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Responses of Coastal Lagoon Plant Communities to Levels of Nutrient Enrichment: A Mesocosm Study

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ABSTRACT: An experiment was conducted to quantify the effects of different levels of nutrient enrichment on the plant communities of temperate coastal lagoons, specifically the lagoons of the northeast U.S. Ten mesocosms, each containing coastal water, lagoon sediments, and plants and animals found in natural lagoons, were subjected to five levels of enrichment. Two mesocosms served as controls, and received no experimental nutrient additions. The remaining 8 mesocosms were enriched in duplicate with ammonium plus phosphate at 1.0 and 0.11 mmol N or P m^{-2} d^{-1}, 2.0 and 0.19 mmol N or P m^{-2} d^{-1}, 4.0 and 0.35 mmol N or P m^{-2} d^{-1}, and 8.0 and 0.67 N or P mmol m^{-2} d^{-1}. At all levels of enrichment, and through much of the experiment, water column concentrations of dissolved inorganic nitrogen (DIN) were drawn down to background levels. Despite the efficient drawdown of added DIN even at the highest loadings, differences in plant biomass among the 5 treatments were difficult to detect. Enrichment at the highest loadings increased standing stocks of phytoplankton for one month mid-experiment. No significant effect of loading could be detected for dry biomass of eelgrass (*Zostera marina*), epiphytic material, drift macroalgae, or for all plant components combined. The experiment has demonstrated that the enrichment responses of coastal lagoons can be diverse, especially at intermediate loadings.

Introduction

Coastal lagoons are one of the types of coastal aquatic systems that have been affected by nutrient enrichment worldwide. Much less is known of the effects of nutrient enrichment of lagoons than of bays and estuaries. In temperate regions the lagoons affected by enrichment include the lagoons of the northeast U.S. (Ryther 1954; Nixon et al. 1982; Valiela et al. 1992), Europe (Sfriso et al. 1992), and Western Australia (McComb and Humphries 1992). In the northeast U.S., the affected lagoons include the barrier lagoons of southern Rhode Island (Lee and Olsen 1985), southern Long Island (Ryther and Dunstan 1971), and southern Massachusetts (Valiela et al. 1997).

The structural properties of coastal lagoons suggest their responses to enrichment might be more complex than the responses of bays and estuaries. Lagoons tend to be smaller, shallower, and possess narrower connections with the adjoining ocean (Kjerfve and McGill 1989), and also exhibit closer coupling of the sediments and water column than bays or estuaries (Nixon 1982). In addition to the phytoplankton that dominate primary production in bays and estuaries (Nixon et al. 1984; Oviatt et al. 1986), lagoons also support complex assemblages of seagrasses and drift and epiphytic macroalgae (Taylor 1983; Thorne-Miller et al. 1983).

Nutrient loading estimates indicate the levels of enrichment of lagoons can be as great as for bays and estuaries. Loadings of dissolved inorganic nitrogen (DIN) as high as 7 and 12 mmol m^{-2} d^{-1} have been reported for highly enriched lagoons such as Moriches Bay (Ryther 1989) and Childs River lagoon (D'Avanzo et al. 1996). By comparison, loadings of DIN to many of the better studied bays and estuaries lie between 2 and 6 mmol m^{-2} d^{-1} (estimates for Chesapeake Bay, Delaware Bay, Narragansett Bay and the Potomac Estuary, Nixon et al. 1996).

Increases in nutrient loadings have been shown to cause the plant communities of lagoons to change. The types of changes reported have been diverse, including the development of dense blooms of phytoplankton (as in Moriches Bay, Ryther and Dunstan 1971), declines in areal coverage or biomass of seagrass beds (Waquoit Bay, Short and Burdick 1996; Valiela et al. 1997), and the de-

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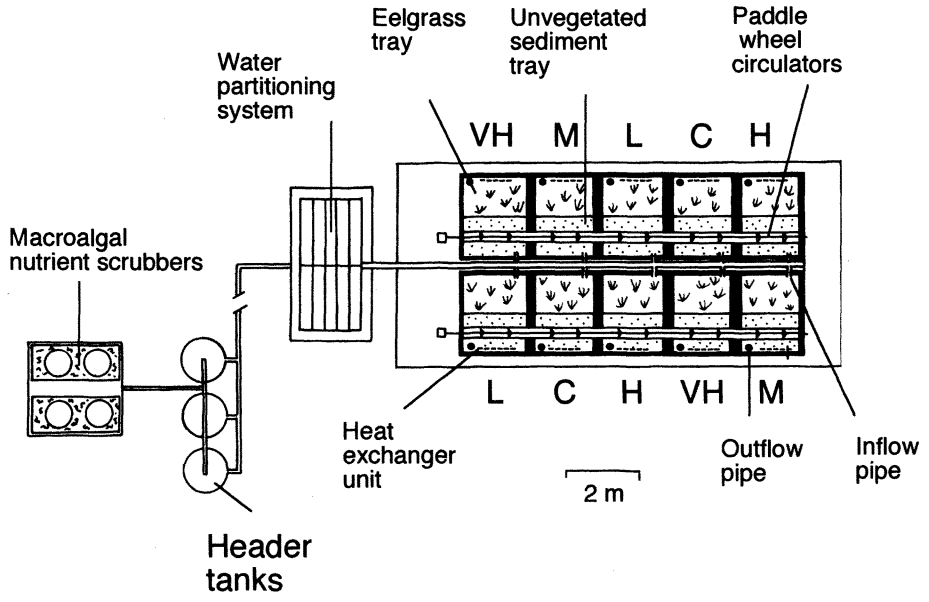

Fig. 1. Plan view of the Lagoon Mesocosm Facility, University of Rhode Island. The distribution of the five loading treatments among the 10 mesocosms are indicated. C = unenriched Controls, L = Low loadings, M = Medium loadings, H = High loadings, and VH = Very High loadings.

velopment of extensive mats of drift macroalgae (Lagoon of Venice, Sfriso et al. 1992; Waquoit Bay, Valiela et al. 1992; Peel-Harvey Estuary, McComb and Humphries 1992).

The plant communities of temperate lagoons have been shown to be sensitive to increased loadings of nitrogen (N), especially if accompanied by phosphorus (P) (Taylor et al. 1995a). In an experiment conducted using mesocosms designed as physical models of lagoons, enrichment with large doses of N and N plus P, caused blooms of phytoplankton, lowered biomasses of epiphytic material and drift macroalgae, and declines in seagrass beds. No change in plant biomass was observed with enrichment with P alone.

While it is known that lagoons are sensitive to enrichment, little is known of how their plant communities respond to different levels of enrichment. Valiela et al. (1997) demonstrated relationships between N loadings and average biomass of macroalgae and eelgrass (*Zostera marina*) for 5 lagoons in Massachusetts enriched to varying degrees mainly with N alone. Experiments involving different levels of enrichment have been conducted using shallow enclosures containing some of the plants found in lagoons (Howard-Williams 1981; Twilley et al. 1985; Burkholder et al. 1992; Neckles et al. 1993), but in all cases the physical properties of the enclosures were not referenced to the physical properties of natural lagoons, making extrapolation to the natural systems tenuous.

This paper reports the results of an experiment designed to better quantify the effects of different nutrient loadings on the plant communities of temperate coastal lagoons. The experiment was conducted using a series of mesocosms designed as physical models of the lagoons of southern Rhode Island (Lee and Olsen 1985). The mesocosm approach was adopted to constrain nutrient loadings, to allow replication within treatments, and to capture at least some of the complex interactions that occur in natural lagoons.

Materials and Methods

Experimental Design

The mesocosms used for the experiment were located at the Lagoon Mesocosm Facility, University of Rhode Island (Fig. 1), less than 15 km from the lagoons of southern Rhode Island. Ten mesocosms were subjected in duplicate to 5 levels of enrichment, termed Control (C), Low (L), Medium (M), High (H), and Very High (VH) treatments (Table 1). The treatments were apportioned semi-randomly among the 10 mesocosms, ensuring that the 2 replicates of each treatment were not located on the same side or end of the facility. The loadings to the 5 treatments spanned the range of loadings reported for natural lagoons (Table 2).

Two mesocosms served as Controls, and received no experimental nutrient additions. These mesocosms, and each of the enriched mesocosms, received background nutrient loadings from the atmosphere and through flowing water, of 0.13

TABLE 1. Loadings of dissolved inorganic nitrogen (DIN) and dissolved inorganic phosphorus (DIP) (mmol m^{-2} d^{-1}) to the five treatments.

