

Effects of nutrient enrichment and small predator density on seagrass ecosystems: An experimental assessment

*K. L. Heck, Jr.*¹

Dauphin Island Sea Lab, Department of Marine Science, University of South Alabama, 101 Bienville Boulevard, Dauphin Island, Alabama 36528

J. R. Pennock

Dauphin Island Sea Lab, Department of Biology, University of Alabama, 101 Bienville Boulevard, Dauphin Island, Alabama 36528

J. F. Valentine

Dauphin Island Sea Lab, Department of Marine Science, University of South Alabama, 101 Bienville Boulevard, Dauphin Island, Alabama 36528

L. D. Coen

South Carolina Department of Natural Resources, Marine Resources Research Institute, P.O. Box 12559, Charleston, South Carolina 29422

S. A. Sklenar

Dauphin Island Sea Lab, Department of Marine Science, University of South Alabama, 101 Bienville Boulevard, Dauphin Island, Alabama 36528

Abstract

We used a field experiment to assess the individual and combined effects of removing top predators and enriching water column nutrients (nitrogen-N and phosphorus-P) on seagrass ecosystem structure and function. Experiments were conducted in turtlegrass (*Thalassia testudinum*) habitats in St. Joseph Bay, FL, an aquatic preserve in the northern Gulf of Mexico that exhibits low ambient nutrient concentrations and contains abundant populations of small crustacean and gastropod mesograzers. We stocked 7.0 m² enclosures with elevated (~4–8× ambient) densities of juvenile pinfish (*Lagodon rhomboides*), the dominant fish species in local seagrass habitats, to simulate the first-order effects of large predator reductions, and we used an in situ delivery system to supplement N and P to ~3× ambient levels in nutrient addition treatments. Monthly determinations of water column nutrients and Chl *a*, along with measurements of the biomass and abundance of leaf epiphytes and seagrass production, biomass, and shoot and leaf densities were used to evaluate the relative effects of manipulating nutrient supply and altering food web structure.

In contrast to our expectations, results showed few significant nutrient effects, or fish × nutrient enrichment effects on any of the parameters measured. However, there were many significant fish effects, most of which were unexpected. As predicted, increased pinfish density reduced mesograzers significantly. Not anticipated, however, was the reduced epiphyte biomass in fish enclosure treatments, apparently brought about by the pinfish consuming significant amounts of epiphytes as well as mesograzers. This reduction in epiphyte biomass produced positive indirect effects on seagrass biomass, shoot number, and rates of primary productivity in pinfish enclosure treatments.

Our results also showed important top-down effects in determining the composition and abundance of seagrass-associated plants and animals in this pristine environment. Although we did not observe simple trophic cascades, most likely because pinfish fed at more than one trophic level, and because the dense seagrass prevented small grazers from being reduced to low numbers, pinfish produced important changes in the epibiota as well as the seagrasses themselves. These data, while contrasting with studies reporting significant negative nutrient enrichment effects on seagrasses, support the results of recent experimental studies in showing that: (1) small grazers can often control the abundance of epiphytes; and (2) it is unlikely that a full understanding of the consequences of nutrient enrichment for seagrass ecosystems can be gained without knowing how grazer population are regulated.

¹ Corresponding author (kheck@disl.org).

Acknowledgments

We thank Leah Gregory, Katherine Canter, Brad Peterson, Paul Bologna, Patric Harper, David Webb, Kirsten Walker, along with a host of other graduate students, for help in field sampling and cage maintenance, Carolyn Wood for manuscript preparation, and Thad Murdoch for drafting Fig. 1. Support was provided by the National Science Foundation Alabama EPSCoR Program, the Dauphin Island Sea Lab and the University of South Alabama. DISL Contribution 317.

Nutrient enrichment and harvesting of large, predatory fishes are two of the most common anthropogenic perturbations in coastal ecosystems. Each has been shown to produce dramatic changes in ecosystem structure and function. For example, increased nutrient loading of estuaries may lead to noxious algal blooms, increased sedimentation of organic material, and ultimately oxygen depletion in bottom waters (*see* Officer et al. 1984; Nixon 1995 for an overview). Nutrient enrichment can produce other undesirable effects in aquatic systems, including the loss of submerged aquatic vegetation (SAV) as a result of shading by rapidly proliferating algal epibionts, whose growth is hypothesized to outstrip the ability of grazers to control them (van Montfrans et al. 1982; 1984; Orth and van Montfrans 1984; Bronmark 1985; Twilley et al. 1985; Howard and Short 1986; Kaiser 1989; Tomasko and Lapointe 1991). After SAV disappears, phytoplankton often come to dominate primary production at very high levels of nutrient loading (*see* review by Duarte 1995). Such "bottom-up" control of ecosystem structure and function by nutrient supply suggests that in eutrophic systems, the potential for a shift from a macrophyte-based to a plankton-based food web is great (Orth and Moore 1983; Cambridge and McComb 1984; Giesen et al. 1990).

It is also known that small invertebrate grazers (i.e., mesograzers) play an important role in controlling epiphytic algal abundance (Howard 1982; van Montfrans et al. 1982; Hootsmans and Vermaat 1985). Recent experimental investigations of the influence of mesograzers (e.g., amphipods, isopods, and small gastropods) on epiphyte abundance in nutrient enriched conditions have found that in most instances (excluding those with the most extreme examples of nutrient enrichment) grazers can control epiphyte abundance and prevent seagrass decline (Neckles et al. 1993; Williams and Ruckelshaus 1993; Short et al. 1995). Why this grazer control has not been frequently reported in nature is unclear, but it suggests that factors influencing grazer abundance might also be involved in determining the degree to which nutrient enrichment impacts SAV habitats. It also suggests that a better understanding of the factors that control mesograzer abundance is needed before we can fully understand the role of nutrient supply in determining the health of seagrass resources.

Reductions in abundance and changes in the composition of predatory fish guilds can also produce profound changes in aquatic systems. Examples include changes in prey habitat utilization and large shifts in prey composition due to reductions in the abundance of predators (Brooks and Dodson 1965; Paine 1966; Dayton 1971; Zaret 1980; Coen et al. 1981; Mittelbach 1984; Werner and Gilliam 1984; Main 1985; 1987). In the pelagic zone of temperate lakes, removal of large predators can trigger a trophic cascade that leads to greater abundances of small fish species, shifts from large to small zooplankton species, and shifts from palatable to grazer-resistant phytoplankton species (Shapiro and Wright 1984; *see* also reviews by Carpenter et al. 1985; 1987). In littoral freshwater habitats, experimentally reducing predator density indirectly led to dramatic changes in SAV abundance (Martin et al. 1992; Lodge et al. 1994). Similarly, in marine kelp forests overharvesting of predatory sea otters led to large increases in the density of their sea urchin prey, which sub-

sequently brought about the loss of kelps as they were overgrazed by the urchins (Estes and Palmisano 1974; Duggins 1980). On coral reefs, the removal of herbivorous fishes has led to the proliferation of algae with concomitant loss of coral cover as algal species begin to monopolize available space (Hughes 1994).

It is now well documented that the ocean's predators have been greatly reduced by fishing, and many popular articles have increased the public's awareness and concern about the consequences of removing great numbers of predators from the world's oceans (Parfit 1995; Safina 1995). As the National Academy of Sciences (1995) reported, the drastic reductions in many species of preferred fishes may be extensive enough to endanger the function of entire marine ecosystems. This report ranked fishing activities as the most serious threat the oceans now face.

Based on these observations, we hypothesized that the increasing harvest of fish predators in coastal waters (e.g., large, warm temperate sciaenid species, such as red drum [*Sciaenops ocellata*], and spotted sea trout [*Cynoscion nebulosus*]) could produce "top-down" effects, in some respects similar to those observed in the littoral zone in lakes (Martin et al. 1992; Lodge et al. 1994), that could ultimately shift seagrass dominated ecosystems to less productive unvegetated bottoms. Such a shift could be mediated by the following sequence of changes after removing most large fish predators: (1) increases in the density of small predatory fishes (e.g., pinfish [*Lagodon rhomboides*], pigfish [*Orthopristis chrysoptera*], and silver perch [*Bairdiella chrysura*]) as they are released from predation; (2) decreases in the abundance of the mesograzer prey of these small fishes (e.g., amphipods, gastropods, and caridean shrimp); (3) increases in the epibiont abundance on the seagrasses as their mesograzer consumers decline in number; and (4) eventual disappearance of the seagrasses as they become overgrown by epibionts. It is important to note that the results predicted by manipulating top predators are similar to those of excess nutrient additions: namely, the loss of seagrass habitat as a result of epiphytic overgrowth. In addition, the effect of reducing large predator populations could increase the rate of seagrass loss in moderately enriched habitats much more rapidly than nutrient addition alone.

Until relatively recently, few investigators have studied both "top-down" and/or "bottom-up" responses of the whole SAV food web (e.g., Carpenter and Lodge 1986; Martin et al. 1992; Lodge et al. 1994; Bronmark and Weisner 1996), and we are unaware of any who have attempted such work in coastal waters. Important differences are to be expected between marine and previously well-studied freshwater systems (Heck and Crowder 1991). For example, the cumulative effects of shifts in macrophyte or large predator abundance are predicted to be more profound in small, "closed" systems such as ponds and less important in larger, "open" systems such as rivers (Power 1992) and estuaries (Heck and Crowder 1991). It is also possible that species-rich marine communities, with many omnivorous taxa, may be less susceptible to "top-down" effects than less diverse freshwater communities (Strong 1992; Polis and Strong 1996).

Here we report on an in situ simulation of the separate

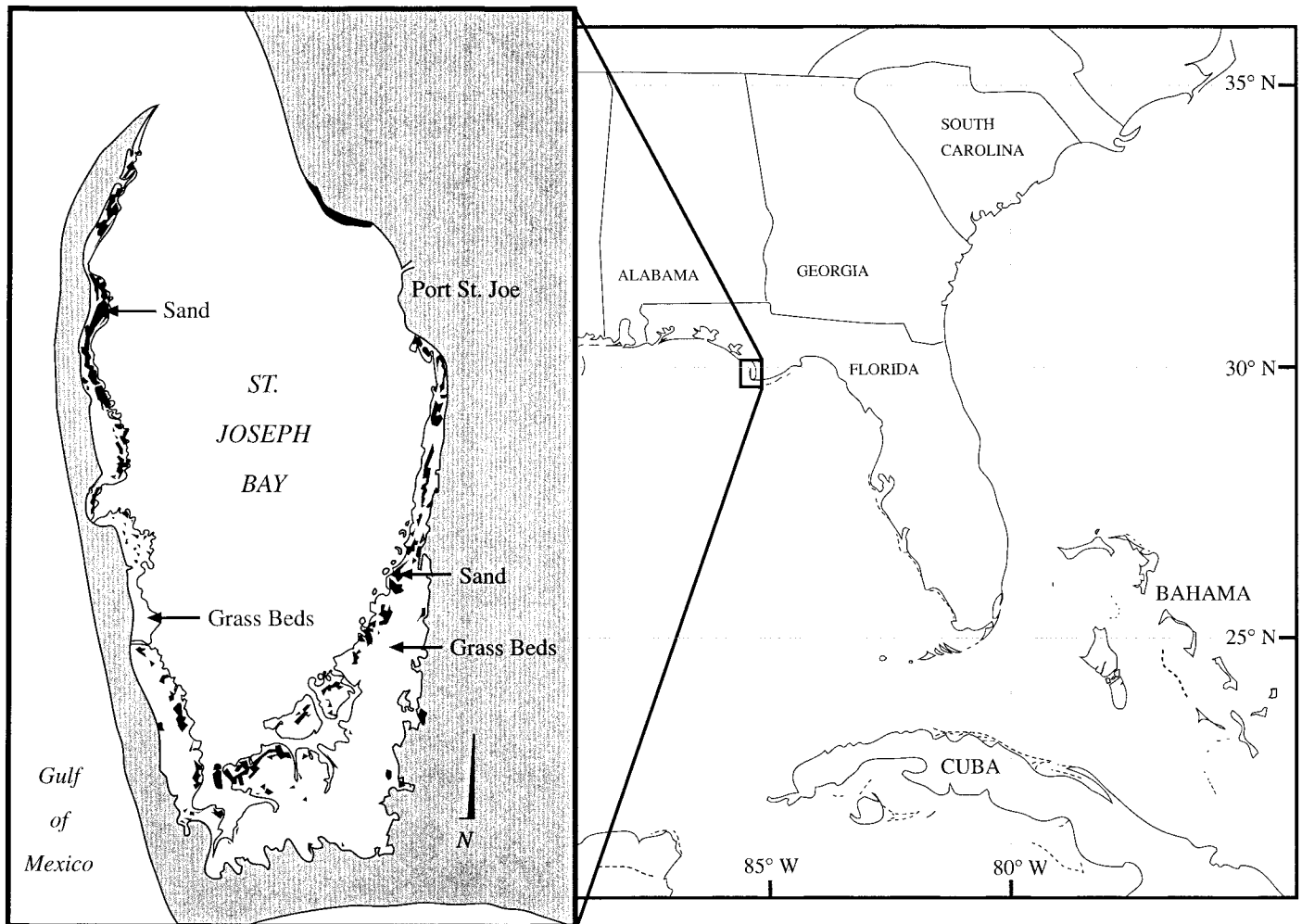


Fig. 1. Study site location in St. Joseph Bay, Florida.

and interactive effects of altering the abundance of large fish predators and nutrient concentrations in seagrass-dominated coastal marine ecosystems. Our objectives were to develop a mechanistic understanding of the indirect effects that may result from these most common perturbations of coastal ecosystems, and ultimately, to predict when these systems could be expected to shift between macrophyte- and phytoplankton-dominated states.

