mean 0.005 g ODM epiphytes shoot⁻¹; Figure 3). Treatment effects (fish exclusion) strongly supported the hypothesis during March 1995, when epiphytic biomass on seagrass blades was significantly higher in the absence of grazers (Figure 3), but no significant increase in epiphyte biomass on the exclusion cages [K] was detected during other periods.

Temporal changes dominated the variation of *T. testudinum* shoot biomass and growth. However, the treatments applied induced high variation in the epiphytic load on *T. testudinum* shoots in March 1995 (Table 2; Figure 3). At that time, the growth of *T. testudinum* leaves inside the fish-exclusion cages was significantly lower than that of the controls.

Crustacean densities in the seagrass bed during June 1996 averaged $44 (\pm 29.3)$ individuals per g ODM of plant material and did not show significant differences between treatments (ANOVA $P > 0.05$;

TABLE 1. Species of macroalgal epiphytes (in decreasing order of abundance for each sampling period) on *T. testudinum* blades from March 1995 to March 1996

Date	Phylum	Species	Relative abundance
4 Jan 95	R	<i>Spyridia filamentosa</i> (Wulfen) Harvey	4
	R	<i>Acanthophora spicifera</i> (Val) Børgesen	3
	C	<i>Cladophora</i> sp.	2
13 Mar 95	C	<i>Cladophora albida</i> (Hudson) Kützing	5
	C	<i>Enteromorpha lingulata</i> J. Agardh	5
	C	<i>Enteromorpha prolifera</i> (O. F. Muller) J. Agardh	5
	C	<i>Enteromorpha flexuosa</i> spp. <i>paradoxa</i> (Dillwyn) Bliding	3
25 May 95		<i>Hincksia irregularis</i> (Kützing) Amsler	1
	R	<i>Spyridia filamentosa</i> (Wulfen) Harvey	3
	R	<i>Hypnea cervicornis</i> J. Agardh	2
	C	<i>Cladophora albida</i> (Hudson) Kützing	1
20 Jun 95	R	<i>Chondria curvilineata</i> Collins & Hervey	1
	R	<i>Hypnea cervicornis</i> J. Agardh	1
	R	<i>Chondria curvilineata</i> Collins & Hervey	1
22 Jul 95	R	<i>Hypnea cervicornis</i> J. Agardh	1
	R	<i>Chondria curvilineata</i> Collins & Hervey	1
5 Sep 95	R	<i>Acanthophora spicifera</i> (Val) Børgesen	2
	R	<i>Hypnea cervicornis</i> J. Agardh	2
	R	<i>Spyridia filamentosa</i> (Wulfen) Harvey	2
	C	<i>Enteromorpha flexuosa</i> spp. <i>paradoxa</i> (Dillwyn) Bliding	1
	C	<i>Enteromorpha lingulata</i> J. Agardh	1
	R	<i>Centrocercus clavulatum</i> (C. Agardh) Montagne	1
	C	<i>Cladophora dalmatica</i> Kützing	1
	R	<i>Chondria baileyana</i> (?) (Montagne) Harvey	1
	B	Blue green	1
	C	<i>Pneophyllum lejolisii</i> (Rosanoff) Chamberlain	1
25 Sep 95	R	<i>Acanthophora spicifera</i> (Val) Børgesen	3
	R	<i>Spyridia filamentosa</i> (Wulfen) Harvey	3
	C	<i>Cladophora</i> sp.	2
30 Nov 95	R	<i>Acanthophora spicifera</i> (Val) Børgesen	2
	R	<i>Hypnea spinella</i> (Agardh) Kützing	2
	R	<i>Chondria littoralis</i> Harvey	2
	C	<i>Cladophora albida</i> (Hudson) Kützing	1
	R	<i>Anotrichum tenue</i> (C. Agardh) Nageli	1
	R	<i>Spyridia filamentosa</i> (Wulfen) Harvey	4
17 Jan 96	C	<i>Cladophora albida</i> (Hudson) Kützing	2
	R	<i>Acanthophora spicifera</i> (Val) Børgesen	2
	R	<i>Spyridia filamentosa</i> (Wulfen) Harvey	4
20 Feb 96	C	<i>Enteromorpha flexuosa</i> spp. <i>paradoxa</i> (Dillwyn) Bliding	2
	C	<i>Cladophora albida</i> (Hudson) Kützing	2
25 Mar 96	C	<i>Cladophora albida</i> (Hudson) Kützing	3
	R	<i>Hypnea cervicornis</i> J. Agardh	3
	R	<i>Acanthophora spicifera</i> (Val) Børgesen	3
	R	<i>Spyridia filamentosa</i> (Wulfen) Harvey	2