Treatment	DIN			DIP			DIN:DIP
	Background[a]	Experimental Additions	Sum	Background[a]	Experimental Additions	Sum	Sum
Control	0.26	—	0.26	0.02	—	0.02	13:1
Low	0.26	1.0	1.26	0.02	0.11	0.13	10:1
Medium	0.26	2.0	2.26	0.02	0.19	0.21	11:1
High	0.26	4.0	4.26	0.02	0.35	0.37	11:1
Very High	0.26	8.0	8.26	0.02	0.67	0.69	12:1

[a] Background refers to inputs from throughflowing water plus atmospheric deposition. Throughflowing = 0.21 mmol N m^{-2} d^{-1} and 0.02 mmol P m^{-2} d^{-1}, and was calculated using average DIN or DIP concentrations in the incoming water after passage through macroalgal scrubbers (n = 7). Atmospheric inputs are wet deposition values of 0.01 mmol N m^{-2} d^{-1} and < 0.001 mmol P m^{-2} d^{-1}, calculated using daily precipitation volumes collected 8.5 km from study site by University of Rhode Island Agriculture Experimental Station. Average concentrations in precipitation assumed to equal concentrations measured at nearby MERL mesocosms; 37 μmol l^{-1} for nitrate plus nitrite, 15 μmol l^{-1} for ammonium and 0.1 μmol l^{-1} for phosphate (Nowicki and Oviatt 1990).

mmol m^{-2} d^{-1} for DIN and 0.03 mmol m^{-2} d^{-1} for dissolved inorganic phosphorus (DIP). These background loadings to the Controls were equivalent in magnitude to the loadings reported for lagoons such as Sage Lot Pond lagoon, Massachusetts (D'Avanzo et al. 1996), and Great South Bay lagoon, New York (Nixon et al. 1994).

The remaining 8 mesocosms received experimental additions of ammonium plus phosphate at four levels—and 0.08 mmol N and P m^{-2} d^{-1} to the L treatments, 2 and 0.16 mmol N and P m^{-2} d^{-1} to the M treatments, 4 and 0.32 mmol N and P m^{-2} d^{-1} to the H treatments, and 8 and 0.64 mmol N and P m^{-2} d^{-1} to the VH treatments. The DIN loadings to the VH treatments were similar to the loadings reported for Moriches Bay lagoon, Long Island, New York (Ryther 1989), and the Childs River and Quashnet River lagoons, Massachusetts (D'Avanzo et al. 1996).

Enrichment lasted 25 wk, from April 22 to October 30, 1992. The nutrients were added as analytical grade NH_4Cl and KH_2PO_4 in dissolved form, to the water column, once per day in late afternoon. Ammonium plus phosphate were selected for enrichment because they (in combination with urea) have been the nutrients involved in some of the most severe enrichment of lagoons (including Moriches Bay lagoon, Ryther 1989; and the Lagoon of Venice, Italy, Sfriso et al. 1992). The ammonium and phosphate were added at a molar N:P of 12:1, to approximate the proportions of N and P involved in the enrichment of these same systems (N:P = 8:1 for Moriches Bay, Ryther 1989; 12:1 for Lagoon of Venice, Puccia 1992).

TABLE 2. Dissolved inorganic nitrogen and phosphorus loadings (mmol m^{-2} d^{-1}) to various temperate coastal lagoons. n.r. = not reported.

	Nitrogen	Phosphorus	Molar N:P
Ninigret Pond, RI[1]	1.15	0.03	38
Point Judith Pond, RI[1]	0.96	n.r.	
Green Hill Pond, RI[1]	2.55	0.04	64
Potter Pond, RI[1]	1.70	n.r.	
Waquoit Bay, MA[2]			
Sage Lot Pond	0.27	n.r.	
Quashnet River	10.41	n.r.	
Childs River	12.32	n.r.	
Harvey Estuary, Australia[3]	1.50	0.13	12
Peel Inlet, Australia[3]	2.10	0.07	30
Moriches Bay, LI[4]	7.40	0.97	7.6
Buttermilk Bay, MA[5]	1.53	0.07	22
Great South Bay, NY[6]	0.19	n.r.	

[1] Lee and Olsen 1985, includes groundwater, precipitation, streams and storm runoff. The values for Ninigret and Green Hill also include offshore inputs.

[2] D'Avanzo et al. 1996, inputs include DIN and DIP inputs via groundwater and streams.

[3] McComb and Humphries 1992.

[4] Ryther 1989.

[5] Valiela and Costa 1988.

[6] Nixon et al. 1994.

The Lagoon Mesocosms

Each of the mesocosms had an area of 2.3 m × 1.8 m, with 1.1-m depth of water overlying 0.3-m sediments (Fig. 2). The water in each mesocosm

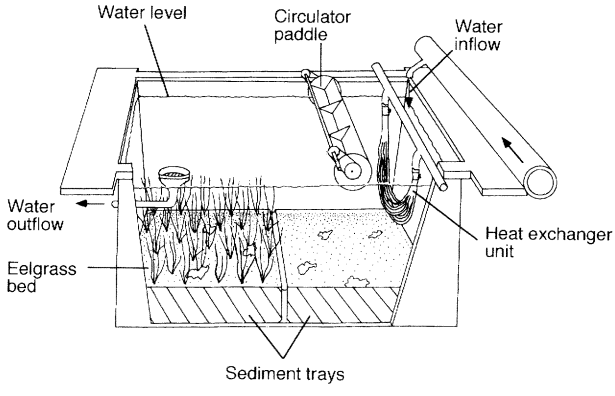

Fig. 2. Schematic side view into one of the experimental mesocosms.

TABLE 3. Quantities of larger plants and animals added to each mesocosm.

Component	Biomass/Numbers Added	Date Added
Eelgrass (*Zostera marina*)	250 shoots m^{-2} bed 100 g (dry) m^{-2} bed	April 16
Macroalgae		
Gracilaria tikvahiae	4 g (dry) m^{-2}	April 22
Ulva lactuca	5 g (dry) m^{-2}	April 20
Cladophora sp.	2 g (dry) m^{-2}	July 10
Enteromorpha sp.	0.5 g (dry) m^{-2}	July 10
Invertebrates		
Hard clams (c. 46 mm) (*Mercenaria mercenaria* L.)	16	June 4
Bay scallops (c. 47 mm) (*Argopecten irradians* Lamarck)	6	June 25
Grass shrimp (c. 28 mm) (*Palaemonetes pugio* Holthuis)	8	May 28
Snails (*Bittium bittium* Pfeiffer)	100	May 27
Mussels (c. 27 mm) (*Mytilus edulis*)	8	June 4
Soft clams (c. 24 mm) (*Mya arenaria*)	8	June 11
Juvenile fish		
Winter flounder (c. 46 mm) (*Pleuronectes americanus* Walbaum)	8	June 8
Sticklebacks (c. 33 mm) (*Gasterosteus aculeatus L.*)	8	August 7
Mummichogs (c. 46 mm) (*Fundulus heteroclitus* L.)	8	May 26
Silversides (c. 49 mm) (*Menidia menidia* L.)	8	July 2

was drawn from the lower west passage of Narragansett Bay, and replaced at a rate of 5% volume d^{-1}. The water depth in each of the mesocosms was comparable with the average depths of the Rhode Island lagoons (0.8 to 1.8 m, Lee and Olsen 1985). The rate of replacement of the water also lay within the range of rates of flushing reported for the local lagoons (3–18% d^{-1}; Isaji and Spaulding 1981; LaCotta 1981; Nixon and Lee 1981).

Water temperatures in each mesocosm were maintained to within 2.5°C of water temperatures at the mouth of Point Judith Pond lagoon, Rhode Island, and to within 2°C of the water temperatures in the other mesocosms. This was achieved using a heat-exchanger system, where refrigerated water was passed through a water tight, high surface area heat exchanger coil deployed in each mesocosm. Water column salinities ranged from 28‰ to 30‰, equivalent to the salinities in the marine lagoons or marine portions of the lagoons of Rhode Island (27–30‰ for Potter, Ninigret and Point Judith Pond lagoons, Lee and Olsen 1985).

Nutrient concentrations in the water added to the mesocosms were similar to the average concentrations reported in summer in Block Island Sound, the ocean water source to the Rhode Island lagoons. DIN and DIP concentrations averaged 0.8 and 0.4 μmol l^{-1}, versus 0.5 and 0.4 μmol l^{-1} for Block Island Sound (Nixon and Lee 1981). Nutrient concentrations in the added water were drawn down to the required level (c. 60% for both components) by passing the water for 24 h through a macroalgal nutrient removal system (designed after Adey 1978).

The water column in each mesocosm was kept well mixed using a transparent paddle-wheel circulator, which rotated at a constant speed for 6 h in one direction and then 6 h in the other direction. Concentrations of dissolved oxygen exceeded 4 mg l^{-1} in all mesocosms through the experiment, approximating conditions in the local lagoons where hypoxia is seldom observed (V. Lee personal communication). The circulators generated currents of 15–20 cm s^{-1} near the water surface and 5–10 cm s^{-1} above the sediments. Tidal water level fluctuations were not simulated in the mesocosms, because tidal amplitudes in most of the local lagoons range from 0.04 m to 0.2 m (Lee and Olsen 1985).