Study site

St. Joseph Bay, Florida, located in the northeastern Gulf of Mexico (29.8°N, 85.3°W), is a soft-bottom polyhaline estuarine system (Fig. 1) with no significant source of freshwater input. Seagrass meadows are dominated by turtlegrass, *Thalassia testudinum*, but also contain shoalgrass, *Halodule wrightii*, and manatee grass, *Syringodium filiforme*, along with unvegetated sand habitats, in the shallow (<2 m) areas. Salinities generally range from 30 to 36 PSU annually (Stewart and Gorsline 1962; pers. observation) but extreme values range from 26 to 43 PSU. Temperatures vary annually from approximately 8–30°C (pers. observation) and the

mean tidal range is 0.5 m (Rudloe 1985). Our previous unpublished measurements have shown low water column nutrient levels ranging from 0.01–2.73 μM for nitrate, 0.3–2.6 μM for ammonium, 0–15.35 μM for silicate and 0–0.14 μM for phosphate (unpubl. data). Overall, Chl *a* (Chl *a*) values are low, and range from 0.17–6.16 $\mu\text{g L}^{-1}$ (unpubl. data). St. Joseph Bay is a semienclosed lagoon type system characterized by low energy current regimes. During the summer of 1994, current velocities measured at our study site ranged from 0 to 7.5 cm s^{-1} , (mean = 2.8 cm s^{-1}), as estimated by an InterOcean System S4 current meter.

Methods

Experimental design—Twenty-four 7 m² round enclosures were erected parallel to shore at depths of approximately 1 m in an area of dense turtlegrass to test the effects of nutrient enrichment and small predator density on community structure and function at several trophic levels. Each enclosure was made of plastic net (1.3 × 1.8 cm mesh) held in place by a metal reinforcing rod frame. Bird netting tops (1.9 cm mesh) maximized light passage and prevented large fish

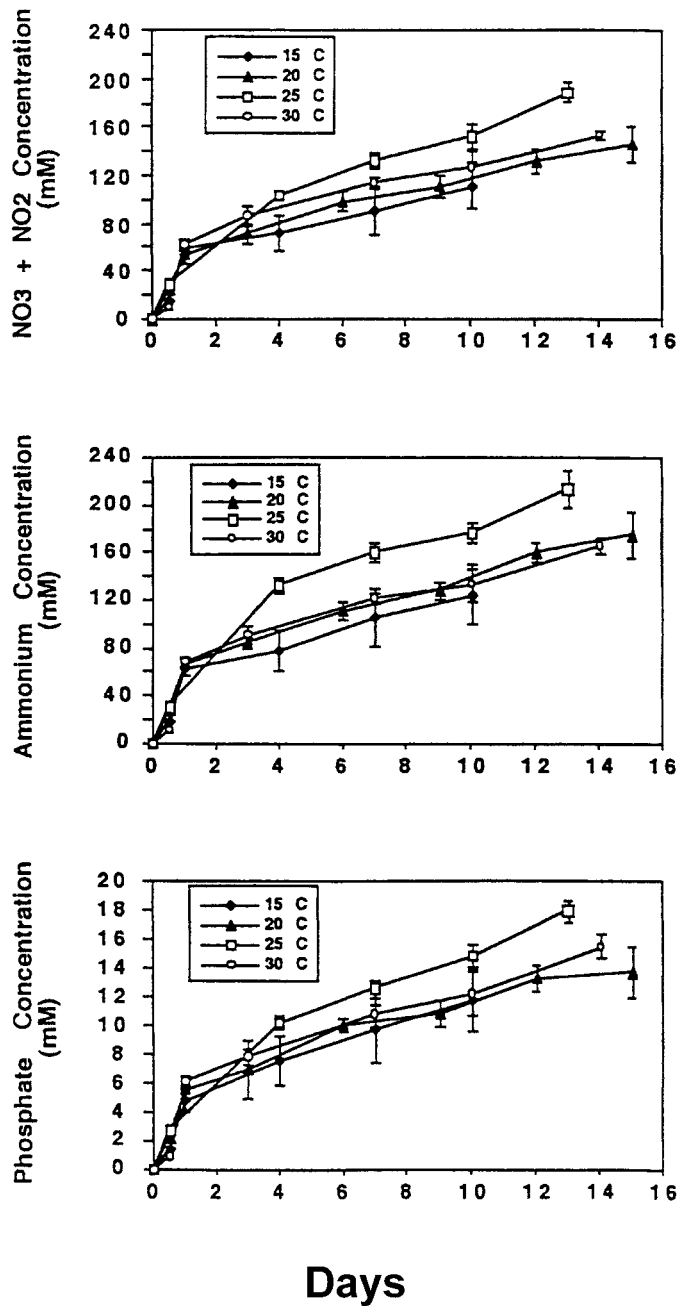


Fig. 2. Dissolution rates vs. time for nitrate + nitrite, ammonium and phosphate at varying temperatures for (2 inch diameter) PVC tubes containing 500 g premeasured Osmocote™.

Table 1. Nutrient release rates ($\text{mmol tube}^{-1} \text{d}^{-1}$) for PVC tubes containing Osmocote™ both in the field and in the laboratory. Field release rates are calculated from weight loss measurements while laboratory measurements were carried out at 15°C and 25°C for comparison purposes.

Dates	Temp (°C)	No. of (d)	% weight loss	field release rates ($\text{mmol tube}^{-1} \text{d}^{-1}$)			Laboratory release rates ($\text{mmol tube}^{-1} \text{d}^{-1}$)		
				NO ₃	NH ₄	PO ₄	NO ₃	NH ₄	PO ₄
27 May 93	25	42	55	42	46	5.5	48	38	5.0
24 Aug 93	28	38	49	42	46	5.5			
01 Oct 93	15	49	37	25	28	3.2	28	26	5.0

from entering or leaving enclosures during extreme high tides.

The experiment's two main effects, small predator manipulation (0 pinfish = -PF and approximately 2–4× mean pinfish density = +PF) and nutrient enrichment (ambient = -N and 3× ambient concentrations = +N), were tested in a factorial design. Each treatment had six replicates and treatments were assigned in two rows of 12 plots. To avoid possible cross-contamination, nutrient treatments were placed in the first and last three cages of each row with additional spacing between the nutrient and nonnutrient cages. Preexperiment sampling were done on 26 May 1993 and all treatments were in place by 28 May 1993. The experiment was carried out for 176 days with the final sampling on 19 and 20 November 1993.

Nutrient additions—In each of the nutrient enclosures, ten PVC tubes (6 cm diameter × 30 cm long with twenty 1 cm holes) containing 500 g of Osmocote™ (N:P molar ratio = 8.3) slow release fertilizer were suspended on metal rods approximately 10 cm above the bottom within the seagrass canopy, and evenly spaced throughout the cage. Nutrients were replaced at approximately six week intervals although the exact time of replacement was dictated by the ambient water temperature and the results of our laboratory studies involving nutrient dissolution (*see below*). Nutrient tubes were cleaned with wire brushes as needed.

In order to characterize the dissolution characteristics of Osmocote™ and to estimate nutrient loading rates in the enclosures, laboratory experiments were conducted to determine Osmocote™ dissolution rates at temperatures commonly encountered during the seagrass growing season (15°C, 20°C, 25°C, and 30°C) (Fig. 2). Individual PVC tubes containing 500 g of Osmocote™ were submerged in 4 L of 30 PSU seawater in 5 liter glass aquaria mixed with magnetic stirrers. Five replicates were used for each temperature treatment. Samples were collected on days 0 and 1, and subsequently at approximately three day intervals over a 10–15 day period. These experiments showed the fertilizer release to occur in two phases, an initial “burst” phase followed by a constant release rate until the nutrients were exhausted (Fig. 2). For temperatures between 15°C and 25°C, the constant release rates displayed a N:P molar release ratio of 17:1 in seawater.

Nutrient loading rates were subsequently calculated directly from field measurements. Three times during the experiment, 20 nutrient tubes were collected and dried to a

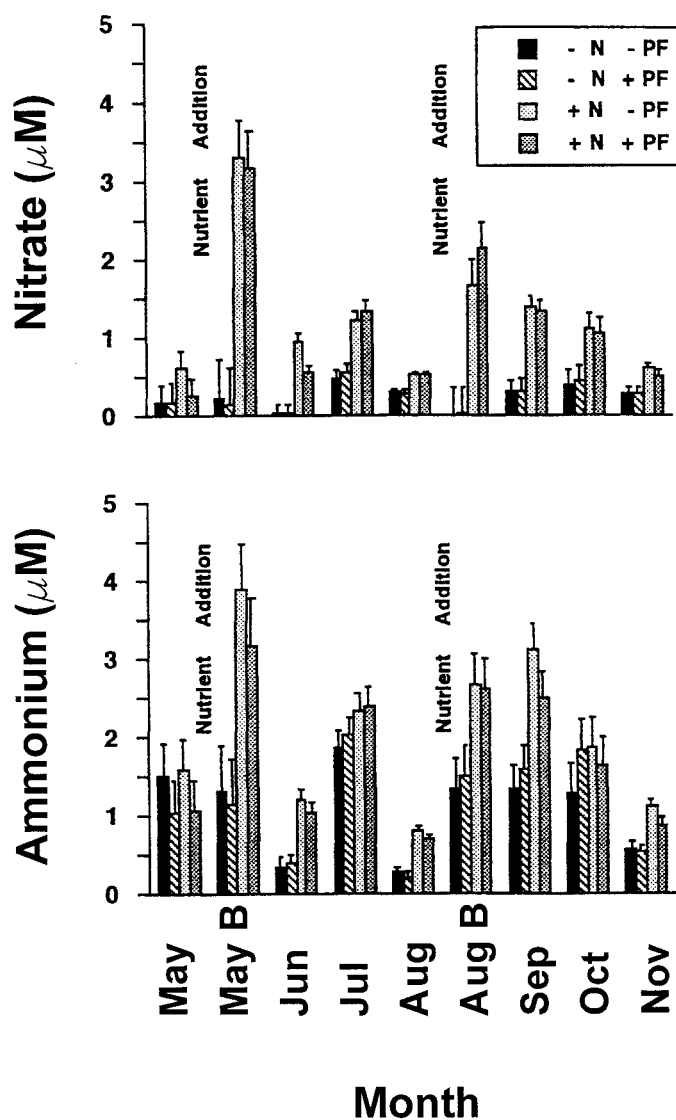


Fig. 3. Nitrate and ammonium concentrations ($\mu\text{M} \pm 1 \text{ SE}$) by month and treatment during 1993. Sampling periods following nutrient additions are indicated by May B and Aug B. Treatments are represented by: -N = no nutrients; +N = nutrient additions; -PF = no pinfish additions; and +PF = pinfish additions.

constant weight after their deployment. Osmocote[®] loss rates in the field ($\text{g tube}^{-1} \text{d}^{-1}$) were calculated based on the change in Osmocote[®] weight over time, and N and P delivery rates ($\text{mmol tube}^{-1} \text{d}^{-1}$) and loading rates ($\text{mmol m}^{-2} \text{d}^{-1}$) were calculated. Comparisons with the laboratory data show the two estimates to agree within $\pm 10\%$ (Table 1).