R=Rhodophyta, C=Chlorophyta, B=Cyanophyta. Braun Blanquet relative abundance scale: 1-rare (<20%), 2-present at low frequency (20–40%), 3-present at high frequency (40–60%), 4-abundant (60–80%), and 5-very abundant (>80%).

Figure 5). Stepwise multiple linear regression showed that algal biomass accounted for a higher percentage of the variation in crustacean densities than did seagrass biomass (ANOVA $P < 0.0001$ vs $P < 0.05$, respectively, $r^2 = 0.744$).

The mean densities of pinfish measured in the seagrass bed were high at 0.32 individuals per m^2 . The

cages excluded pinfish individuals larger than 7 cm in length, which are dominantly herbivorous and represented 70% of the population (Figure 6). The average estimated density of herbivorous mullet was also high with 0.13 individuals per m^2 (Figure 7), and both species maintained high visual densities of large individuals throughout the study period.

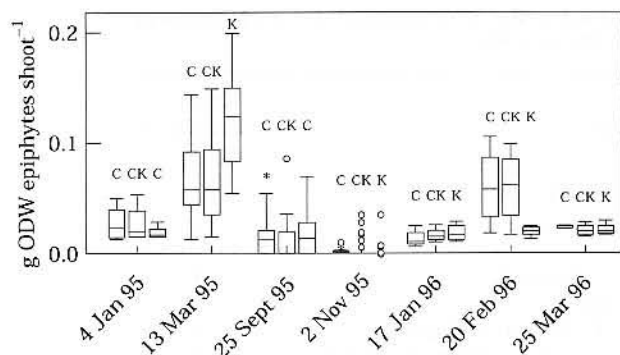


FIGURE 3. Mean biomass of epiphytes in g ODW per *T. testudinum* shoot in the different treatment plots (control, control cages and cages, respectively) during the course of the study. Boxes include 25 and 75% quartiles of all data, the central line represents the median, bars extend to the 95% confidence limits, and circles and asterisks represent observations beyond the 95% confidence limits. Significantly higher values were found for the epiphytic community inside the cage treatments compared to controls (ANOVA, $P < 0.005$) in March 1995.

Discussion

Dissolved inorganic nutrient availability exerts a major control on epiphyte development (e.g. Tomasko & Lapointe, 1990). The nutrient concentration consistently recorded in the lagoon far exceeded the threshold levels conducive to macroalgal proliferation (i.e. $0.2 \mu\text{M}$ SRP and $1.0 \mu\text{M}$ DIN; Bell 1992; Lapointe *et al.*, 1997) in other seagrass and coral-reef marine ecosystems. Continuous culture studies with warm temperate macroalgal species commonly found in the lagoon revealed that the maximum (exponential) growth rates for the sheet-like chlorophyte *Ulva fasciata* (Lapointe & Tenor, 1979) and the coarsely branched rhodophytes *Gracilaria foliifera* and *Neogardhiella bayley* (De Boer, 1978) occurred at DIN concentrations between only 0.5 and $0.7 \mu\text{M}$. The concept that the Indian River Lagoon consistently exceeds DIN and SRP values limiting to macroalgal growth is further supported by the data of Crossland *et al.* (1984) who reported DIN levels of *c.* $1.2 \mu\text{M}$ and SRP *c.* $0.22 \mu\text{M}$ for macroalgal dominated high latitude communities of Western Australia. Available data on nutrient concentration in the lagoon (Heffernam & Gibson, 1983; Davis, 1985) indicate comparable values to those reported during the present study, but with a tendency for ammonium concentrations to increase over the past several decades: $2.70 \mu\text{M}$ in 1976–1978 (Heffernam & Gibson, 1983), $3.30 \mu\text{M}$ in 1984–1985 (Davis, 1985) compared to a maximum of $15 \mu\text{M}$ in 1995–96 (this study).