Each mesocosm contained silty-sand sediments collected from the mouth of Point Judith Pond lagoon. The sediments were collected using a large crane-operated grab sampler, care being taken to maintain the vertical integrity of the sediments. The sediments were collected and placed in the mesocosms 32 d before the start of enrichment. The sediments in each mesocosm lay in two trays, each 1.15 m long, 1.8 m wide and 0.35 m tall. Inclusion of the sediments was necessary to incorporate the sediment-water coupling of natural lagoons.

Each mesocosm also contained plants common in the local lagoons (Thorne-Miller et al. 1983) (Table 3). In addition to the microflora added with the sediments, and in the water added to the mesocosms each day, each mesocosm was planted with shoots of eelgrass (*Zostera marina*), and also received living thalli of four species of drift macroalgae, *Gracillaria tikvahiae, Ulva lactuca, Cladophora* sp., and *Enteromorpha* sp. The *Zostera, Ulva,* and *Gracillaria* were added to the mesocosms at the start of the experiment. *Cladophora* and *Enteromorpha* were added in early summer when populations became available in the local lagoons.

The *Zostera* shoots planted in the mesocosms were collected from Point Judith Pond lagoon adjacent to the site of sediment collection. Shoots of standard length (0.25 m to 0.35 m from first root node to tip of longest leaf) and showing no signs of wasting disease (assessed as in Burdick et al. 1994) were transplanted into one tray per mesocosm. The shoots were planted at a biomass of 100 g dry wt m^{-2} bed and a density of 250 shoots m^{-2} bed. Average biomasses in the Rhode Island lagoons range from 90–430 g dry wt m^{-2} bed (Lee and Olsen 1985). Shoot densities in natural eelgrass beds in the northeast U.S. typically lie between 270 and 510 shoots m^{-2} bed (Harlin and Thorne-Miller 1981). Relatively low rates of stocking were selected, to allow space for new shoot formation should conditions in any of the mesocosms have favored this.

The sides of each mesocosm were lined with white acrylic panels, which were removed once per week in summer for cleaning. Cleaning served to maintain light levels in the mesocosms, and prevent build up of fouling materials on the sidewalls of the mesocosms. In the absence of phytoplankton blooms, light levels at the sediment surface exceeded the light compensation level (30 μE m^{-2} s^{-1}; Drew 1979) and daily photoperiod requirement for eelgrass (6 h, Dennison and Alberte 1985). The fouling material scraped from the panels was retained outside the mesocosms for elemental analysis (results to be reported elsewhere).

Juveniles of 6 species of invertebrates and 4 species of fish known to be common in the local lagoons were also added to each mesocosm (Table 3). The purpose of adding these animals was to incorporate some of the animal-plant interactions known to occur in natural lagoons, and that may regulate the way lagoon plant communities respond to enrichment (as in Neckles et al. 1993). The individuals added were all collected from the local lagoons or from Narragansett Bay. Accurate standing stock estimates are not available for these species in the local lagoons, but the quantities added to the mesocosms are believed to be reasonably realistic.

Response Measurements

Concentrations of dissolved inorganic nutrients in the water column of each of the mesocosms was determined once per week. Water samples were filtered through Gelman A/E filters, and analyses followed U.S. Environmental Protection Agency methods for nitrate plus nitrite (based on Bendschneider and Robinson 1952), ammonium (Fiore and O'Brien 1962), and phosphate (Murphy and Riley 1962). The analyses were conducted in duplicate, using a Lachat Instruments Flow Injection Analyzer Model Quickchem IV. Water column concentrations of chlorophyll *a* (chl *a*) were measured twice per week. Water samples were filtered through Gelman A/E filters, and acetone extraction and fluorometric pigment analysis followed Holm-Hansen et al. (1965). Water column attenuation coefficients (k, m^{-1}) were estimated twice per week from readings of photosynthetically active radiation (PAR). PAR readings were conducted at 0.02 m, 0.1 m, 0.2 m, 0.4 m, and 0.6 m water depths, using a Li-Cor Quantum/Radiometer/Photometer Li-185 meter.

Biotic removal of the nutrients added to the mesocosms was estimated by subtracting the average observed concentrations in the water column, from the theoretical concentrations predicted assuming no biological activity within the systems. The predicted concentrations were calculated from the sum of loadings (from Table 1) minus the losses through flushing at 5% volume d^{-1}. The draw down calculated in this manner is obviously a net draw down, because it reflects not only draw down through biological uptake plus loss through flushing, but also any internal regeneration of nutrients from within the systems (the sediments or decomposition).

Above-ground dry biomass of *Zostera* was estimated every two weeks. Biomass (g dry wt m^{-2} bed) (y) was estimated as follows: $y = 0.003x + 11.99$, $r^2 = 0.82$, where x is total leaf length per unit area eelgrass bed (cm m^{-2} bed). Indirect estimation of biomass was necessary, to minimize destructive sampling of the eelgrass beds. The regression of above-ground biomass versus total leaf length was derived from measurements of 100 shoots (10 mesocosm^{-1}) sacrificed from each of the mesocosms in June.

Total leaf length was estimated from measurements conducted every 2 wk in a fixed transect (1.58 m × 0.08 m) across the eelgrass bed in each mesocosm. During each 2-wk survey measurements were conducted of shoot densities (shoots m^{-2} bed), numbers of leaves $shoot^{-1}$, and length of the longest leaf $shoot^{-1}$ (from first root node to leaf tip). Total leaf length was estimated by multiplying the numbers of shoots m^{-2} bed by the average numbers of leaves $shoot^{-1}$, by the average leaf length $shoot^{-1}$. The latter was assumed to be 0.75 of the maximum leaf length $shoot^{-1}$.

Direct measurements of biomass of drift macroalgae were conducted every two weeks. The macroalgae were gently retrieved from the mesocosms by diver, patted dry with paper toweling, weighed, and then returned to their respective mesocosms. If biomass in any of the mesocosms was very low, thalli were retrieved from the entire bottom of the mesocosm, to ensure accuracy of the biomass es-

timates. If biomass was very high, algae were retrieved from six quadrats (each of 0.4 m × 0.4 m) thrown arbitrarily into each mesocosm. Quadrant sampling was required under conditions of high biomass, to minimize physical disturbance of the mesocosms.

Dry biomass of epiphytic material was estimated m^{-2} eelgrass bed once per month. This was achieved by estimating the epiphyte biomass cm^{-2} leaf surface from representative leaves, and then multiplying this by the total leaf area m^{-2} bed. The latter was computed by multiplying the sum of leaf length m^{-2} bed by average leaf width (assumed to be 0.8 cm), and then by 2 (to account for both sides of the leaves). Each month 5 leaves collected from randomly selected shoots in each mesocosm were used to estimate biomass cm^{-2} leaf surface. The third to fifth youngest leaves were selected, to standardize for differences in epiphytization that can exist with leaf age. Sampling of the leaves and processing of the epiphytic material followed Lin (1995).

Statistical Analysis

One-way and two-way repeated measures ANOVA (SAS/STAT 1985) were employed to determine whether for any parameter the differences between treatments (termed LOADING effects) were significant. Fisher's protected least significance difference (LSD) tests (SAS/STAT 1985) were then conducted to determine which of the treatments was significantly different from the others. If a significant LOADING × TIME interaction was observed, the data were partitioned for 4-wk periods, and the one-way or two-way ANOVA repeated for these periods. If the effects of LOADINGS were significant but no LOADING × TIME interaction existed for a specific period, Fisher's protected least significance difference (LSD) tests were again performed. For all tests, p values of 0.10 or greater were considered to be significant.