Fish Manipulations—Pilot studies showed that our enclosure cages effectively excluded large predators (e.g., sharks, red drum, spotted sea trout, and jacks) while allowing smaller invertebrates (e.g., grass shrimp) and benthic fish (e.g., gobies) access (cf. Leber 1985).

The pinfish, *L. rhomboides*, dominates the small fish fauna in Gulf of Mexico seagrass meadows during spring-fall (Heller 1962; Hansen 1969; Stoner 1982; Huh 1984; Stoner and

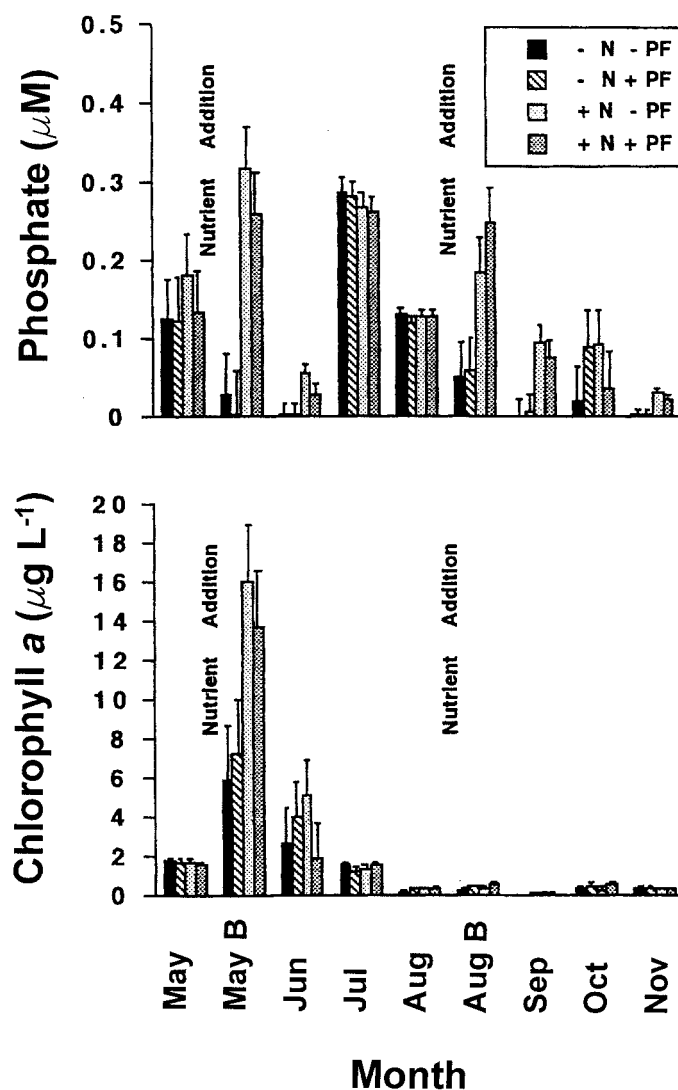


Fig. 4. Phosphate ($\mu\text{M} \pm 1 \text{ SE}$) and Chl *a* ($\mu\text{g L}^{-1} \pm \text{SE}$) concentrations by month and treatment during 1993. Sampling periods following nutrient additions are indicated by May B and Aug B. Treatments are represented by: -N = no nutrients; +N = nutrient additions; -PF = no pinfish additions; and +PF = pinfish additions.

Livingston 1984; Livingston 1984) and is the numerically dominant semidemersal fish in St. Joseph Bay (Kip Thompson, unpubl. data). Density in seine samples at our study site ranged from 4.57 m^{-2} in May to 0.14 m^{-2} in September and 0 m^{-2} during the winter months after young-of-the-year pinfish had migrated offshore (Kip Thompson, unpubl. data). Similarly, mean pinfish density over an annual cycle in Redfish Bay, Texas was found to be 2.3 m^{-2} (Huh 1984).

Pinfish undergo ontogenetic changes in feeding behavior (Carr and Adams 1973; Huh and Kitting 1985; Luczkovich and Stellwag 1993) and they have been suggested to play an influential role in controlling both invertebrate and epiphyte abundance (Stoner 1982; Stoner and Livingston 1984; Huh and Kitting 1985). Based on stomach content analyses, distinctive feeding stages have been characterized, which

vary depending on the area sampled and time of collection (Carr and Adams 1973; Stoner and Livingston 1984; Huh and Kitting 1985). Stoner and Livingston (1984) found five feeding stages: (1) planktivore (11–15 mm standard length [SL]); (2) carnivore (16–35 mm SL); (3) omnivore (amphipod-dominated) (36–80 mm SL); (4) omnivore (epiphyte-dominated) (81–120 mm SL); and (5) herbivore (>120 mm SL). Livingston (1984) characterizes an omnivorous stage (26–60 mm SL) during which pinfish feed heavily on both amphipods and epiphytes. With further growth (61–120 mm SL), pinfish become increasingly more herbivorous and finally (>120 mm SL) feed most heavily on seagrasses.

Young-of-the-year pinfish, *Lagodon rhomboides*, were captured by trawling and used to stock +PF cages at a density of 200 cage⁻¹ or 28 m⁻². The majority of fish ranged from 80 mm to 120 mm in initial SL although extremes ranging to 180 mm SL were also present. Prior to pinfish additions all cages were seined to remove fish larger than the cage mesh. In the northern Gulf of Mexico, pinfish are present at this size (>80 mm SL) by late spring—early summer and could be retained by the mesh enclosures.

Compared with the density of small semidemersal predators at our study site in May, our small predator treatments contained approximately 6.2× ambient “natural” densities (28 fish m⁻²). However, because sampling of juvenile fish abundance using seines and trawls typically underestimates fish density by 30–70% (Kjelson 1977), we estimate that our initial stocking density was actually much lower than 6.2× “natural” pinfish densities. For example, if our estimate of 4.5 fish m⁻² were only 30% of actual densities, the actual abundance would be around 15 m⁻². If they represented 70%, actual densities would be around 6.4 m⁻². Therefore, we estimate that our study densities ranged from around 1.9–4.4× “natural densities”. These enhanced pinfish densities were used to simulate what might happen if large predators were removed from the system by overharvesting.

Sampling regime—All experimental plots were sampled monthly from May to November, the period of greatest seagrass growth in the northern Gulf of Mexico (Iverson and Bittaker 1986; Valentine and Heck 1991; 1993). During each sampling, triplicate water samples were collected from each enclosure for documentation of inorganic nutrient and water-column Chl *a* concentrations. To minimize disturbance within the enclosures, water samples were collected at the canopy height from outside each enclosure. A 2-m long aluminum pipe containing Tygon tubing was inserted through the cage mesh and samples were collected using acid-washed 60 ml syringes. Water samples were placed on ice until (<2 h) they could be filtered through Whatman™ GF/C filters and frozen in 60 ml plastic bottles. Nutrient analyses were carried out on samples using standard wet chemical techniques (Alpkem Manual 1988) adapted for use on an Alpkem RFA/2 Nutrient Autoanalyzer. Chl *a* concentrations were determined using a Turner Designs Model 10 Fluorometer following the acidification method of Lorenzen (detailed in Strickland and Parsons 1972).

Seagrass parameters were determined from shoots collected in three haphazardly selected 0.01 m² samples per enclosure. Samples were placed in 5% formalin and stored

Table 2. Mesograzer categories used in classification of mobile epibiota.

Gastropoda	Chiton
<i>Turbo</i>	Isopod
<i>Rissoina</i>	Amphipod
<i>Modulus</i>	Penaeid
<i>Diastoma</i>	Caridean (no alpheids)
<i>Cerithium</i>	Pagurid
<i>Crepidula</i>	Majid
<i>Mitrella</i>	
<i>Anachis</i>	
<i>Dentimargo</i>	

for later analyses. In the lab, five randomly selected shoots from each sample were used to measure leaf length and width and to quantify attached epibionts on the leaves. Epiphyte species growing on the outside surface of the oldest leaf on each shoot were covered by a 4 × 4 mm grid and the proportion of grid intersections containing filamentous green algae were recorded. (We were especially interested in determining whether the abundance of filamentous green algae, a well-recognized indicator of nutrient enriched conditions, would increase in response to nutrient additions). Epibiont biomass was determined by scraping all sample leaves with a razor blade and drying to a constant weight at 90°C. Samples were then ashed in a muffle furnace at 500°C for 3 h and epibiont ash free dry weight (AFDW) was determined. Total seagrass biomass was also determined by drying to a constant weight at 90°C.

Net aboveground primary production was estimated using a modified blade-marking technique (cf. Dennison 1990). Five randomly selected shoots within 12 cages (3 cages per treatment) were marked with a probe, identified with a flagged stake and collected within 14 days after marking. Newly produced material below the probe mark and all new blades were dried to a constant weight at 90°C to estimate net aboveground primary production (g DW shoot⁻¹ d⁻¹).

Invertebrate mesograzers were collected from each enclosure using a 0.07 m² plastic cylinder, whose lower edge was embedded in the sediment. The macrofauna in the cylinder were sampled by a gasoline-powered suction pump (cf. Orth and van Montfrans 1987; Williams et al. 1990; Valentine and Heck 1993) and all material was passed through a 0.5 mm collecting bag where larger motile epibiota were retained. Following collection, samples were sieved on a 0.5 mm mesh screen to remove additional material, placed on ice and frozen. Animals were identified only to the extent necessary to be classified trophically (Table 2), according to published information (cf. Zimmerman et al. 1979; Orth and van Montfrans 1984; Klumpp et al. 1992; Neckles et al. 1993; Williams and Ruckelshaus 1993). Free-living amphipods, isopods, caridean shrimp, and gastropods constituted the majority of mesograzers.

Cage inspection and repair was conducted biweekly, and cage cleaning was conducted monthly to ensure enclosure integrity. During cage inspections sea urchins, all observed predatory portunid and xanthid crabs, and other fish species

Table 3. Comparison of estimated loading rates and measured nitrogen and phosphorus concentrations in this study with those of previous experimental manipulations in seagrass systems and selected estuaries.

Field manipulations	N-loading (mmol m ⁻² d ⁻¹)	P-loading (mmol m ⁻² d ⁻¹)	Ambient [N] (μM)	Treatment [N] (μM)	Ambient [P] (μM)	Treatment [P] (μM)
This study*	77-123	5-7	0.3-5.3	0.5-7.0	0-0.14	0.1-0.4
Harin and Thorne-Miller (1981)*	1,971-3,857	257-429	0.4-2.3	1.0-21.6	0-1.0	0.1-5.6
Neckles et al. (1993)†			4.0-10.8	10.6-37.8	0.7-1.6	1.8-3.4
Williams and Ruckelshaus (1993)†	476-510		3.6-45.0	3.6-45.0		
McGlathery (1995)	300	34.5	1.0-2.0	4.0-4.5	<0.05	0.10
Selected estuaries‡						
Apalachicola Bay			5.4		0.2	
Chesapeake Bay	1.9	0.11	20.0		0.5	
Delaware Bay	19.2	1.60	110.0		1.2	
Narragansett Bay	2.7	0.22	8.1		1.9	
Thames Estuary, U.K.	87.7	8.70				

* DIN added as NO₃ and NH₄.

† DIN added as NH₄ only.

‡ Estimated from Nixon (1986).

larger than 2 cm in body width or height were removed by hand or by spearing.

After the final sampling, all fish in each cage were collected, counted and identified. Up to 20 pinfish per cage were measured (TL and SL in mm) and weighed (wet weight). Fultons condition factor was calculated ($K = \text{weight} \times \text{length}^{-3}$) (Lagler et al. 1962) and used to investigate treatment differences in pinfish condition.

Statistical analyses—Two-way repeated measures ANOVA was used to analyze the effects of small predator manipulation and nutrient enrichment on monthly measurements of seagrass parameters, mesograzers abundance, epibiont DW, AFDW, and percent occurrence by taxonomic category, inorganic nutrients, and Chl *a*. Nutrient concentrations, final fish counts, and condition factors were also analyzed using two-way ANOVAs. Scheffe's multiple comparison procedure was used when $P < 0.05$ for main effects and interactions were not significant. Data were transformed when necessary to meet assumptions of the ANOVAs.