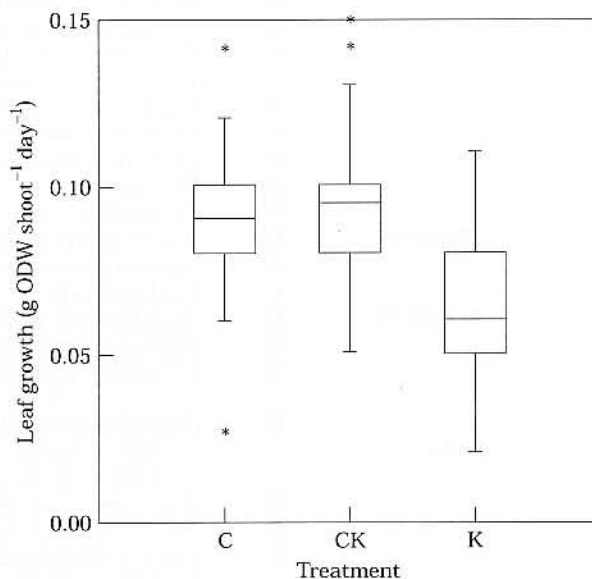
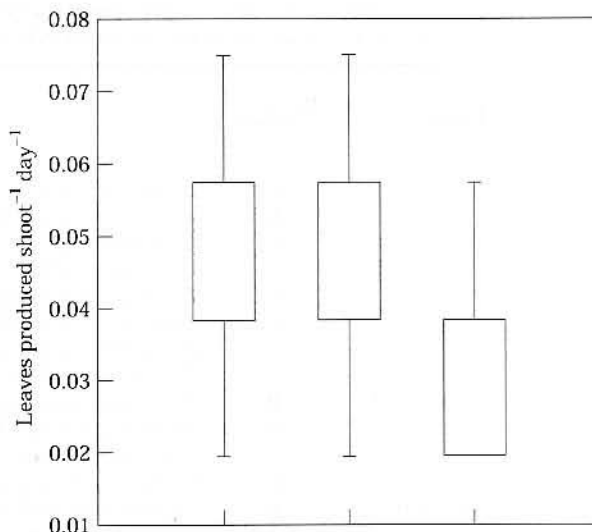


FIGURE 4. Box-plot showing number of *T. testudinum* leaves and new biomass produced per shoot during the enclosure experiment in March 1995. Production of new leaves and new biomass was significantly lower for the plants growing inside the fish enclosure cages (ANOVA, $P < 0.001$) than for accessible plants in the controls.

Maximum epiphyte values were recorded in March 1995 when the dissolved inorganic nitrogen concentrations were maximal [Figure 2(b)]. At that time, the epiphytic assemblage was dominated by delicate green algae of the genera *Enteromorpha* (thin-tubular) and *Cladophora* (filamentous). Both are easily grazed ephemeral species that bloom under eutrophic conditions; (Littler & Arnold, 1982.) During the rest of

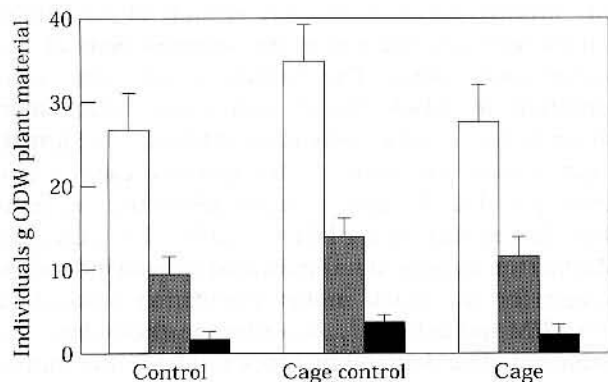


FIGURE 5. Mean densities (\pm SD) of crustaceans in the three different treatments during June 1996. No significant differences among treatments were found for any of the groups (ANOVA, $P > 0.05$). Amphipoda (□); Tanaidacea (▒); and Isopoda (■).