Results

Water Column Nutrient Responses

Dissolved Inorganic Nitrogen

In all mesocosms except the 2 mesocosms enriched at VH loadings, concentrations of DIN remained low (2–4 μmol l^{-1}) through the experiment (Fig. 3). In the 2 VH loading mesocosms, concentrations of DIN built up to 30 μmol l^{-1} and 45 μmol l^{-1} from mid-June through July, and then between 12 μmol l^{-1} and 18 μmol l^{-1} in September. Two-way repeated measures ANOVA indicated concentrations of DIN were significantly different among the 5 treatments (significant LOADING effect, p = 0.06, Table 4). Fisher's LSD test indicated

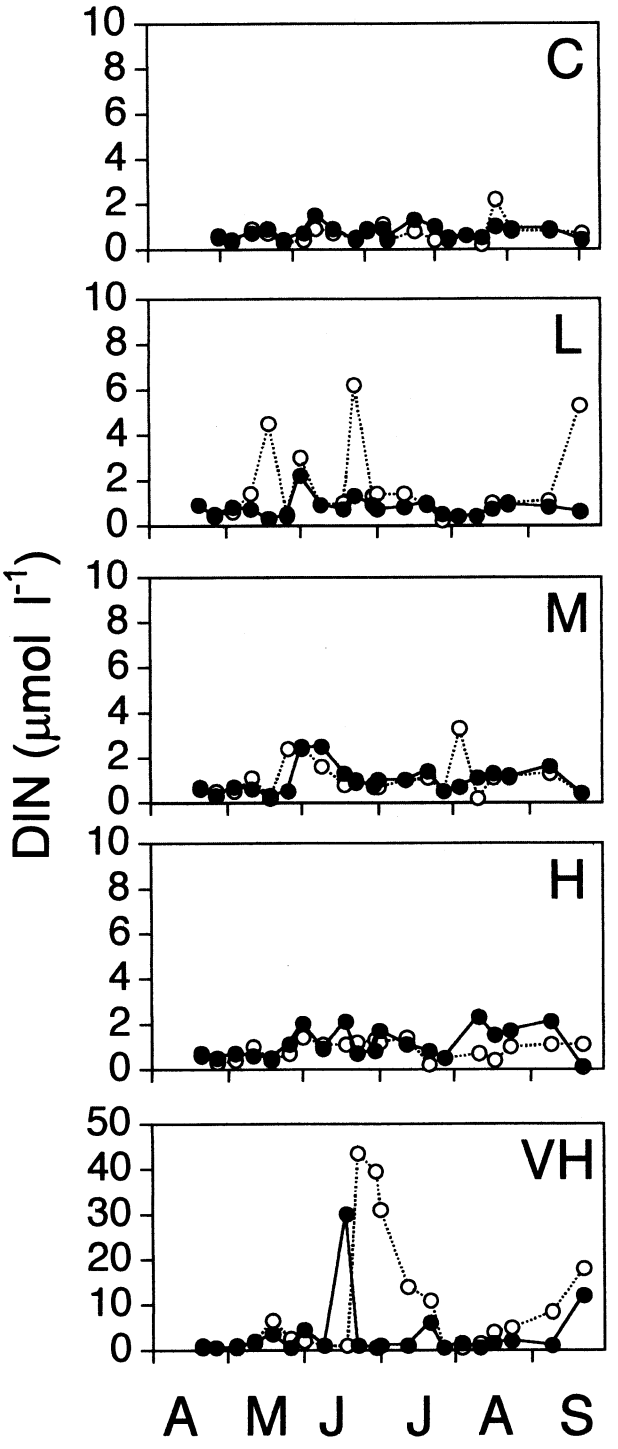

Fig. 3. Water column concentrations of dissolved inorganic nitrogen (DIN) in the two replicate mesocosms of the 5 loading treatments. Note the scale of the vertical axis of the VH loading panel is five times the vertical scales of the other panels.

TABLE 4. Statistical significance of loading (LOADING) or loading by time (LOADING × TIME) responses of concentrations of dissolved inorganic nutrients in the 5 treatments. All data ln transformed. Horizontal underlines are used to denote differences among treatments. Where underlines overlap, the specific treatments showing the overlaps are not significantly different. Where no overlap exists, the responses to the treatments are significantly different at p = 0.10 or greater.

Variable	2-way ANOVA		Fishers LSD	p =
	LOADING	LOADING × TIME		
DIN concentration (μmol l^{-1})				
Entire expt.	0.06	n.s.	VH > L > H > M > C	0.05
June + July	0.04	n.s.	VH > M > H > C > L	0.05
DIP concentrations (μmol l^{-1})				
Entire expt.	0.01	0.03		
Aug. + Sept.	0.02	n.s.	VH > H > M > L > C	0.05
Molar DIN:DIP				
Entire expt.	n.s.	n.s.		

that concentrations in the VH treatment mesocosms, but at none of the other levels of enrichment were greater than in the Controls (p = 0.05).

In all treatments, including the Controls, average concentrations of DIN were lower than predicted (Table 5), indicating a net draw down of DIN by the biota of the systems. The extent of the draw down differed among treatments (p = 0.05, one-way ANOVA, Table 6), ranging from 4 μmol l^{-1} in the Controls to 143 μmol l^{-1} in the VH treatments. The percent draw down was high in all treatments. Percent draw down was significantly greater in the 4 enriched treatments (−95% to −99%) than in the Controls (−83%), but not among the 4 enriched treatments (Fisher's LSD, p = 0.10).

Dissolved Inorganic Phosphorus

In all treatments, concentrations of DIP remained < 1 μmol l^{-1} from the start of the experiment through July, and then increased through August and September (Fig. 4). For the period April through July, concentrations among the 5 treatments were not different. For August through September, concentrations of DIP in the M through VH treatments, but not in the L treatment, were significantly greater than in the Controls (Fishers LSD test, p = 0.02).

The extent of the draw down of DIP differed among treatments (one-way ANOVA, p = 0.01). Concentrations in the Controls were greater than predicted, perhaps as a result of DIP release from the sediments as occurs in the local lagoons in summer (Nowicki and Nixon 1985). In all 4 enriched treatments, and as for DIN, concentrations of DIP were lower than predicted. The net draw down of DIP was smaller than for DIN, and differed among the 4 enriched treatments, from −79% at L loadings to −59% in the mesocosms enriched at VH loadings (Fisher's LSD, p = 0.05).

Molar DIN:DIP

While the levels of buildup across the enrichment gradient were different for DIN and DIP, no significant difference in molar DIN:DIP ratios could be detected among the 5 treatments (Fig. 5) (repeated measures, two-way ANOVA, p ≤ 0.05 in all cases). In most mesocosms, molar ratios tended to be lower than the ratios of the external loadings (10:1 to 13:1, Table 1), indicating a greater de-

TABLE 5. Net drawdown of water column concentrations of DIN and DIP in the five treatments.

Treatment	Observed Concentration[a] (μmol l^{-1})		Theoretical Concentration[b] (μmol l^{-1})		Draw Down[c] (μmol l^{-1})		Percent Draw Down[d]	
	DIN	DIP	DIN	DIP	DIN	DIP	DIN	DIP
Controls	0.75	0.5	4.5	0.4	−3.75	+0.1	−83	+25
Low	1.2	0.5	24.7	2.4	−23.5	−1.9	−95	−79
Medium	1.05	1.25	42.5	3.8	−41.5	−2.75	−98	−67
High	1.15	2.65	78.2	6.6	−77.1	−3.95	−99	−60
Very High	6.4	5.05	149.6	12.4	−143.3	−7.35	−96	−59

[a] Average for 2 replicates per treatment. n = 19 observations per mesocosm. Averages are for period when equilibrium concentrations would have been achieved in the mesocosms, calculated assuming zero biological activity and 5% volume d^{-1} flushing.

[b] Calculated from sum of DIN and DIP loadings (throughflowing water plus wet deposition plus experimental additions) (as in Table 1), and assuming zero biological activity and 5% volume d^{-1} flushing.

[c] Draw down = Average observed concentration minus theoretical concentration.

[d] (Draw down/theoretical concentration) × 100.

TABLE 6. Statistical significance of differences in average drawdown of dissolved inorganic nutrients in the 5 treatments. n.s. = p > 0.10. All data is ln transformed.

Variable	1-way ANOVA LOADING	Fishers LSD	p =
DIN draw down			
μmol l^{-1}	0.05	VH > H > M > L > C	0.10
%	0.06	H > M > VH > L > C	0.10
DIP draw down			
μmol l^{-1}	0.01	VH > H > M > L > C	0.05
%	0.02	L > M > H > VH > C	0.05

mand for DIN relative to DIP by the biota of the systems. The absence of a treatment effect for DIN:DIP indicates the demand for DIN relative to DIP did not change over the enrichment gradient.

Plant Responses

Phytoplankton

Standing stocks of phytoplankton, measured as concentrations of chl *a*, varied widely during the experiment (Fig. 6). Over the first 4 weeks of enrichment, chlorophyll concentrations increased in all mesocosms. In both Controls and one of the L treatment replicates, the concentrations remained elevated (> c. 20 μg l^{-1}) through much of the experiment. In the other 7 enriched mesocosms, concentrations were elevated for a period early to mid-experiment, but then crashed to very low levels through August and September.

For only a one month period from mid-May through mid-June, were the differences in chl *a* concentrations among the 5 treatments significantly different. During this period, concentrations at VH loadings, but at none of the other levels of enrichment, were significantly greater than in the Controls (Fishers LSD test, p = 0.10). Concentrations in the 2 VH mesocosms peaked at 100 or 260 μg l^{-1}, discoloring the water green or yellow-green during this period. Scanning electron microscopy of water samples collected in late May/early June indicated the discoloration was caused by populations of *Nannochloropsis* sp. and *Chlorella* sp., with smaller populations of small diatoms.