Results

Water column nutrients—While nutrient concentrations varied somewhat during the experiment as a result of natural input and wind-mixing, on average, +N treatments achieved 3× ambient nutrient levels observed in -N plots (Figs. 3,4). Both nitrogen and phosphate levels generally remained elevated in the nutrient addition treatments throughout the duration of the experiment (Figs. 3,4). High concentrations were observed following the addition of replacement fertilizer tubes, as documented in May and August (Figs. 3,4); however, these periods were expected to be brief based on laboratory dissolution results.

Initial ambient water samples collected in May were not significantly different in nitrate, nitrite, ammonium, phosphate, silicate, or Chl *a* levels among treatments. Throughout the experimental duration, nitrite and silicate levels were very low and similar between treatments and within months, thus we do not present the results for these nutrients. Chl *a* concentrations were also low (<2 μg L⁻¹) and showed no treatment effects except immediately after the initial nutrient addition in May (Fig. 4). We believe that this response was an artifact caused by the physical dislodging of epiphytes during initiation of the experiment, not phytoplankton growth.

Over all months, nitrate concentrations were greatest in the nutrient addition treatments. Nitrate levels in the -N treatments ranged from 0.02 μM (-N-PF) in August to 0.56 μM (-N+PF) in July (Fig. 3). In the nutrient addition cages, nitrate levels ranged from 0.53 μM (+N-PF, +N+PF) in August to 1.39 μM (+N-PF) in September. Excluding the initial sampling date, nitrate concentrations were significantly higher in the +N treatments compared with the -N treatments.

Ammonium levels in the -N treatments were lowest in August (0.21 μM 1:2 -N+PF) and highest during July (2.03 μM 1:2 -N+PF) (Fig. 3). Ammonium concentrations in nutrient enriched treatments ranged from 0.69 μM (+N+PF) in August to 3.14 μM (+N-PF) in September.

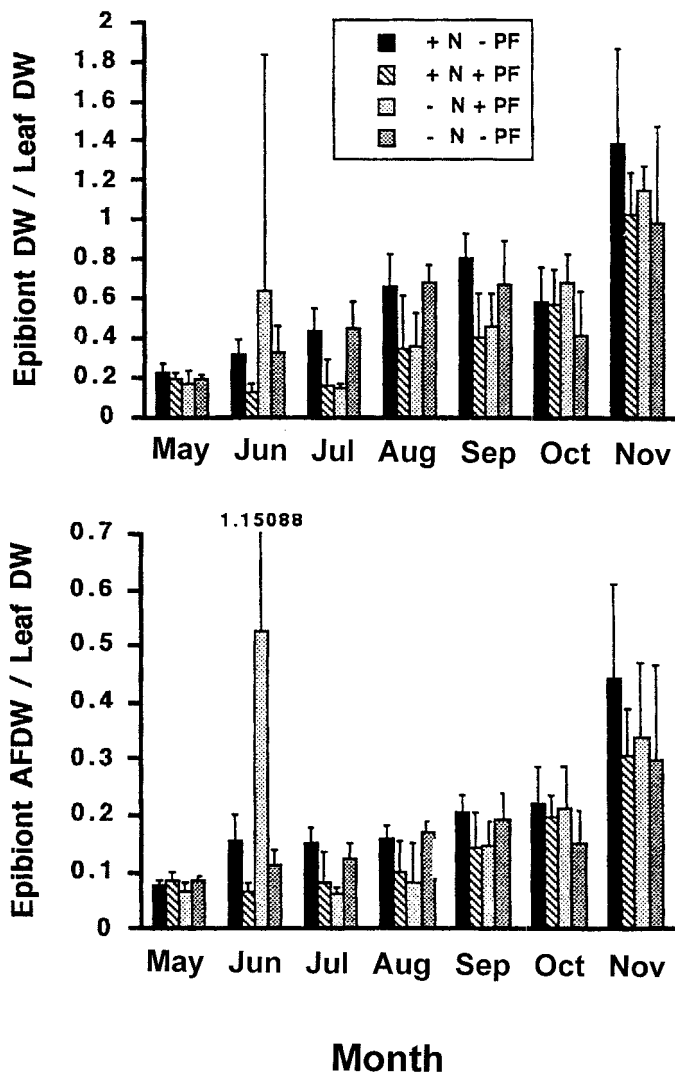


Fig. 5. Ratio of epibiont dry weight and epibiont ash free dry weight ($\text{g } 0.01 \text{ m}^{-2}$) to leaf dry weight ($\text{g } 0.01 \text{ m}^{-2}$) (\pm SD) by month and treatment during 1993. Treatments are represented by: -N = no nutrients; +N = nutrient additions; -PF = no pinfish additions; and +PF = pinfish additions. May samples were taken before the experiments were begun.

Significant nutrient effects occurred for all sampling dates except July and October (Fig. 3).

Phosphate concentrations ranged from undetectable (September: -N-PF) to $0.29 \mu\text{M}$ (July: -N-PF) in the -N treatments (Fig. 4). Phosphate values were highest in July ($0.27 \mu\text{M}$; 2+N-PF) and lowest in November ($0.02 \mu\text{M}$; 2+N+PF). Phosphate concentrations were significantly greater within nutrient enriched cages compared with the ambient treatments in June ($F_{2,23} = 11.84$, $P = 0.003$), September ($F_{2,23} = 13.38$, $P = 0.002$) and November ($F_{2,23} = 15.63$, $P < 0.001$) (Fig. 4).

During the May "initial burst", significant nutrient treatment effects were documented for nitrate ($F_{2,23} = 41.46$, $P < 0.001$), ammonium ($F_{2,23} = 14.95$, $P < 0.001$), phosphate ($F_{2,23} = 25.71$, $P < 0.001$), and Chl *a* ($F_{2,23} = 8.46$, $P = 0.009$). Nutrient effects were also observed in the Au-

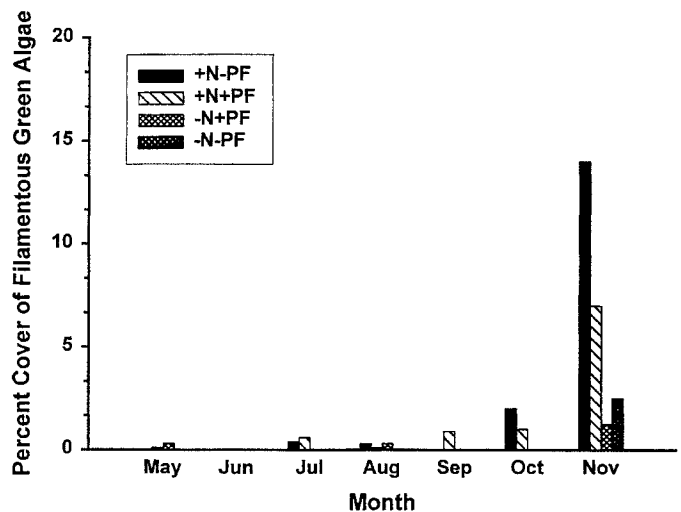


Fig. 6. Proportion of leaves covered by filamentous green algae by month and treatment during 1993. Treatments are represented by: -N = no nutrients; +N = nutrient additions; -PF = no pinfish additions; and +PF = pinfish additions. May samples were taken before the experiments were begun.

gust burst for nitrate ($F_{2,23} = 29.25$, $P < 0.001$), ammonium ($F_{2,23} = 9.64$, $P = 0.006$) and phosphate ($F_{2,23} = 13.48$, $P = 0.002$). Nutrient enrichment treatments had elevated levels of nitrate, ammonium, and phosphate in May and August compared with the -N treatments.

Epibionts—Epibiont DW and AFDW/leaf DW was usually greater in cages without pinfish than in those with pinfish additions, especially during the summer months (Fig. 5), and these ratios were significantly lower in pinfish addition treatments (Table 4). Month, as well as interactions between fish and month, were also significant in both cases (Table 4).

Overall, significant between subjects nutrient and fish effects were documented for the percentage of filamentous green algal cover, with significantly more filamentous green algae in +N treatments, and significantly less algae in +PF treatments (Table 4; Fig. 6). Month, two-way (nutrient \times month and fish \times month) and three-way interaction terms (nutrient \times fish \times month) were also significant within subjects.

Mesograzers—Free-living amphipods, isopods, caridean shrimp, hermit crabs, and gastropods constituted the majority of mesograzers at our study site. As expected, pinfish reduced mesograzers densities during most months (Fig. 7), resulting in significant fish, but not nutrient, effects (Table 4). There were also significant monthly differences that reflected usual seasonal variations in population size (Table 4).

Seagrass—Leaf length varied seasonally, with greatest mean lengths of 25–30 cm occurring in July–September (Fig. 8). Leaves collected from pinfish cages were significantly longer than leaves from the no pinfish treatments (Table 4). Increased nutrient levels did not significantly affect

leaf length although there were significant seasonal effects on leaf length (Table 4).

Seagrass leaf width was not significantly affected by either nutrient or pinfish treatments (Table 4), but did show significant seasonal variability (Table 4; Fig. 8).

Seagrass biomass peaked during July, with mean values ranging between approximately 95 and 135 g dry wt m⁻². Significant pinfish effects were observed, with seagrass biomass usually greatest in pinfish treatments (Table 4; Fig. 9). There were significant seasonal effects on seagrass biomass as well as a fish × month interaction (Table 4). Seagrass shoot number responded similarly, with significantly enhanced shoot densities present in pinfish treatment, especially during the August–November period (Table 4; Fig. 10) and significant seasonal variability (Table 4). Although seagrass production was not significantly affected by either nutrient or fish treatments (Table 4), owing to large variability, the greatest production rates generally occurred in the +PF treatments from August through October (Fig. 11). A significant seasonal effect was also noted (Table 4).

Experiment termination—A final sampling was conducted in November; in addition, all cages were seined to quantify final fish densities. Initially, *L. rhomboides* was stocked at 200 fish per cage (+PF treatments). Seven months later in November, pinfish numbers had declined in all pinfish enclosures (presumably because of escapes), so that the +PF treatments contained approximately 3× the density of nonpinfish enclosures (mean of 66.0 cage⁻¹ or 9.4 m⁻² in +PF enclosures, compared with a mean of 21.8 cage⁻¹ or 3.1 m⁻²) in -PF treatments (which often contained unwanted immigrants) (Fig. 12). This difference was significant ($F_{2,23} = 24.23$, $P < 0.0001$). Additional immigrant fish species removed from cages included spot, cowfish, pigfish, cubbyu, gag grouper, toadfish, pipefish, filefish, sand perch, mullet, goby, red snapper, sheephead, sea robin, seahorse, flounder, and speckled trout. These additional species made up a small fraction of the total fish number by cage and treatment, and never exceeded a mean value of more than 2 cage⁻¹ (Fig. 12).

Pinfish in the enclosures at the end of the experiment ranged from 50 mm to 200 mm in total length (TL), with the majority in the 60–100 mm TL range (Fig. 13). Condition factors ($K = \text{weight} \times \text{length}^{-3}$) (Lagler et al. 1962) were affected by pinfish density ($F_{2,23} = 9.22$, $P = 0.0065$) but not by nutrients (Fig. 14). Pinfish from +PF cages had a significantly lower condition index (mean = 0.025) compared with intruding pinfish found in the no -PF treatments (mean = 0.027) (Fig. 14), although we ascribe little biological importance to this small difference in condition index.

Discussion

Duarte (1995) has summarized the conventional wisdom regarding the effects of nutrient enrichment on SAV, stating that increasing nutrient supplies lead to the overgrowth of seagrasses by fast-growing algae and the eventual disappearance of seagrasses from eutrophic systems. This is the explanation most often proposed to account for the loss of seagrasses in North America (Orth and Moore 1983; Neundorfer and Kemp 1993; Short et al. 1995; Tomasko et al.