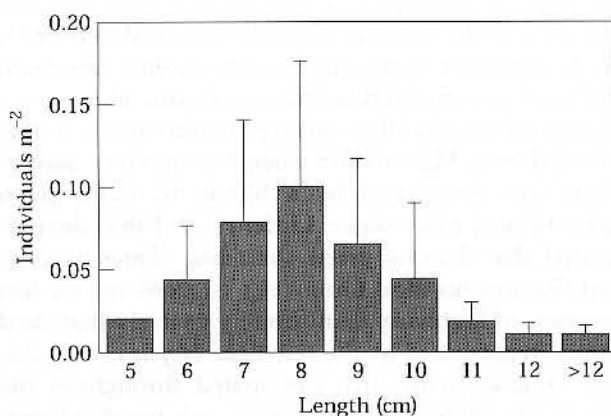


FIGURE 6. Size-frequency data for pinfish collected in the *T. testudinum* bed studied. Data are the average of 20 seine hauls (\pm SD) conducted during August and September 1996 and covering an area of approximately 150 m² each.

the experimental period (Table 1) the epiphyte flora was dominated by coarse red macroalgae. These constitute the main component of the drift-algae of the lagoon (Virnstein & Carbonara, 1985) and use seagrass blades for anchoring (Norton & Mathieson, 1983).

The observed seasonal patterns of epiphyte biomass (i.e. maximum values during winter and low values during spring and most of the summer) are inversely correlated with *T. testudinum* growth (Gacia, in press), which may reflect the importance of the leaves' lifespan for epiphyte accretion (Borum, 1983). It was estimated that within the study area there was an annual load of epiphytic algae of 0.022 g ODM per *T. testudinum* shoot⁻¹. Given a mean annual shoot density of 616 shoots m⁻², and a leaf turnover rate of 4.1 per year (Gacia, in press), the minimum annual

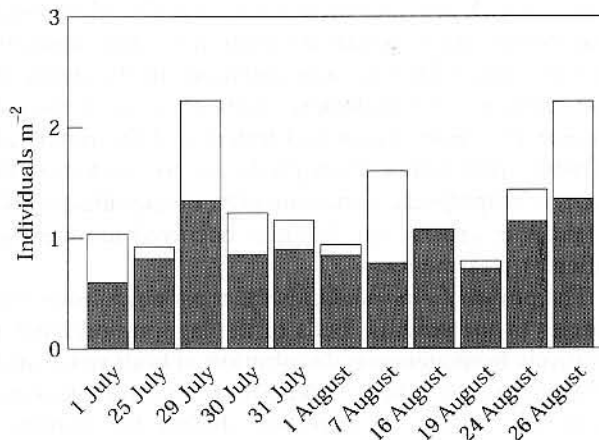


FIGURE 7. Abundances of black mullet in the seagrass beds of near the study area. Large sized fish (□) weighed more than 1.0 kg and medium size (▒) comprise fish between 1.0 and 0.7 kg.

production of macrophytic algae can be estimated at 55 g ODM m⁻² year⁻¹. These values are within the range of the total epiphyte production for *T. testudinum* in Florida Bay (Frankovich & Zieman, 1994), and 40% lower than the data provided for *T. hemprichii* (Ehrenb.) Aschers. in Papua New Guinea (Heijs, 1987), but represent a significant figure, since they only account for macroalgal epiphyte production.

Most importantly, significant differences in epiphyte biomass due to the exclusion of grazers occurred during the chlorophyte bloom of March 1995, when the epiphyte biomass was significantly higher inside the exclusion cages than in the controls. As predicted, the increased epiphyte loads had an inhibitory effect on leaf growth of *T. testudinum*, and leaf initiation was significantly reduced for the non-grazed plants (inside the exclosures) compared to those in the treatments exposed to grazers (controls). Chlorophytes were also present during other seasons (e.g. March 1996), however, they were only dominant in the epiphytic community in March 1995, when the biomass was also the highest recorded. The tendency to lower epiphytic load on *T. testudinum* leaves from inside the cages in February 1996 may reflect a negative effect of the exclusion cages impairing the drift algae to reach and anchor the seagrass blades.