The populations responsible for the prolonged elevated chl *a* concentrations in the Controls were different from the shorter-lived populations in the VH treatments. In late May/early June, the populations in the Controls were composed almost entirely of the brown-tide organism, *Aureococcus anophagefferens* (Nixon et al. 1994). By the end of August, the Controls were devoid of *Aureococcus*, but continued to support large standing stocks of small

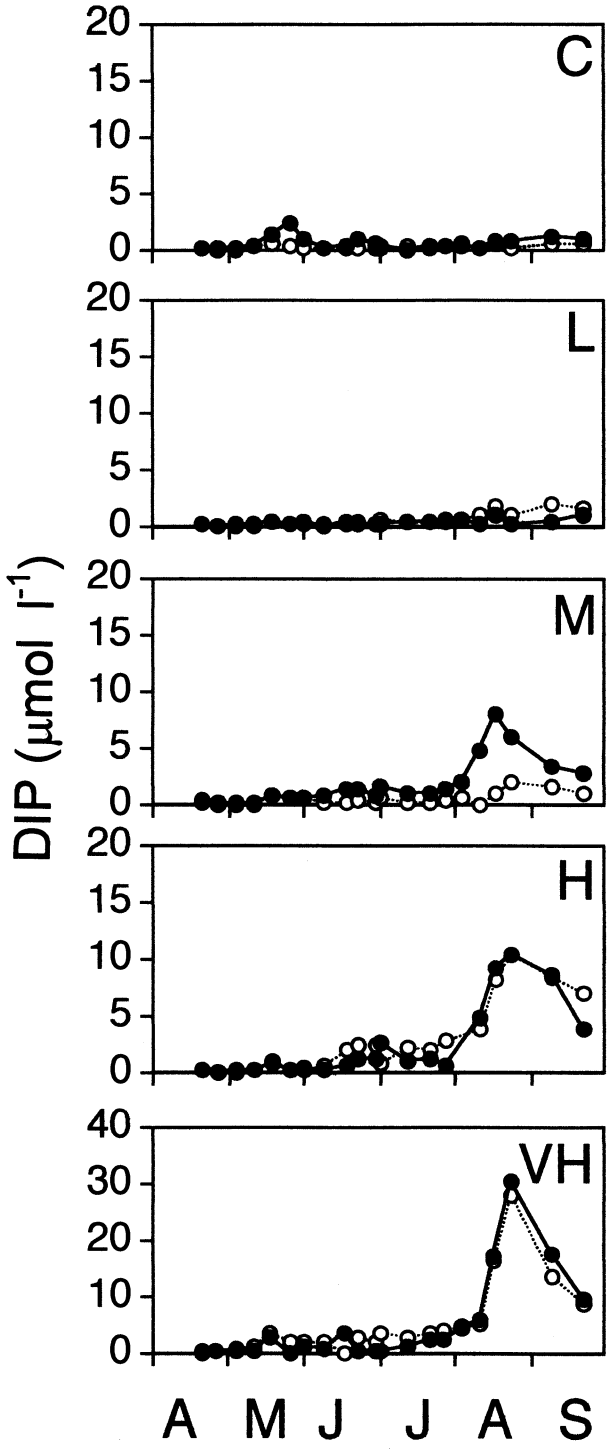

Fig. 4. Water column concentrations of dissolved inorganic phosphorus (DIP). Note vertical axis of VH treatment panel twice the scale of the other panels.

diatoms, with minor populations of *Nannochloropsis* sp. and *Chlorella* sp.

Eelgrass

While a significant effect of nutrient loading could be detected for concentrations of chlorophyll, no significant effect could be detected for above-ground biomass of *Zostera* (Fig. 7), for the entire experiment or for any period during the experiment. In all treatments, *Zostera* biomass increased over the first 4–8 wk of the experiment, and then starting in mid-May through late June proceeded to decline. By the end of the experiment, 3 of the mesocosms possessed no living above-ground biomass, and the biomasses in the other 7 mesocosms were low (< 30 g dry wt m^{-2} bed).

Based on water column k values (Fig. 8), the declines in all treatments were likely caused by water column shading, by *Aureococcus* brown-tide blooms in the Controls, and mixed diatom/coccoid blooms in the enriched mesocosms. Within the first 4 wk to 8 wk after start of enrichment, the k values had exceeded 1.9 m^{-1}, the k value in all mesocosms at which light levels at the sediment surface fell below the upper light saturation level for eelgrass photosynthesis (230 μE m^{-2} s^{-1}, Dennison and Alberte 1982).

Epiphytic Material and Drift Macroalgae

As for *Zostera,* no significant difference among treatments could be detected for dry biomass of epiphytic material (Fig. 9) or drift macroalgae (Fig. 10). In most mesocosms biomass of epiphytic material (expressed per unit area of eelgrass bed) increased through the early to mid-portion of the experiment. Biomass then declined through August and September, presumably through detachment of eelgrass leaves. An exceptionally large biomass of epiphytic material of 2,034 g dry wt m^{-2} bed was measured in one of the H loading replicates in July.

Starting in mid-July or August, and extending into September, the biomass of drift macroalgae increased in 7 of the 8 enriched mesocosms. The increases followed the declines in epiphyte biomass, and were caused by the development of mats of filamentous green algae, specifically of *Enteromorpha* and *Cladophora* species. A biomass of 3,680 g dry wt m^{-2} sediment was observed in one of the M loading replicates in September. Biomass of drift macroalgae remained low in both Controls through the experiment.

All Plant Components Combined

At most times during the experiment, the bulk of the total plant biomass in each of the mesocosms was contributed by the benthic plants; *Zostera,* epiphytic material or drift macroalgae (Fig. 11). As for each of these individual components, no significant loading effect could be detected for

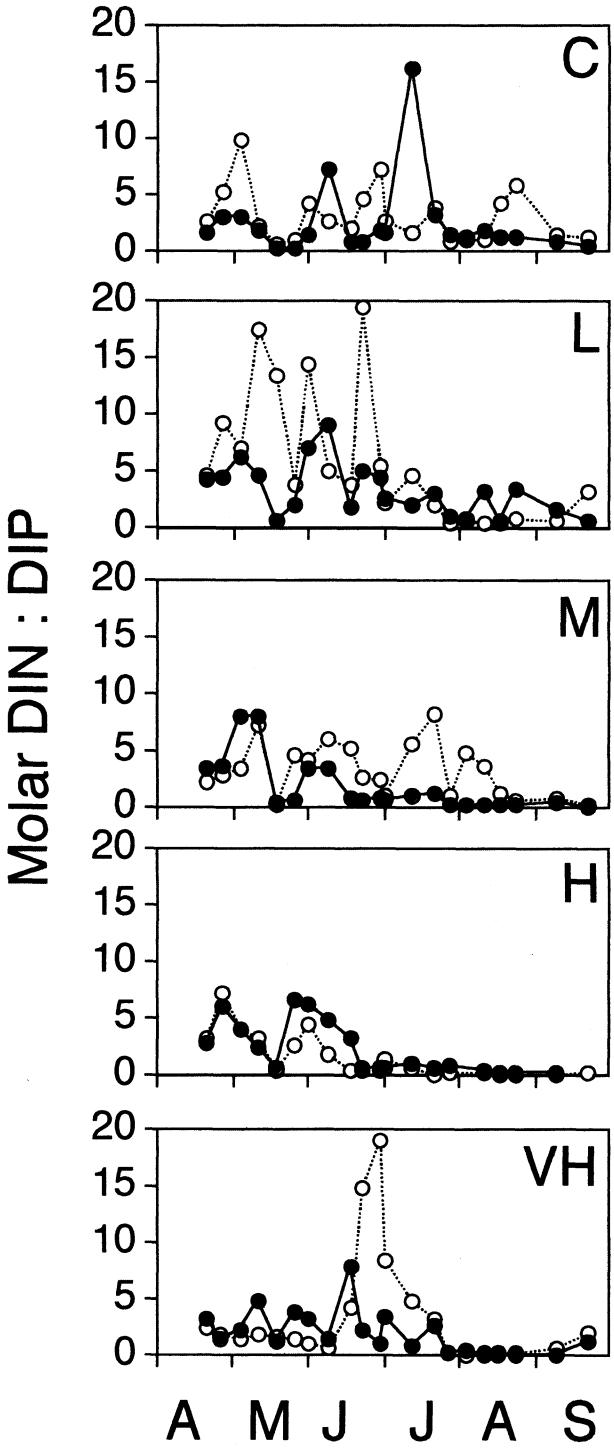

Fig. 5. Molar DIN:DIP ratio in the water column in the 5 treatments.