1996), Europe (Giesen et al. 1990; Den Hartog 1994) and Australia (Cambridge and McComb 1984). However, none of the studies cited above evaluated the ability of epiphyte grazers (mesograzers) to control epiphyte biomass on seagrass leaves. This is relevant because numerous studies have demonstrated that small crustacean and gastropod grazers can control epiphyte biomass. For example, van Montfrans et al. (1982), Robertson and Mann (1982), and Howard and Short (1986) demonstrated that small gastropods (e.g., *Bititium varians*) could regulate epiphyte biomass in laboratory microcosms. Similarly, Caine (1980) and Howard (1982) showed that amphipods could control epiphyte biomass, with Caine (1980) reporting differences of up to 400% in epiphyte biomass between grazed and ungrazed eelgrass leaves. In addition, Borum (1987) demonstrated that a mixed group of amphipods, isopods, and gastropods at field densities kept epiphyte biomass on eelgrass shoots at levels only 10% those in ungrazed treatments. Reviews of the many studies that demonstrate the remarkable degree to which mesograzers can control epiphyte abundance on macrophytes are provided by van Montfrans et al. (1984), Brawley (1992), and Jernakoff et al. (1996). On balance, these reviews suggest that when grazers are present, the stimulatory effects of increased nutrient loading on epiphyte abundance are greatly reduced.

Recently, several nutrient enrichment experiments with grazers present have found only partial support for the simple nutrient enrichment hypothesis cited by Duarte (1995). For example, Neckles et al. (1993) found that epiphyte grazing by amphipods seasonally prevented the overgrowth of eelgrass by algae in nutrient-enriched mesocosms, and concluded that the effects of grazers were stronger than those of nutrients. Williams and Ruckelshaus (1993) found that isopod grazing reduced epiphyte biomass by one-third, while in the absence of grazing nutrient enrichment led to increased epiphyte biomass that negatively affected eelgrass growth. They concluded that epiphytes have the potential to control eelgrass growth only when small grazers are absent, nitrogen in the water column is abundant (>15 μM DIN; dissolved inorganic nitrogen) and when temperatures are suboptimal for eelgrass growth. In the Netherlands, Phillipart (1995) used field enclosure experiments to show that gastropod (*Hydrobia ulvae*) grazing on epiphytes led to enhanced eelgrass density and biomass. Phillipart (1995) further suggested that eelgrass declines in the Wadden Sea during the past 25–30 yrs, which have been attributed to the effects of eutrophication, may have instead been initiated when *Hydrobia* abundances declined precipitously in the early 1970's (Phillipart 1995). Lin et al. (1996) assessed the effects of nutrient enrichment on laboratory mesocosms of eelgrass containing mesograzers as well as faunal components from all trophic levels. They found that epiphyte biomass was not a good indicator of nutrient loading in shallow coastal lagoons, and that epiphyte responses to nutrient enrichment were surprisingly complex. Of primary importance, they concluded, were system level faunal interactions that produced results that differed from previous studies which did not include complex plant–animal interactions (Lin et al. 1996). In aggregate, the results from these studies showed that mesograzers frequently control the abundance of epiphytes, even in enriched conditions.

Table 4. Univariate results of repeated measures ANOVAs.

Source of variation	DF	Type III SS	Mean square	F value	Pr > F
Epibiont DW/Seagrass DW					
<i>Between subjects</i>					
Nutrients	1	0.00513699	0.00513699	0.19	0.6662
Fish	1	0.43962289	0.43962286	16.00	0.0001
Nutrients × Fish	1	0.05952768	0.05952768	2.17	0.1436
<i>Within subjects</i>					
Date	6	5.58709139	0.93118190	33.90	0.0001
Nutrients × Date	6	0.05952768	0.00991907	0.36	0.9022
Fish × Date	6	1.51728280	0.25288047	9.21	0.0001
Nutrients × Fish × Date	5	0.14442732	0.02888546	1.05	0.3908
Epibiont AFDW g Seagrass DW⁻¹					
<i>Between subjects</i>					
Nutrients	1	0.01508862	0.01508862	0.84	0.3622
Fish	1	0.33137071	0.33137071	18.37	0.0001
Nutrients × Fish	1	0.14739596	0.04739596	2.63	0.1076
<i>Within subjects</i>					
Date	6	3.62384995	0.60397499	33.48	0.0001
Nutrients × Date	6	0.06674279	0.01112380	0.62	0.7166
Fish × Date	6	1.00829083	0.16804847	9.32	0.0001
Nutrients × Fish × Date	5	0.08765056	0.01753011	0.97	0.4379
Percent leaf cover by green filamentous algae					
<i>Between subjects</i>					
Nutrients	1	0.08123753	0.08123753	35.41	0.0001
Fish	1	0.01883982	0.01883982	8.21	0.0048
Nutrients × Fish	1	0.00033254	0.00033254	0.14	0.7040
<i>Within subjects</i>					
Date	6	1.20729172	0.20121529	87.70	0.0001
Nutrients × Date	6	0.19118439	0.03186407	13.89	0.0001
Fish × Date	6	0.04088964	0.00681494	2.97	0.0092
Nutrients × Fish × Date	6	0.05277404	0.00879567	3.83	0.0014
Number of mesograzers g Seagrass DW⁻¹					
<i>Between subjects</i>					
Nutrients	1	26103.8707	26103.8707	1.83	0.1789
Fish	1	359639.2452	359639.2452	25.15	0.0001
Nutrients × Fish	1	468.5076	468.5076	0.03	0.8566
<i>Within subjects</i>					
Date	6	517813.2113	86302.2019	6.03	0.0001
Nutrients × Date	6	75148.4065	12524.7344	0.88	0.5145
Fish × Date	6	44863.2163	7477.2027	0.52	0.7903
Nutrients × Fish × Date	6	13243.8359	2207.3060	0.15	0.9879
Mean leaf length (cm)					
<i>Between subjects</i>					
Nutrients	1	11.078461	11.078461	0.78	0.3787
Fish	1	89.291331	89.291331	6.29	0.0133
Nutrients × Fish	1	35.087021	35.087021	2.47	0.1183
<i>Within subjects</i>					
Date	6	4067.557942	677.926324	47.72	0.0001
Nutrients × Date	6	60.761741	10.126957	0.71	0.6398
Fish × Date	6	96.014009	16.002335	1.13	0.3501
Nutrients × Fish × Date	6	30.388498	5.064750	0.36	0.9051
Mean leaf width (mm)					
<i>Between subjects</i>					
Nutrients	1	0.09080795	0.09080795	3.01	0.0847
Fish	1	0.01640203	0.01640203	0.51	0.4618
Nutrients × Fish	1	0.00064042	0.00064042	0.02	0.8843

Table 4. Continued.

Source of variation	DF	Type III SS	Mean square	F value	Pr > F
<i>Within subjects</i>					
Date	6	1.75181880	0.29246980	9.71	0.0001
Nutrients × Date	6	0.13103220	0.02183870	0.72	0.6303
Fish × Date	6	0.04125716	0.00687619	0.23	0.9669
Nutrients × Fish × Date	6	0.02717141	0.00452857	0.15	0.9887
Total leaf dry weight (g DW m ²)					
<i>Between subjects</i>					
Nutrients	1	0.01161956	0.01161956	0.10	0.7499
Fish	1	2.80943081	2.80943081	24.67	0.0001
Nutrients × Fish	1	0.26476576	0.26476576	2.33	0.1295
<i>Within subjects</i>					
Date	6	40.21016076	6.70139346	58.86	0.0001
Nutrients × Date	6	0.45326620	0.07554437	0.66	0.6792
Fish × Date	6	2.65058666	0.44176444	3.88	0.0013
Nutrients × Fish × Date	6	0.19895515	0.03315919	0.29	0.9403
Number of shoots 0.01 m ² ⁻¹					
<i>Between subjects</i>					
Nutrients	1	3.37948987	3.37948987	2.43	0.1224
Fish	1	8.85787037	8.85787037	6.37	0.0133
Nutrients × Fish	1	0.51580189	0.51580189	0.37	0.5440
<i>Within subjects</i>					
Date	4	68.93211246	17.23302811	12.39	0.0001
Nutrients × Date	4	2.42345057	0.60586264	0.44	0.7827
Fish × Date	4	5.60512619	1.40128155	1.01	0.4077
Nutrients × Fish × Date	4	0.39948103	0.9987026	0.07	0.9905
Production (g DW shoot ⁻¹ day ⁻¹)					
<i>Between subjects</i>					
Nutrients	1	0.00000010	0.00000010	0.03	0.8541
Fish	1	0.00000880	0.00000880	30.6	0.0865
Nutrients × Fish	1	0.00000000	0.00000000	0.00	0.9945
<i>Within subjects</i>					
Date	5	0.00023091	0.00004618	16.00	0.0001
Nutrients × Date	5	0.00000763	0.00000153	0.53	0.7518
Fish × Date	5	0.00001903	0.00000381	1.32	0.2700
Nutrient × Fish × Date	5	0.00000239	0.00000048	0.17	0.9738

In our experiments, we found that nutrient enrichment had no significant effect on epiphyte biomass, or the production, leaf length, shoot density, or biomass of *T. testudinum*. In fact, the only significant nutrient effect was on the increased cover of filamentous green algae on seagrass leaves. In contrast, manipulation of pinfish densities resulted in significant effects on mesograzers density, epiphyte biomass, and the production, leaf length and shoot density of *Thalassia*. These results are clearly not consistent with the simple paradigm of nutrient-enrichment based seagrass decline summarized by Duarte (1995) and require close examination.

Initially, it is important to assess the level of nutrient enrichment in the +N treatments. We estimate (based on data from both 15°C and 25°C; Fig. 2) that our +N treatments received 77–123 mmol DIN m⁻² d⁻¹, and 5–7 mmol P m⁻² d⁻¹. These daily rates translate to annual rates of 28–45 mol DIN m⁻² yr⁻¹ and 1.8–2.6 mol PO₄ m⁻² yr⁻¹ and are generally much higher than rates estimated for major estuaries of the world, and within the range of those achieved in other seagrass nutrient enrichment studies (Table 3). While some advection of nutrients from our experimental cages undoubt-

edly occurred, there are a number of reasons why we believe that our nutrient enrichments were quite effective: (1) St. Joseph Bay is a low energy environment, and current movement is negligible in the southern portion of the Bay (Stewart and Gorsline 1962), where our study site was located. This is supported by the low average current velocities we measured (around 2.8 cm sec⁻¹), indicating that large scale advection of dissolved nutrients is unlikely; (2) placing the nutrient delivery tubes within the seagrass canopy ensured that nutrient release occurred in an area of very low flow (Fonseca et al. 1982; Ackerman and Okubo 1993), and immediately adjacent to and accessible by seagrass algal epiphytes; (3) we measurably increased water-column nutrient concentrations; (4) there was an increase in the proportion of filamentous green epiphytes in the nutrient treatments (Fig. 6), indicating microalgal responses to enhanced nutrient loading; and (5) an increase of nearly 25% in N concentrations was recorded in *Thalassia* leaves in +N treatments (Lores, USEPA Gulf Breeze Laboratory unpubl. data), indicating that increased concentration of N was achieved and available in our +N treatments. And, subsequent to our ex-