Densities of crustaceans on *T. testudinum* leaves in June 1996 (Figure 6) were similar to those reported by Kensley *et al.* (1995) and Nelson (1995) on *Halodule wrightii* Aschers. and *Syringodium filiforme* Kutz. beds in the same region of the lagoon. Crustaceans appear to prefer the more physically complex habitat offered by drift algae (Zimmerman & Livingston, 1979; Heck & Thoman, 1981; Lenanton *et al.*, 1982; Stoner,

1982), which provides them with more abundant food and refuge from predators than does the seagrass canopy. The relatively large openings in the mesh of our experimental exclusion cages allowed access of smaller predatory fishes and minimized the potential of artefactual refuge from predation for mesograzers such as amphipods. Consequently, no significant differences in crustacean densities occurred among the different treatments.

The pinfish *L. rhomboides* is the most ubiquitous fish species in the seagrass beds of the lagoon and have a relatively homogeneous distribution in both space and time (Gilmore, 1988). Maximum grazing pressure from this species is expected during the summer months, when juveniles shift from a carnivorous to a herbivorous diet linked to a decline in the amphipod populations in the seagrass beds of the lagoon (Nelson *et al.*, 1982). However, the presence of primarily herbivorous individuals (>80 mm total length) throughout the year (Gilmore, 1988), means that some grazing pressure is maintained over time. Densities of *L. rhomboides* during the summer of 1996 were similar to those reported at the same site throughout a 6 year survey (Gilmore, 1988; i.e. 0.32 *vs* 0.30 individuals per m², respectively). Darcy (1985) estimated that *L. rhomboides* has a subsistence feeding rate of 5.75% of body mass per day, and at least 65% of this consumption was algae for the fish sizes excluded from the cages (body mass >90 g FM per individual). From these data, the authors estimated that the potential algal demand needed to sustain this population was 0.1 g DM m⁻² day⁻¹, or about 36 g DM m⁻² year⁻¹, which is about 60% of the conservative estimate of epiphyte turnover (55 g ODM m⁻² year⁻¹ derived above).

Mugil cephalus densities during summer 1996 were two fold greater (0.133 *vs* 0.06 individuals m⁻²) than those reported by Gilmore (1988). Those differences may be due, in part, to the different gear used (seine and drop nets in Gilmore, 1988, and cast nets in this study), but they may also reflect the recovery of the black mullet population after elimination of the gill net fisheries beginning in the lagoon during the summer of 1995 (gill-net ban as a Florida State Constitutional law effective during July 1995). Adult mullet becomes essentially herbivorous towards the third year, when the higher juvenile mortality has already occurred and densities are, therefore, most constant over time (Ribas, 1980). Migrations of black mullet related to spawning (Ribas, 1980) occur from October to December. However, while spawning of different schools may extend over several months, any particular school spends but a very short time in spawning (not exceeding several days). This explains

why throughout the year large schools of big mullet can be seen grazing within the seagrass beds of the lagoon (pers. obs.). The estimated daily algal consumption by black mullet individuals larger than 20 cm is 9.8% of the body mass (Odum, 1973), with a gut-content turnover rate for this size class of five times per day. Length *vs* mass allometric relationship for mullet [Ln g FM = -10.5 × 2.9 (Ln cm); McPherson unpubl. data] indicated a mean individual weight for the black mullet population studied of 995 g FM individual⁻¹. According to these data, the estimated algal demand by black mullet in the immediate study area during summer would be about 6.4 g DM m⁻² day⁻¹. Total algal biomass required to support the combined food demands of the two predominant fish grazers in the *T. testudinum* bed studied equates to 6.5 g DM of algal epiphytes m⁻² day⁻¹. This demand represents about 40% of the epiphyte standing crop present during the summer and 16% of the biomass available during March 1995. Such significant herbivory pressure should have been detected in our experimental treatments. However, a significant grazing effect on epiphyte biomass was only found during March 1995 when the epiphytic assemblage was dominated by a bloom of fleshy-green opportunistic macroalgae. Littler *et al.* (1983) demonstrated that delicate green sheet-like (*Enteromorpha*) and filamentous algal forms (e.g. *Cladophora*) are less resistant to herbivory than rubbery coarsely-branched forms (represented by the red algae *Hypnea*, *Chondria* and *Acanthophora*), that dominated throughout the rest of the study. Hypothetically, such tougher forms (Littler *et al.*, 1983) are not available to the weak shearing feeding apparatuses of pinfish or mullet. These results suggest that herbivory changes seasonally depending on the epiphyte resistances to fish-grazers, which offsets the growth of fleshy-green algae typical of bloom conditions, but has little impact on the relatively unavailable thicker coarsely-branched red algae. The dominance of the coarsely-branched group during the majority of the year could reduce the effect of grazers and enhance the use of alternative food sources such as epiphytic microalgae, as well as seagrass and seaweed detritus.