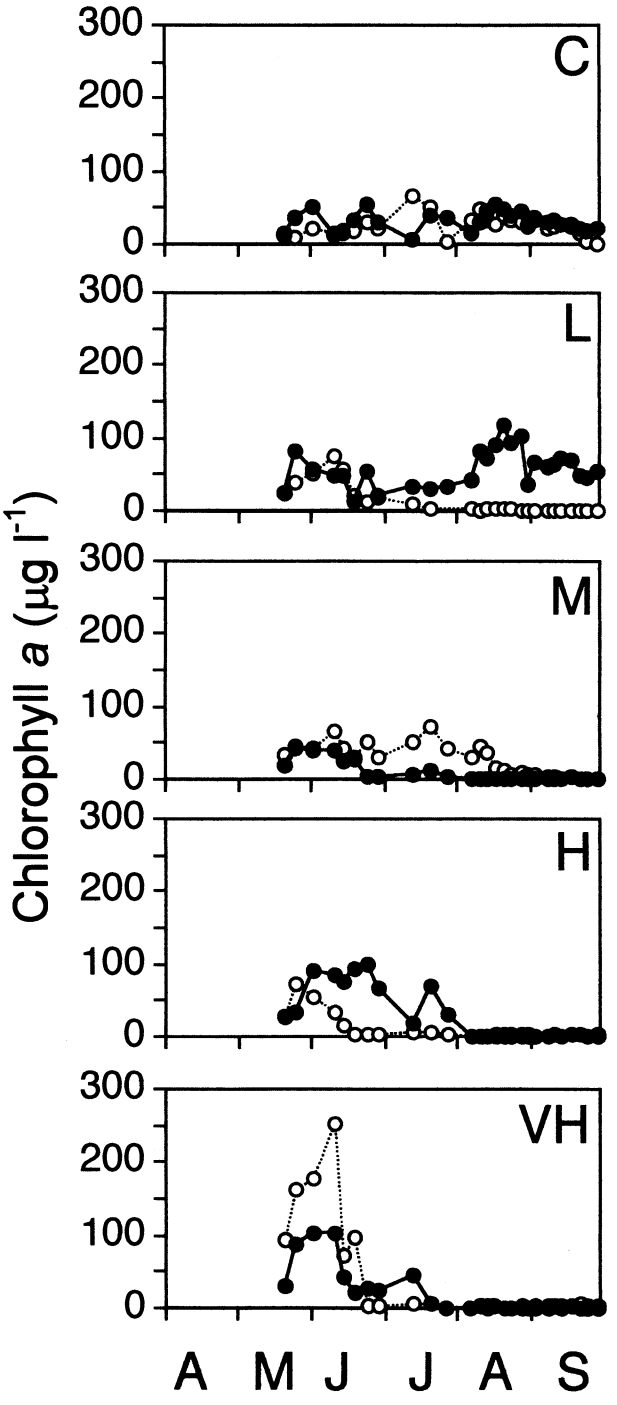

Fig. 6. Water column concentrations of chlorophyll *a*.

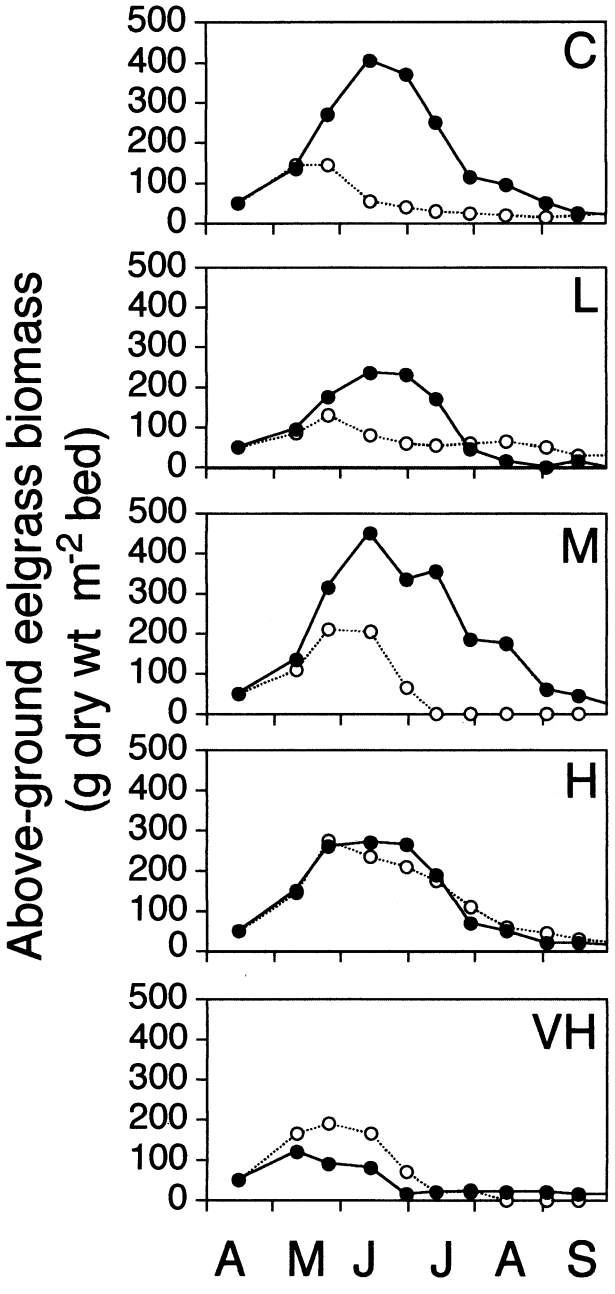

Fig. 7. Above-ground dry biomass of eelgrass, *Zostera marina*.

total biomass of all plant components combined. Any loading effect was confounded by the exceptional biomasses of macroalgae and epiphytic material that developed in one of the M and H replicates, respectively. For both components, the high biomass in the one replicate were not compensated for by high biomass of another plant component in the other replicate.

Discussion

Comparison with Bays and Estuaries

Comparison of the results of this experiment with the results of a similar gradient enrichment experiment conducted in 1981 and 1982 using the MERL mesocosms (described in Nixon et al. 1984 and Oviatt et al. 1986), suggests the responses of

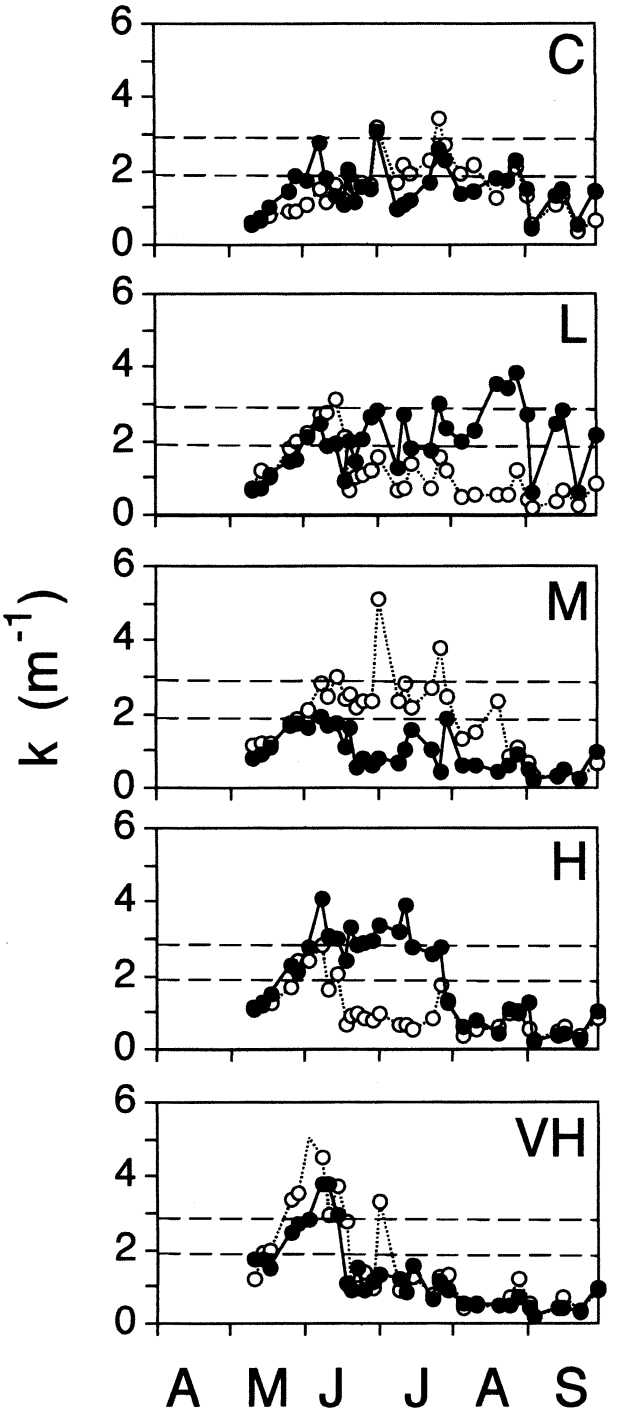

Fig. 8. PAR vertical attenuation coefficients (k). The horizontal dashed lines indicate the 1.9 and 2.9 m^{-1} k values, which represent the points at which light levels at the sediment surface in the mesocosms fall below the upper (230 μE m^{-2} s^{-1}) and lower (100 μE m^{-2} s^{-1}) light saturation levels reported for eelgrass photosynthesis (Dennison and Alberte 1982) (incident irradiance assumed = 2,000 μE m^{-2} s^{-1}).