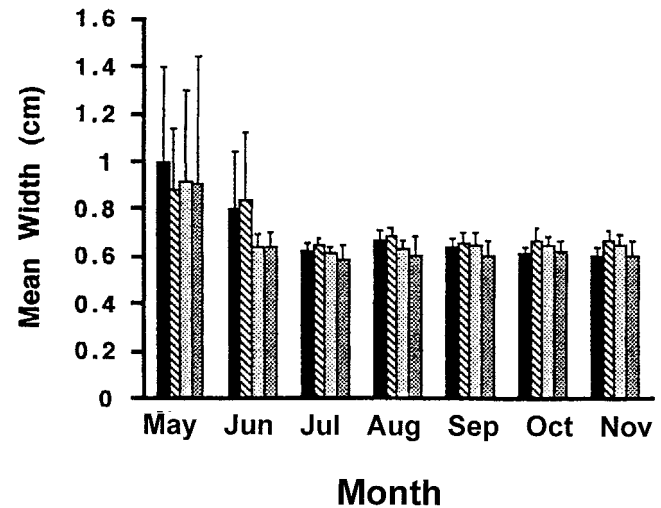
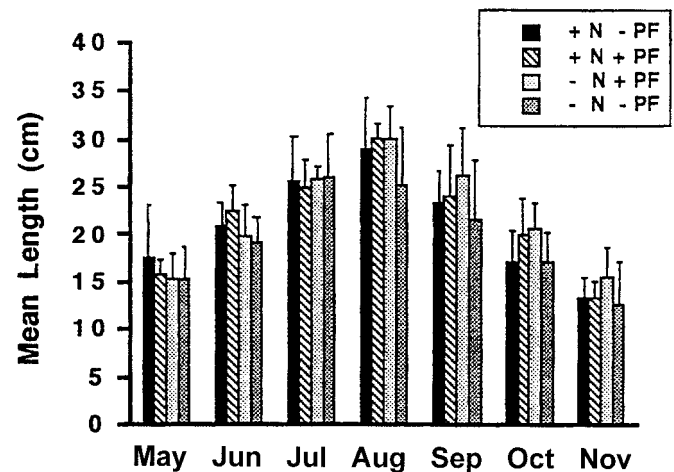
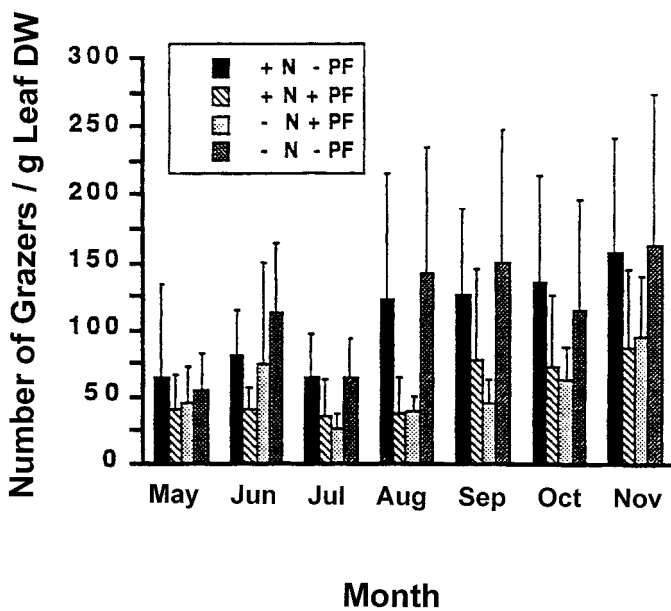


Fig. 7. Ratio of grazer number to leaf dry weight (g) (\pm SD) by month and treatment during 1993. Treatments are represented by: -N = no nutrients; +N = nutrient additions; -PF = no pinfish additions; and +PF = pinfish additions. May samples were taken before the experiments were begun.

periments, Thomas et al. (unpubl. data) have carried out in situ flume studies at the sampling site that have shown very high uptake of water-column nutrients by the seagrass-epiphyte complex over very short (5–6 min) time periods.

An important characteristic of our +N treatment was that despite high nutrient loading, nutrient concentrations were seldom elevated above $10 \mu\text{M}$ DIN and $0.3 \mu\text{M}$ PO_4 . Thus, some potential consequences of nutrient enrichment, such as enhanced growth of attached algae with high half-saturation coefficients for nutrient uptake or phytoplankton blooms, did not occur. However, our data clearly support the fact that despite significant nutrient loading the expected large increases in the biomass of epiphytes and associated seagrass decline did not occur.

In contrast to the +N treatments, the +PF (elevated pinfish density) treatments displayed numerous significant effects. Significant reductions in mesograzzer densities were observed in +PF (Fig. 6), yet there was no evidence of the expected epiphyte proliferation, even in the +N enclosures (Fig. 5). Instead, increased pinfish numbers led to reductions in the biomass of epiphytes. We believe that two factors account for this unanticipated result. First, pinfish consume increasing amounts of epiphytes as they grow (Livingston 1982; Stoner and Livingston 1984; Luczkovich and Stellwag 1993), and they were likely to have been consuming substantial amounts of epiphytes. Second, mesograzzer density, although significantly reduced in pinfish treatments, was still very high (e.g., $\sim 3 \times 10^3$ individuals m^{-2} in July, and $2.7 \times 10^3 \text{ m}^{-2}$ in August, as obtained by multiplying numbers of mesograzers per g DW [Fig. 6] by the mean seagrass DW in pinfish treatments [Fig. 8]). These numbers are above the highest density recorded ($2.1 \times 10^3 \text{ m}^{-2}$) by Nelson (1980) in a survey of amphipod densities in North American sea-

Fig. 8. Mean leaf length and width (cm) (\pm SD) by month and treatment during 1993. Treatments are represented by: -N = no nutrients; +N = nutrient additions; -PF = no pinfish additions; and +PF = pinfish additions. May samples were taken before the experiments were begun.

grass meadows from Nova Scotia to Florida, and are about 75% of the mean density of macrobenthic species recorded from densely vegetated turtlegrass meadows in Apalachee Bay, Florida by Stoner (1982). They are also above the range of mesograzzer densities ($1\text{--}2 \times 10^3 \text{ m}^{-2}$) found by Howard (1982) and Howard and Short (1986) to produce significant epiphyte reductions in mesocosm experiments and substantially greater than the isopod densities ($\sim 100 \text{ m}^{-2}$) reported by Williams and Ruckelshaus (1993). Neckles et al. (1993) observed significant epiphyte reductions at amphipod densities of $\sim 4,800\text{--}11,400 \text{ m}^{-2}$. Based on the weight of the above evidence, it appears that the relatively high mesograzzer numbers still remaining, combined with the high pinfish densities, prevented the proliferation of epiphytes in our elevated pinfish treatments, despite the high loading rates in our +N treatments.

We can also ask why our elevated pinfish densities did not drive mesograzzer densities below the relatively high

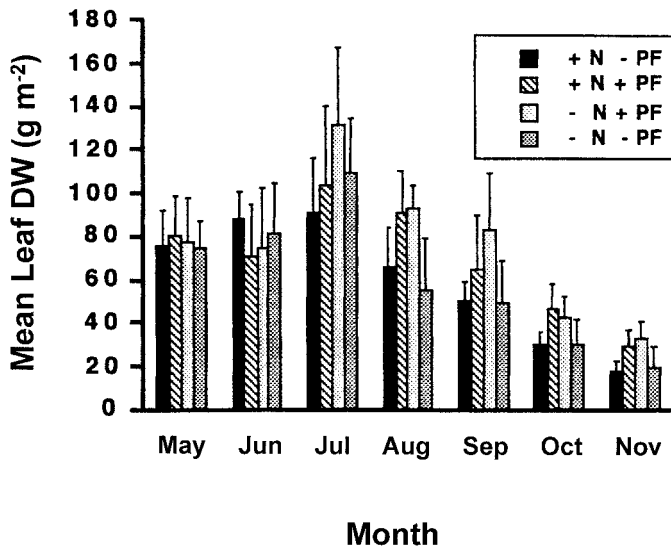


Fig. 9. Mean leaf dry weight (g m^{-2}) ($\pm\text{SD}$) by month and treatment during 1993. Treatments are represented by: -N = no nutrients; +N = nutrient additions; -PF = no pinfish additions; and +PF = pinfish additions. May samples were taken before the experiments were begun.

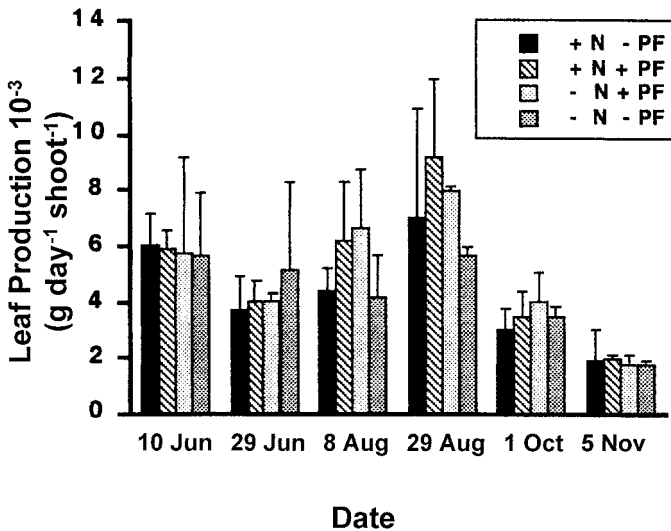


Fig. 10. Mean shoot density (number m^{-2}) ($\pm\text{SD}$) by month and treatment during 1993. Treatments are represented by: -N = no nutrients; +N = nutrient additions; -PF = no pinfish additions; and +PF = pinfish additions.

numbers of 2,500+ individuals m^{-2} . We think this is explained by the high standing crop of turtlegrass in our treatments. Stoner (1982) found that 177.6 g dry wt m^{-2} of turtlegrass reduced pinfish foraging success on seagrass-associated amphipods to about 20% of that on bare sand substrate, while biomasses of 88 and 22 g dry wt m^{-2} reduced foraging success to around 40 and 60%, respectively, of that on unvegetated substrate. Turtlegrass standing crops in our +PF treatments ranged from 30 g (in November) to 130 g dry wt m^{-2} (in July), but from May to July were never below 60 g dry wt m^{-2} . Therefore, even though pinfish densities

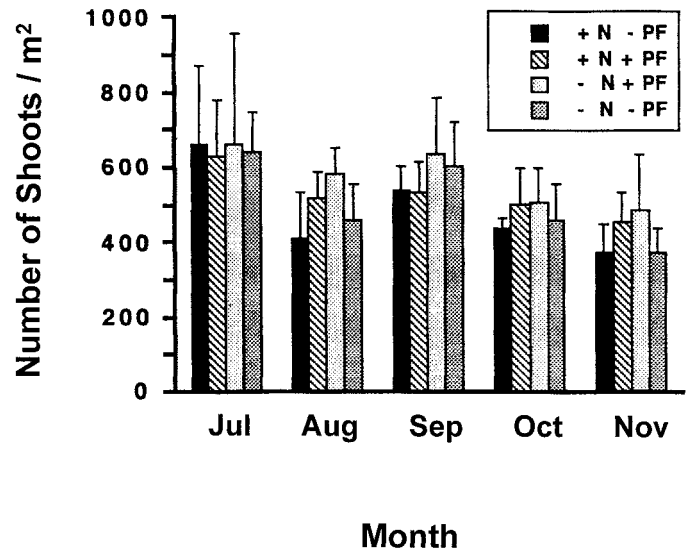


Fig. 11. Mean leaf production $10^3 \text{ g d}^{-1} \text{ shoot}^{-1}$ ($\pm\text{SD}$) by date and treatment during 1993. Treatments are represented by: -N = no nutrients; +N = nutrient additions; -PF = no pinfish additions; and +PF = pinfish additions.

were substantially elevated in our treatments, the high biomass of seagrass still should have provided sufficient protection for prey to allow the relatively high densities of mesograzers to persist.

Reduced epiphyte biomass produced positive effects on seagrass biomass, and to a lesser extent on shoot density and shoot-specific productivity. This is similar to the results of both Neckles et al. (1993) and Williams and Ruckelshaus (1993). The simple explanation for this is that seagrass leaves receive more light and grow more rapidly when less heavily fouled by epiphytes. Therefore, whenever epiphyte grazing is sufficient to control epiphyte populations, seagrasses appear to benefit. This is clear evidence of important "top-down" effects in these seagrass ecosystems, though we did not observe a simple alternation of high and low biomass between successive trophic levels as seen in simple trophic cascades. Instead, pinfish, while substantially reducing mesograzers, also fed on algal epiphytes, which partially prevented the release of epiphytes from mesograzers, despite high rates of nutrient enrichment. In addition, the high seagrass density also allowed high numbers of mesograzers to persist even in the face of strong predation pressure by pinfish. Effectively, the omnivorous pinfish, together with the remaining numbers of mesograzers, prevented a simple trophic cascade from occurring. This is, at least in part, what was predicted by Strong (1992) and Polis and Strong (1996), who have argued that trophic cascades are uncommon except in simple food chains because of the reticulate nature of most food webs.