In summary, the results obtained for this study area indicate a limited capacity of trophic interactions to alleviate *T. testudinum* from being overgrown by epiphytic algae under eutrophic conditions. In the lagoon, fish-grazing intensity had an effect on epiphytic algal standing crops only under fleshy green algae bloom conditions. This short-term contribution to the reduction in epiphyte-seagrass competition did not have a consistent effect on the overall annual primary production of the *T. testudinum* bed. While

fish requirements for algae are sufficient to play an important role, the predominant macroalgal community accumulating over the seagrass blades consists of thick, branched forms, which are not used by the fish. Hence, the role of top-down interactions in maintaining *T. testudinum* growth is limited to the occasional reduction of shading by epiphytic green algae. In the warm temperate Indian River Lagoon, it appears that fish-algal interactions have only limited capacity to buffer the consequences of eutrophication for seagrass growth.

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References

- Braun Blanquet, J. 1946 *Jahrbuch Naturwissen-schaftlichen Gesellschaft Graubündens* **80**, 115–119.
- Bell, P. 1992 Eutrophication and coral reefs: some examples in the Great Barrier Reef Lagoon. *Water Research* **26**, 555–568.
- Borum, J. 1985 Development of epiphytic communities on eelgrass (*Zostera marina*) along a nutrient gradient in a Danish estuary. *Marine Biology* **87**, 211–218.
- Cambridge, M. L. & McComb, A. J. 1984 The loss of seagrass in Cockburn Sound, Western Australia. I. The time course and magnitude of seagrass decline in relation to industrial development. *Aquatic Botany* **20**, 229–243.
- Carpenter, S. R., Kitchell, J. F. & Hodgson, J. R. 1985 Cascading trophic interactions and lake productivity. *Bioscience* **35**, 634–639.
- Crossland, C. J., Hatcher, B. J., Atkinson, M. J. & Smith, S. V. 1984 Dissolved nutrients of a high latitude coral reef, Houtman Abroolhos Island, Western Australia. *Marine Ecology Progress Series* **14**, 159–163.
- Darcy, G. H. 1985 Synopsis of Biological Data on the Pinfish, *Lagodon rhomboides* (Pisces: Sparidae). *NOAA Technical Report NHFS23. FAO Fisheries, Synopsis*. 32 pp.
- Davis, T. L. 1985 *Indian River Water Quality Survey 1984–1985*. Department of Environmental Regulation State of Florida. 115 pp.
- De Boer, J. A., Girgli, H. J., Israel, T. L. & D'Elia, C. F. 1978 Nutritional studies of the two red algae. I. Growth rates as a function of nitrogen source and concentration. *Journal of Phycology* **14**, 261–266.
- D'Elia, C. F., Connor, E. E., Kaumeyer, N. L., Keefe, C. W., Wood, K. V. & Zimmerman, C. F. 1995 *Standard Operating Procedures of the Nutrient Analytical Services Laboratory*. Chesapeake Biological Laboratory (Maryland). 61 pp.
- Frankovich, T. A. & Zieman, J. C. 1994 Total epiphyte and epiphytic carbonate production on *Thalassia testudinum* across Florida Bay. *Bulletin of Marine Science* **54**, 679–695.
- Gacia, E. 1999 Leaf dynamics and primary production of *Thalassia testudinum* in the Indian River Lagoon. *Botanica Marina* **42**, 97–102.