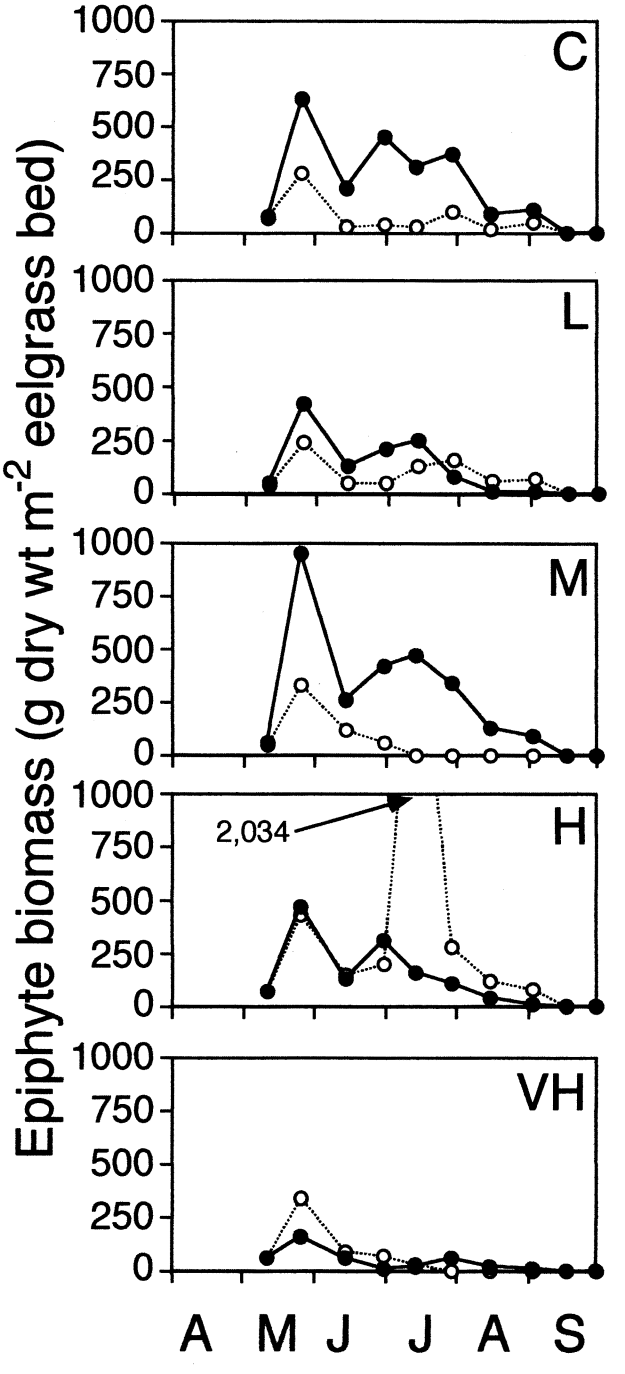

Fig. 9. Dry biomass of epiphyte material per unit area eelgrass bed.

lagoons to enrichment might be more complex than the responses of bays and estuaries. The MERL mesocosms, which were located 200 m from the Lagoon Mesocosm Facility, were designed as physical models of lower Narragansett Bay. The MERL mesocosms were 5.0 m deep, with a water

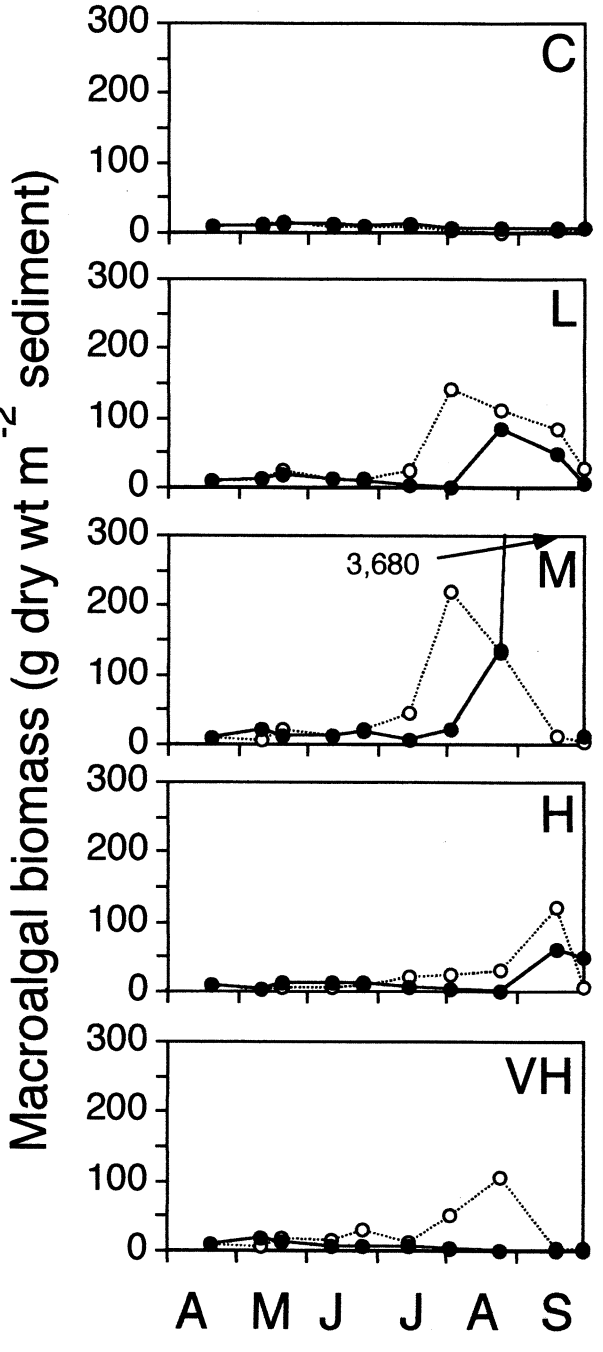

Fig. 10. Dry biomass of drift macroalgae per unit area sediments.

residence time of 27 d, versus 20 d in the lagoon mesocosms.

In this particular MERL experiment, the mesocosms were subjected to the following 6 levels of enrichment: 1×, 2×, 4×, 8×, 16×, and 32× ambient loadings (plus one unenriched Control). Enrichment of the MERL mesocosms involved daily addition to the water column of ammonium plus phosphate plus silicate, at a molar N:P:Si ratio of 12.8:1:1.09. The areal N and P loadings to our VH treatment mesocosms were equivalent to between the 8× and 16× MERL treatments. Unlike the MERL mesocosms, the lagoon mesocosms received no experimental additions of Si.

Comparison of the nutrient concentration data from the 2 experiments indicates that the efficiency of draw down of added DIN was larger in the lagoon mesocosms than in the MERL systems (Fig. 12 top). In the MERL mesocosms, unlike in the lagoon mesocosms, average DIN concentrations showed a significant linear build up with increased loadings. In the lagoon mesocosms, at all levels of enrichment, the average DIN concentrations were drawn down to background levels. Only in the VH treatment replicates, for a brief period, did a significant build up of DIN occur in the shallower systems.

While enrichment of the lagoon mesocosms, as in the MERL mesocosms, led to increased standing stocks of phytoplankton, the increases in the lagoon mesocosms were less regular than in the MERL systems (Fig. 12 bottom). For the MERL mesocosms, a relationship existed between concentrations of chlorophyll averaged from May through September, and DIN loadings. In the lagoon mesocosms, an effect of enrichment on standing stocks of phytoplankton could be detected only at VH loadings, and for the one month period early to mid-experiment.

Unlike in the MERL mesocosms where plant biomass and the plant responses to enrichment were dominated by phytoplankton, in the lagoon mesocosms no relationship could be detected between nutrient loadings and the biomass of the benthic plants that dominated biomass. The absence of such a relationship suggests the coupling between nutrient loadings and plant biomass may be looser in shallow, benthic-dominated lagoons than in deeper phytoplankton-based systems (at least on the time scales of the 2 experiments).