If this interpretation of our results is correct, it has implications for better understanding the effects of nutrient enrichment on seagrass habitats. In sparsely vegetated meadows (e.g., those at depths where light may be limiting to seagrass biomass accumulation, or in unfavorable salinities or temperature regimes) subjected to eutrophication, the low

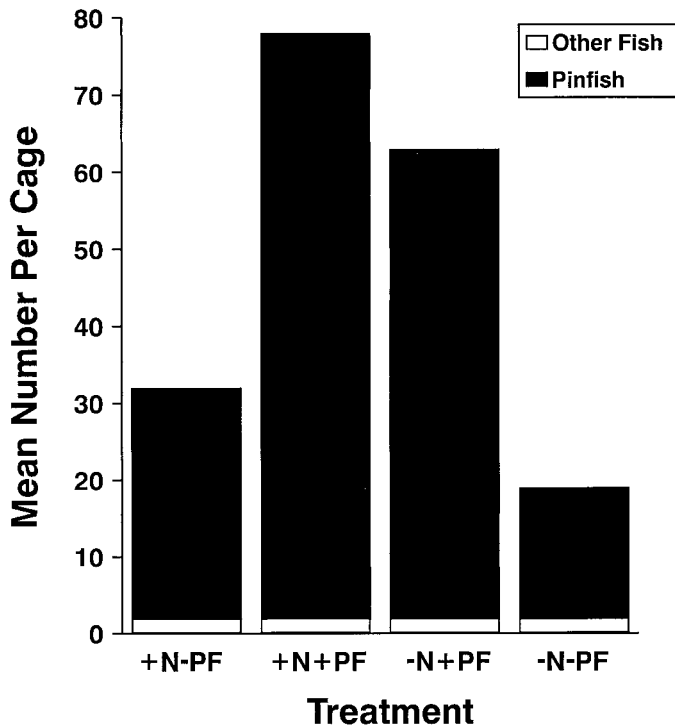


Fig. 12. Mean number of pinfish and other fish species by treatment seined from cages in November 1993. Treatments are represented by: -N = no nutrients; +N = nutrient additions; -PF = no pinfish additions; and +PF = pinfish additions.

seagrass biomass is unlikely to afford adequate protection for mesograzers to remain high enough to control the growth of epiphytes as they respond to eutrophication. Epiphyte overgrowth of seagrasses should therefore proceed rapidly in eutrophic coastal areas which have also lost large, piscivorous predators to overfishing, and whose populations of mesograzers-consuming small fishes are consequently at very high levels. One could also expect the susceptibility of seagrass meadows to eutrophication to vary annually as either the density of seagrasses fluctuates in response to changing environmental factors (e.g., varying light levels due to increased runoff or storm activity, or varying temperatures or salinities), or as small fish populations vary in response to changes in year-class strength. Both of these effects would result in changes in the number of mesograzers present. In addition, environmental factors that reduce seagrass growth rates (e.g., increased turbidity, stressful temperature, or salinity) could also increase the meadow's susceptibility to eutrophication by allowing epiphytes more time to accumulate on slowly growing seagrass leaves.

This scenario elaborates on the conditions proposed by Williams and Ruckelshaus (1993) that can lead to epiphyte proliferation and subsequent seagrass decline: unfavorable temperatures for seagrass growth, high availability of DIN, and few grazers. We consider the role of seagrass biomass to be critical in determining the size of mesograzers populations, especially where the larger predators of small fishes are not abundant. And we believe that low seagrass biomass could often be responsible for keeping mesograzers abun-

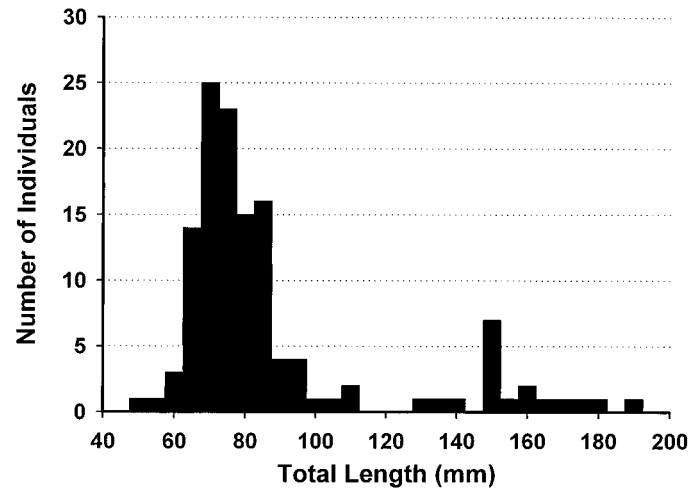


Fig. 13. Total length data (mm) of pinfish seined from all cages in November 1993.

dances too low to prevent the overgrowth of seagrass leaves by epiphytes when eutrophication accelerates.

Overall, we believe that our data: (1) support the results of previous studies that manipulated both nutrient supply and grazing activity, in showing that grazers frequently can control the abundance of epiphytes; and (2) indicate that it is unlikely we can gain a full understanding of the consequences of nutrient enrichment for seagrass ecosystems without

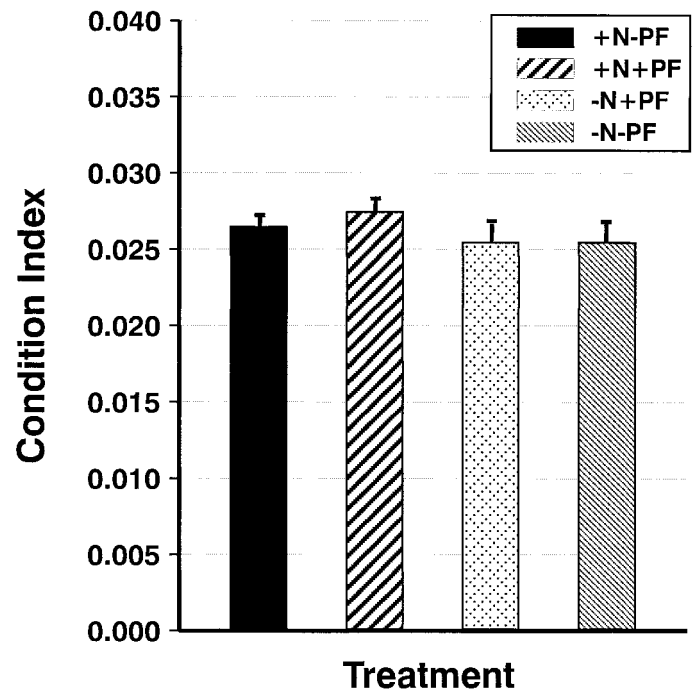


Fig. 14. Fulton condition index (\pm SD) by treatment for a subsample of pinfish (≤ 20) seined from cages in November 1993. The condition index was determined using the equation: Condition index = $\text{weight} \times \text{length}^{-3}$. Treatments are represented by: -N = no nutrients; +N = nutrient additions; -PF = no pinfish additions; and +PF = pinfish additions.

understanding what controls the population fluctuations of mesograzers. The potential importance of grazers in determining the abundance of seagrass epiphytes was pointed out some time ago (e.g., Orth and van Montfrans 1984; van Montfrans et al. 1984), although recent investigations have focused more on the effects of nutrient supply in controlling epiphyte abundance, with a smaller role described for the effects of grazing (e.g., Duarte 1995).

Our results also indicate important “top-down” effects in determining the structure of seagrass communities. Although we did not observe simple trophic cascades, presumably because pinfish feed at several different trophic levels, it is quite clear that the abundance of small fishes can have important consequences for small plants and animals as well as seagrasses themselves. Finally, the importance of seagrass meadows in controlling secondary productivities in coastal systems strongly suggests that additional tests of the hypotheses laid out above are necessary. It appears that the role of mesograzers in controlling the effects of eutrophication in seagrass meadows has been underestimated, and in an effort to preserve the health of seagrass ecosystems, it should be well worth the effort to understand mesograzers effects more completely.

References

- ACKERMAN, J. D., AND A. OKUBO. 1993. Reduced mixing in a marine macrophyte canopy. *Func. Ecol.* **7**: 305–309.
- ALPKEM MANUAL. 1988. Alpkem Corporation, Clakamas, Oregon.
- BORUM, J. 1987. Dynamics of epiphyton on eelgrass (*Zostera marina*) leaves: Relative roles of algal growth, herbivory and substratum turnover. *Limnol. Oceanogr.* **32**: 986–992.
- BRAWLEY, S. H. 1992. Mesoherbivores, p. 235–263. *In* D. M. John, S. J. Hakins, and J. H. Price [eds.], *Plant-animals interactions in marine benthos*. Clarendon Press.
- BRONMARK, C. 1985. Interactions between macrophytes, epiphytes and herbivores: An experimental approach. *Oikos* **45**: 26–30.
- , AND S. E. B. WEISNER. 1996. Decoupling of cascading trophic interactions in a freshwater benthic food chain. *Oecologia* **108**: 534–541.
- BROOKS, J. L., AND S. I. DODSON. 1965. Predation, body size and composition of plankton. *Science* **150**: 28–35.
- CAINE, E. A. 1980. Ecology of two littoral species of caprellid amphipods (Crustacea) from Washington, USA. *Mar. Biol.* **56**: 327–335.
- CAMBRIDGE, M. L., AND A. J. MCCOMB. 1984. The loss of seagrasses in Cockburn Sound, Western Australia. I. The time course and magnitude of seagrass decline in relation to industrial development. *Aquatic Bot.* **20**: 229–243.
- CARPENTER, S. R., AND D. M. LODGE. 1986. Effects of submersed macrophytes on ecosystem processes. *Aquat. Bot.* **26**: 341–370.
- , J. F. KITCHELL, AND J. R. HODGSON. 1985. Cascading trophic interactions and lake productivity. *Bioscience* **35**: 634–639.
- , AND OTHERS. 1987. Regulation of lake primary productivity by food-web structure. *Ecol.* **68**: 1863–1867.
- CARR, W. E. S., AND C. A. ADAMS. 1973. Food habits of juvenile marine fishes occupying seagrass beds in the estuarine zone near Crystal River, Florida. *Trans. Amer. Fish Soc.* **102**: 511–540.
- COEN, L. C., K. L. HECK, JR., AND L. G. ABLE. 1981. Experiments on competition and predation among shrimp of seagrass meadows. *Ecol.* **62**: 1484–1493.
- DAYTON, P. K. 1971. Competition, disturbance and community organization: The provision and subsequent utilization of space in a rocky intertidal community. *Ecol. Mono.* **41**: 351–389.
- DEN HARTOG, C. 1994. Suffocation of a littoral *Zostera* bed by *Enteromorpha radiata*. *Aquat. Bot.* **47**: 21–28.
- DENNISON, W. C. 1990. Leaf production, p. 77–85. *In* R. C. Phillips, and C. P. McRoy [eds.], *Seagrass research methods*. UNESCO.
- DUARTE, C. M. 1995. Submerged aquatic vegetation in relation to different nutrient regimes. *Ophelia* **41**: 37–112.
- DUGGINS, D. O. 1980. Kelp beds and sea otters: An experimental approach. *Ecology* **61**: 447–453.
- ESTES, J. A., AND J. F. PALMISANO. 1974. Sea otters: Their role in structuring nearshore communities. *Science* **185**: 1058–1060.
- FONSECA, M. S., J. S. FISHER, J. C. ZIEMAN, AND G. W. THAYER. 1982. Influence of the seagrass, *Zostera marina* L., on current flow. *Estuar. Coast. Shelf Sci.* **15**: 351–364.
- GIESEN, W. B. J. T., M. M. VAN KATWIJK, AND C. DEN HARTOG. 1990. Eelgrass condition and turbidity in the Dutch Wadden Sea. *Aquatic Bot.* **37**: 71–85.
- HANSEN, D. J. 1969. Food, growth, migration, reproduction and abundance of pinfish *Lagodon rhomboides*, and croaker *Micropogon undulatus* near Pensacola, Florida 1963–1965. *Fish. Bull.* **68**: 135–146.
- HARLIN, M. M., AND B. THORNE-MILLER. 1982. Seagrass-sediment dynamics of a flood-tidal delta in Rhode Island. *Aquat. Bot.* **14**: 127–138.
- HECK, K. L., JR., AND L. B. CROWDER. 1991. Habitat structure and predator-prey interaction in vegetated aquatic systems, p. 281–299. *In* S. S. Bell, E. D. McCoy, and H. R. Mushinsky [eds.], *Habitat complexity: The physical arrangement of objects in space*. Chapman and Hall.
- , K. W. ABLE, C. T. ROMAN, AND M. P. FAHAY. 1995. Composition, abundance, biomass and production of macrofauna in a New England estuary: Comparisons among eelgrass meadows and other nursery habitats. *Estuaries* **18**: 379–389.
- HELLIER, J. R., JR. 1962. Fish production and biomass studies in relation to photosynthesis in the Laguna Madre of Texas. *Contr. Mar. Sci.* **8**: 1–22.
- HOOTSMANS, M. J. M., AND J. E. VERMAAT. 1985. The effect of periphyton-grazing by three epifaunal species on the growth of *Zostera marina* L. under experimental conditions. *Aquat. Bot.* **22**: 83–88.
- HOWARD, R. K. 1982. Impact of feeding activities of epibenthic amphipods on surface-fouling of eelgrass leaves. *Aquat. Bot.* **14**: 91–87.
- , AND F. T. SHORT. 1986. Seagrass growth and survivorship under the influence of epiphyte grazers. *Aq. Bot.* **24**: 287–302.
- HUGHES, T. P. 1994. Catastrophes, phase shifts, and large scale degradation of a Caribbean coral reef. *Science* **265**: 1547–1551.
- HUH, S-H. 1984. Seasonal variations in populations of small fishes concentrated in shoalgrass and turtlegrass meadows. *J. Oceanological Soc. Korea* **19**: 44–55.
- , AND C. L. KITTING. 1985. Trophic relationships among concentrated populations of small fishes in seagrass meadows. *J. Exp. Mar. Biol. Ecol.* **92**: 29–43.
- IVERSON, R. L., AND H. F. BITTAKER. 1986. Seagrass distribution and abundance in the eastern Gulf of Mexico water. *Est. Coast. Shelf Sci.* **22**: 577–602.
- JERNAKOFF, P., A. BREARLEY, AND J. NIELSEN. 1996. Factors affecting grazer-epiphyte interactions in temperate seagrass meadows. *Oceanogr. Mar. Biol. (Ann. Rev.)* **34**: 109–162.
- KAISER, S. C. 1989. The growth responses of eelgrass, *Zostera marina*, to epiphyte fouling and herbivore grazing in a New England estuary. M. S. Thesis, Rutgers Univ., New Brunswick.