- Gilmore, G. 1988 *Subtropical seagrass fish communities: population dynamics, species guilds and microhabitat associations in the Indian River Lagoon, Florida*. Ph.D. Thesis Florida Institute of Technology, Melbourne, Florida, U.S.A..
- Heck, K. L. Jr & Thoman, T. A. 1981 Experiments on predator-prey interactions in vegetated aquatic habitats. *Journal of Experimental Marine Biology and Ecology* **53**, 125–134.
- Heffernan, J. J. & Gibson, R. A. 1983 A comparison of primary production rates in Indian River, Florida seagrass systems. *Florida Scientist* **46**, 286–295.
- Heijls, F. M. L. 1987 Qualitative and quantitative aspects of the epiphytic component in a mixed seagrass meadow from Papua New Guinea. *Aquatic Botany* **27**, 363–383.
- Hunter, M. D. & Price, P. W. 1992 Playing chutes and ladders: heterogeneity and the relative roles of bottom-up and top-down forces in natural communities. *Ecology* **73**, 724–733.
- Kemp, W. M., Boynton, W. R., Twilley, R. R., Stevenson, J. C. & Means, J. C. 1983 The decline of submerged vascular plants in upper Chesapeake Bay: summary of results concerning possible causes. *Marine Technology Society Journal* **17**, 78–89.
- Kensley, B., Nelson, W. G. & Schotte, M. 1995 Marine isopod biodiversity in the Indian River Lagoon, Florida. *Bulletin Marine Science* **57**, 136–142.
- Kjørboe, T. 1980 Production of *Ruppia cirrhosa* (Petagna) Grande in mixed beds in Ringkøbing Fjord (Denmark). *Aquatic Botany* **9**, 135–143.
- Klumpp, D. W., Salita-Espinosa, J. S. & Fortes, M. D. 1992 The role of epiphytic periphyton and macroinvertebrate grazers in the trophic flux of a tropical seagrass community. *Aquatic Botany* **43**, 327–349.
- Lapointe, B. E., Littler, M. M. & Littler, D. S. 1997 Macroalgal overgrowth of fringing reefs at Discovery Bay, Jamaica: bottom-up versus top-down control. In *Proc 8th Int. Coral Reef Symposium* (Lessios, H. & Mcintyre, I. G., eds) 24 to 29 June 1996, Panama, pp. 71–100.
- Lapointe, B. E. & Tenore, K. R. 1979 Experimental outdoor studies with *Ulva fasciata* Delile. I. Interaction of light and nitrogen on nutrient uptake, growth, and biochemical composition. *Journal of Experimental Marine Biology and Ecology* **135**, 135–152.
- Lenanton, R. C. J., Robertson, A. I. & Hansen, J. A. 1982 Nearshore accumulations of detached macrophytes as nursery areas for fish. *Marine Ecology Progress Series* **9**, 51–57.
- Levitan, C. 1987 Formal stability analysis of a planktonic freshwater community. In *Predation: direct and indirect impacts on aquatic communities* (Kerfoot, W. C., & Sih, A., eds). University Press of New England, Hanover, NH.
- Littler, M. M. & Arnold, K. E. 1982 Primary productivity of marine macroalgal functional-form groups from southwestern North America. *Journal of Phycology* **18**, 307–311.
- Littler, M. M., Littler, D. S. & Taylor, R. R. 1983 Evolutionary strategies in a tropical barrier reef system: functional-form groups of marine macroalgae. *Journal of Phycology* **19**, 229–237.
- McGlathery, K. J. 1995 Nutrient and grazing influences on a subtropical seagrass community. *Marine Ecology Progress Series* **122**, 239–252.