Depth and the Enrichment Responses of Coastal Marine Systems

The plant responses observed in the lagoon mesocosms were also different from the responses observed in earlier shallow-water enclosure experiments. In most of the earlier experiments, enrichment caused increased biomasses of drift macroalgae (Burkholder et al. 1992; Fong et al. 1993) or epiphytic material (Twilley et al. 1985; Neckles et al. 1993). In our experiment, no clear response was demonstrated by these components. Enrichment in the earlier experiments also caused standing stocks of submerged macrophytes to decline (How-

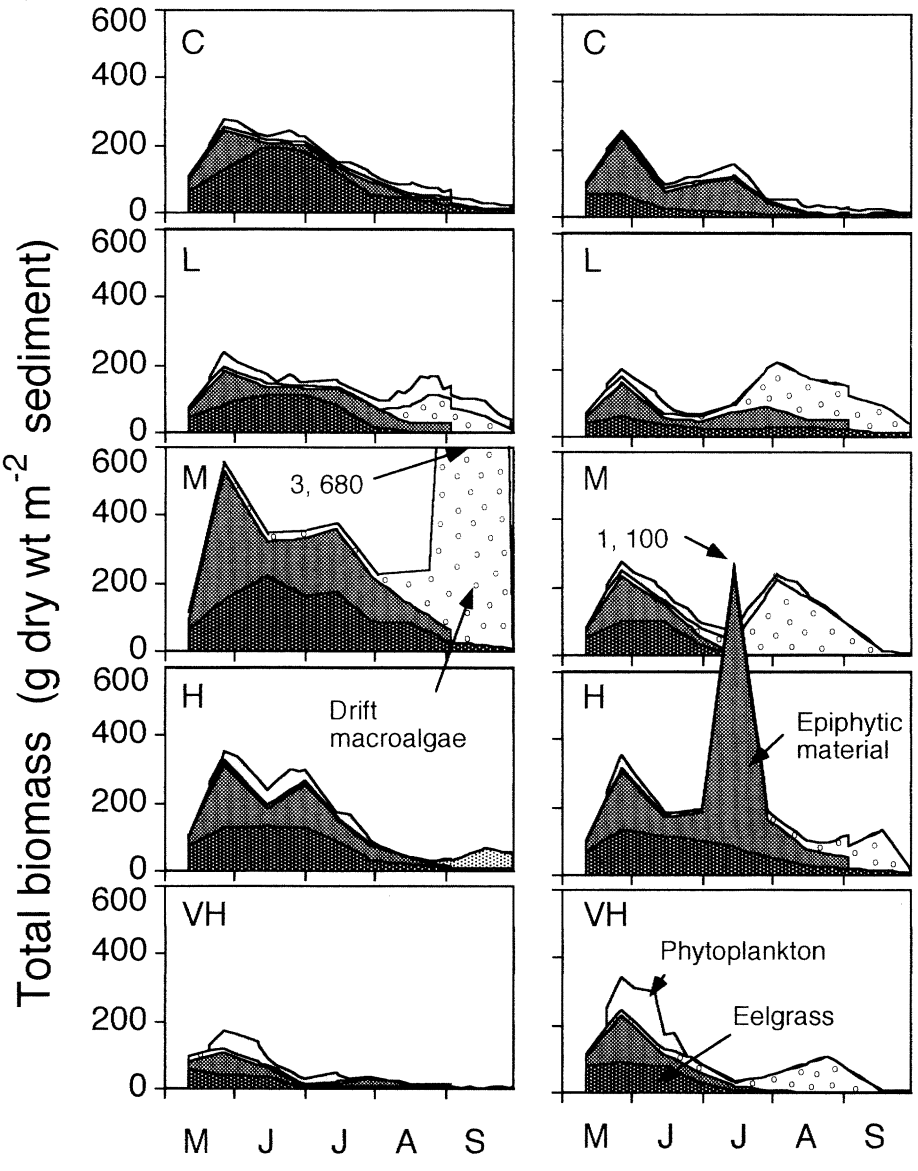

Fig. 11. Total biomass of all plant components combined in each of the mesocosms. Dark stippling = eelgrass (*Zostera marina*), medium stippling = epiphytic material, open circles = drift macroalgae, and light stippling = phytoplankton. Phytoplankton biomass estimated assuming chlorophyll *a* concentrations = 0.5 carbon content, and carbon content = 0.20 dry wt.

ard-Williams 1981; Twilley et al. 1985; Burkholder et al. 1992; Neckles et al. 1993; Short et al. 1995). In our experiment the eelgrass responses were no different in the Controls and enriched mesocosms.

One explanation for the different responses in the 2 sets of experiments, and one that would also explain the difference between the lagoon and MERL results, might be the different depths of the experimental systems. In the earlier experiments, which employed enclosures between 0.3 m (Short et al. 1995) and 0.85 m deep (Twilley et al. 1985), the depth likely allowed benthic algae to out compete the phytoplankton for added nutrients. In the MERL mesocosms, which were 4 m deeper than ours, only phytoplankton could respond to enrichment.

In the lagoon mesocosms, which were intermediate in depth, each of the plant components was likely provided with a more equal opportunity to respond to enrichment, creating the observed diverse responses. If this interpretation is correct, it would account for the diverse plant changes observed in the lagoon mesocosms, even in mesocosms receiving identical loadings. The relatively large benthic plant biomass in these systems of intermediate depth probably accounts for the effi-

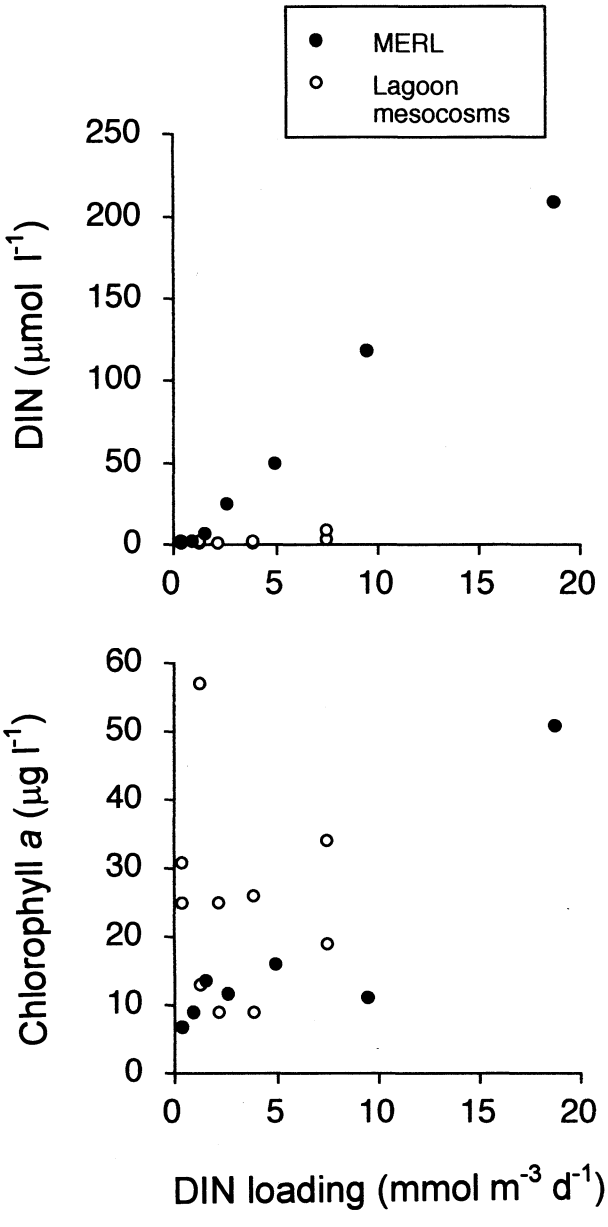

Fig. 12. Comparison of average DIN (top) and chlorophyll *a* concentrations (bottom) as a function of DIN loading in the lagoon mesocosms (open) and MERL mesocosms (closed). MERL data for May through September 1981, from Nixon et al. (1984).

cient biotic draw down of the added nutrients even at the VH loadings.

Brown Tides and the Responses of Lagoons to Enrichment

It seems likely that the effects of enrichment might have been more readily detectable in this experiment had *Aureococcus* brown tides not developed in the unenriched Controls. The brown tides caused changes in the Controls that paralleled changes in the VH treatments, specifically increased water column chlorophyll concentrations, decreased attenuation coefficients, and decreased standing stocks of benthic plants. In an experiment conducted using the same facility the previous year, and in which the Controls showed no brown tides, chlorophyll concentrations remained low and the *Zostera* beds survived and grew in the Controls (Taylor et al. 1995b).

While brown tides were not reported in the Rhode Island lagoons during this or the previous experiment, they were observed in the lagoons of southern Long Island the year of this experiment (Nixon et al. 1994). The eelgrass declines in the mesocosms that showed brown tides might be a parallel of the declines that followed brown tides in Long Island Sound in the mid-1980's (Cosper et al. 1987; Dennison et al. 1989). The fact the brown tides occurred in the Controls and one L treatment mesocosm agrees with observations that brown tides develop in the coastal waters of the northeast U.S. under conditions of low rather than high water column availability of DIN (Nixon et al. 1994).

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