- KJELSON, M. A. 1977. Estimating the size of juvenile fish populations in southeastern coastal-plain estuaries, p. 71–90. *In* W. Van Winkle [ed.], *Proceedings of the Conference on Assessing the Effects of Power-Plant-Induced Mortality on Fish Populations*. Pergamon Press.
- KLUMPP, D. W., J. S. SALITA-ESPINOSA, AND M. D. FORTES. 1992. The role of epiphytic periphyton and macroinvertebrate grazers in the trophic flux of a tropical seagrass community. *Aq. Bot.* **43**: 327–349.
- LAGLER, K. R., J. E. BARDACH, AND R. R. MILLER. 1962. *Ichthyology*. John Wiley and Sons.
- LEBER, K. M. 1985. The influence of predatory decapods, refuge, and microhabitat selection on seagrass communities. *Ecol.* **66**: 1951–1964.
- LIN, H. J., S. W. NIXON, D. I. TAYLOR, S. L. GRANGER, AND B. A. BUCKLEY. 1996. Responses of epiphytes on eelgrass, *Zostera marina* L., to separate and combined nitrogen and phosphorus enrichment. *J. Exp. Mar. Ecol.* **52**: 243–248.
- LIVINGSTON, R. J. 1982. Trophic organization of fishes in a coastal seagrass system. *Mar. Ecol. Prog. Ser.* **7**: 1–12.
- . 1984. Trophic responses of fishes to habitat variability in coastal seagrass systems. *Ecol.* **65**: 1258–1275.
- LODGE, D. M., K. K. KERSHNER, J. E. ALOI, AND A. P. COVICH. 1994. Effects of an omnivorous crayfish (*Orconectes rusticus*) on a freshwater littoral food web. *Ecol.* **75**: 1265–1281.
- LUCZKOVICH, J. J., AND E. J. STELLWAG. 1993. Isolation of cellulolytic microbes from the intestinal tract of the pinfish, *Lagodon rhomboides*: Size-related changes in diet and microbial abundance. *Mar. Biol.* **116**: 381–388.
- MAIN, K. L. 1985. The influence of prey identity and size selection of prey by two marine fishes. *J. Exp. Mar. Biol. Ecol.* **98**: 145–152.
- . 1987. Predator avoidance in seagrass meadows: Prey behavior microhabitat selection and cryptic coloration. *Ecol.* **68**: 170–180.
- MARTIN, T. H., L. B. CROWDER, C. DUMAS, AND J. M. BURKHOLDER. 1992. Indirect effects of fish on macrophytes in Bays Mountain Lake: Evidence for a littoral trophic cascade. *Oecologia* **89**: 476–481.
- MCGLATHERY, K. J. 1995. Nutrient and grazing influences on a subtropical seagrass community. *Mar. Ecol. Prog. Ser.* **122**: 239–252.
- MITTELBACH, G. G. 1984. Predation and resource partitioning in two sunfishes (Centrarchidae). *Ecol.* **65**: 499–513.
- NATIONAL ACADEMY OF SCIENCES. 1995. *Understanding marine biodiversity*. National Academy Press.
- NATIONAL RESEARCH COUNCIL. 1994. *Priorities for coastal ecosystem science*. National Academy Press.
- NECKLES, H. A., R. L. WETZEL, AND R. J. ORTH. 1993. Relative effects of nutrient enrichment and grazing on epiphyte-macrophyte (*Zostera marina*) dynamics. *Oecologia* **93**: 285–295.
- NELSON, W. G. 1980. A comparative study of amphipods in seagrass from Florida to Nova Scotia. *Bull. Mar. Sci.* **30**: 80–89.
- NEUNDORFER, J. V., AND W. M. KEMP. 1993. Nitrogen versus phosphorus enrichment of brackish waters: Responses of the submersed plant *Potamogeton perfoliatus* and its associated algal community. *Mar. Ecol. Prog. Ser.* **94**: 71–82.
- NIXON, S. W. 1995. Coastal marine eutrophication: A definition, social causes and future concerns. *Ophelia* **41**: 199–219.
- OFFICER, C. B. AND OTHERS. 1984. Chesapeake Bay anoxia: Origin, development, and significance. *Science* **223**: 22–27.
- ORTH, R. J., AND K. A. MOORE. 1983. Chesapeake Bay: An unprecedented decline in submerged aquatic vegetation. *Science* **222**: 51–53.
- , AND J. VAN MONTFRANS. 1984. Faunal communities in seagrass beds: A review of the influence of plant structure and prey characteristics on predator-prey relationships. *Estuaries* **7**: 339–350.
- , AND ———. 1987. Utilization of seagrass meadow and tidal marsh creek by blue crabs *Callinectes sapidus*. I. Seasonal and annual variations in abundance with emphasis on post-settlement juveniles. *Mar. Ecol. Prog. Ser.* **41**: 283–394.
- PAINE, R. T. 1966. Food web complexity and species diversity. *Amer. Nat.* **100**: 65–75.
- PARFIT, M. 1995. Diminishing returns. *Nat. Geogr.* **188**: 2–36.
- PHILLIPART, C. J. M. 1995. Effect of periphyton grazing by *Hydrobia ulvae* on the growth of *Zostera noltii* on a tidal flat in the Dutch Wadden Sea. *Mar. Biol.* **122**: 431–437.
- POLIS, G. A., AND D. S. STRONG. 1996. Food web complexity and community dynamics. *Am. Nat.* **147**: 813–846.
- POWER, M. E. 1992. Top down and bottom up forces: Do plants have primacy? *Ecol.* **73**: 733–746.
- ROBERTSON, A. I., AND K. H. MANN. 1982. Population dynamics and life history adaptations of *Littorina neglecta* (Bean) in an eelgrass meadow (*Zostera marina* L.) in Nova Scotia. *J. Exp. Mar. Biol. Ecol.* **63**: 151–171.
- RUDLOE, A. 1985. Variation in the expression of lunar and tidal rhythms in the horseshoe crab, *Limulus polyphemus*. *Bull. Mar. Sci.* **36**: 867–893.
- SAFINA, C. 1995. The world's imperiled fish. *Sci. Amer. (Nov.)*: 46–53.
- SHAPIRO, J., AND D. I. WRIGHT. 1984. Lake restoration by manipulation: Round Lake, Minnesota, the first two years. *Freshwater Biol.* **14**: 371–383.
- SHORT, F. T., D. M. BURDICK, AND J. E. KALDY III. 1995. Mesocosm experiments quantify the effects of eutrophication on eelgrass, *Zostera marina*. *Limnol. Oceanogr.* **40**: 740–749.
- SOGARD, S. M., G. V. N. POWELL, AND J. G. HOLMQUIST. 1987. Epibenthic fish communities on Florida Bay banks: Relations with physical parameters and seagrass cover. *Mar. Ecol. Prog. Ser.* **40**: 25–39.
- STEWART, R. A., AND D. S. GORSLINE. 1962. Recent sedimentary history of St. Joseph Bay, Florida. *Sedimentology* **1**: 256–286.
- STONER, A. W. 1982. The influence of benthic macrophytes on the foraging behavior of pinfish, *Lagodon rhomboides*. *J. Exp. Mar. Biol. Ecol.* **58**: 271–284.
- , AND R. J. LIVINGSTON. 1984. Ontogenetic patterns in diet and feeding morphology in sympatric sparid fishes from seagrass meadows. *Copeia* **1**: 174–187.
- STRICKLAND, J. D. H., AND T. R. PARSONS. 1972. *A practical handbook for seawater analysis*. Fish. Res. Bd. Can. Bull. 167. 310 p.
- STRONG, D. W. 1992. Are trophic cascades all wet? Differentiation and donor-control in speciose ecosystems. *Eco.* **73**: 747–754.
- TOMASKO, D. A., C. J. DAWES, AND M. O. HALL. 1996. The effects of anthropogenic nutrient enrichment on turtlegrass (*Thalassia testudinum*) in Sarasota Bay, Florida. *Estuaries* **19**: 448–456.
- , AND B. E. LAPOINTE. 1991. Productivity and biomass of *Thalassia testudinum* as related to water column nutrient availability: Field observations and experimental studies. *Mar. Ecol. Prog. Ser.* **75**: 9–17.
- TWILLEY, R. R., W. M. KEMP, K. W. STAVELAND, J. C. STEVENSON, AND W. R. BOYNTON. 1985. Nutrient enrichment of estuarine submersed vascular plant communities. I. Algal growth and effects on production of plants and associated communities. *Mar. Ecol. Prog. Ser.* **23**: 179–191.
- VALENTINE, J. F., AND K. L. HECK, JR. 1991. The role of sea urchin grazing in regulating subtropical seagrass meadows: Evidence from field manipulations in the northern Gulf of Mexico. *J. Exp. Mar. Biol. Ecol.* **154**: 215–230.
- , AND ———. 1993. Mussels in seagrass meadows: Their influence on macroinvertebrate abundance and secondary pro-

- duction in the northern Gulf of Mexico. *Mar Ecol. Progr. Ser.* **96**: 63–74.
- VAN MONTFRANS, J., R. J. ORTH, AND S. A. VAY. 1982. Preliminary studies of grazing by *Bittium varium* on eelgrass periphyton. *Aquat. Bot.* **14**: 75–89.
- , R. L. WETZEL, AND R. J. ORTH. 1984. Epiphyte-grazer relationships in seagrass meadows: Consequences for seagrass growth and production. *Estuaries* **7**: 298–309.
- WERNER, E. E., AND J. F. GILLIAM. 1984. The ontogenetic niche and species interactions in size-structured populations. *Ann. Rev. Ecol. Syst.* **15**: 393–425.
- WILLIAMS, A. H., L. D. COEN, AND M. S. STOELTING. 1990. Seasonal abundance, distribution, and habitat selection of juvenile *Callinectes sapidus* (Rathbun) in the northern Gulf of Mexico. *J. Exp. Mar. Biol. Ecol.* **137**: 165–183.
- WILLIAMS, S. L., AND M. H. RUCKELSHAUS. 1993. Effects of nitrogen availability and herbivory on eelgrass (*Zostera marina*) and epiphytes. *Ecol.* **74**: 904–918.
- ZARET, T. M. 1980. Predation in freshwater communities. Yale Univ. Press.
- ZIMMERMAN, R., R. GIBSON, AND J. HARRINGTON. 1979. Herbivory and detritivory among gammaridean amphipods from a Florida seagrass community. *Mar. Biol.* **54**: 41–47.

Received: 30 August 1999

Accepted: 6 January 2000

Amended: 6 March 2000