- McQueen, D. J., Johannes, M. R. S., Post, J. R., Steward, T. J. & Lean, D. R. S. 1989 Bottom-up and top-down impacts on freshwater pelagic community structure. *Ecological Monographs* 59, 289–309.
- Nelson, W. G. 1980 A comparative study of amphipods in seagrasses from Florida to Nova Scotia. *Bulletin of Marine Sciences* 30, 80–89.
- Nelson, W. G. 1995 Amphipod crustaceans of the Indian River Lagoon: current status and threats to biodiversity. *Bulletin Marine Science* 57, 143–152.
- Norton, T. A. & Mathieson, A. C. 1983 The biology of unattached seaweeds. In *Progress in Phycological Research 2* (Round, F. E. & Chapman, D. J., eds) Elsevier, Amsterdam, pp. 333–386.
- Odum, W. E. 1973 Utilization of the direct grazing and plant detritus food chains by the striped mullet *Mugil cephalus*. In *Marine Food Chains* (Steele, T. H. & Koeltz, O., eds). Antaquariat, pp. 222–240.
- Orth, R. J. & Van Montfrans, J. 1984 Epiphyte–seagrass relationship with an emphasis on the role of micrograzing: a review. *Aquatic Botany* 18, 43–69.
- Ribas, L. R. 1980 *Synopsis of knowledge on the taxonomy, biology, distribution, and fishery of the gulf of Mexico mullets (pisces: mugilidae)*. Contribution Number 80-37M of the National Marine Fisheries Service, Southeast Fisheries Center, Miami, Florida, pp. 34–53.
- Sand Jensen, K. 1977 Effects of epiphytes on eelgrass photosynthesis. *Aquatic Botany* 3, 55–63.
- Short, F. T. & Short, C. A. 1984 The seagrass filter: purification of coastal waters. In *The Estuary as a Filter* (Kennedy, V. S., ed.). Academic Press, Orlando, Florida, pp. 395–423.
- Silberstein, K., Chiffings, A. W. & McComb, A. J. 1986 The loss of seagrass in Cockburn Sound, Western Australia. III. The effects of epiphytes on productivity of *Posidonia australis* Hook F. *Aquatic Botany* 24, 355–371.
- Sokal, R. R. & Rohlf, F. J. 1995 *Biometry. The principles and practice of statistics in biological research.* (3rd edition). W. H. Freeman & Co, New York, 859 pp.
- Stoner, A. W. 1982 The influence of benthic macrophytes on the foraging behavior of pinfish, *Lagodon rhomboides* (Linnaeus). *Journal of Experimental Marine Biology and Ecology* 58, 271–284.
- Stoner, A. W. & Livingston, R. J. 1984 Ontogenic Patterns in Diet and Feeding Morphology in Sympatric Sparid Fishes from Seagrass Meadows. *Copeia* 1, 174–187.
- Threlkeld, S. T. 1988 Planktivory and planktivore biomass effects on zooplankton, phytoplankton, and the trophic cascade. *Limnology and Oceanography* 33, 1362–1375.
- Tomasko, D. A. & Dawes, C. D. 1989 Evidence for physiological integration between shaded and unshaded short shoots of *Thalassia testudinum*. *Marine Ecology Progress Series* 54, 299–305.
- Tomasko, D. A. & Lapointe, B. E. 1991 Productivity and biomass of *Thalassia testudinum* as related to water column nutrient availability and epiphyte levels: field observations and experimental studies. *Marine Ecology Progress Series* 75, 9–17.
- Twilley, R. R., Kemp, W. M., Staver, K. W., Stevenson, J. C. & Wointon, W. R. 1985 Nutrient enrichment of estuarine submerged vascular plant communities: I. Algal growth and effects on production of plants and associated communities. *Marine Ecology Progress Series* 23, 179–191.
- Virnstein, R. W. & Carbonara, P. A. 1985 Seasonal abundance and distribution of drift algae and seagrasses in the mid-Indian River Lagoon, Florida. *Aquatic Botany* 23, 67–82.
- Wilkinson, L. 1990 *Systat, the system for statistics.* SYSTAT, Eranston, Illinois, 638 pp.
- Zar, J. H. 1984 *Biostatistical analysis.* Prentice-Hall, Inc., Englewood Cliffs, N.J., U.S.A., 620 pp.
- Zieman, J. C. 1974 Methods for the study of the growth and production of the turtle grass *Thalassia testudinum* König. *Aquaculture* 4, 139–143.
- Zimmerman, M. S. & Livingston, R. J. 1979 Dominance and distribution of benthic macrophyte assemblages in a north Florida estuary (Apalachee Bay, Florida). *Bulletin Marine Science* 29, 27–40.