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Nutrient limitation and the eutrophication of coastal lagoons

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ABSTRACT: An ecosystem-level experiment was conducted to identify the nutrient most limiting to productivity and biomass in the marine lagoons of the northeast United States. Mesocosms containing a complex of species characteristic of shallow coastal marine environments were enriched with P alone, N alone, or combined N plus P, at loadings typical of highly enriched natural lagoons. The mesocosms showed significant responses to enrichment with N alone but not P alone, indicating limitation by N. Enrichment with N alone caused increased water column concentrations of chlorophyll *a* and particulate nitrogen (PN), increased water column daytime net production (*NP*), and increased rates of growth of juvenile winter flounder. It also caused eelgrass beds and mats of drift macroalgae to decline, apparently in response to phytoplankton shading. Comparison of the N-alone and combined N+P treatments indicated that when enriched with N alone, the limitation of the systems shifted to P limitation of total system metabolism and of phytoplankton production and standing crop, and to light limitation of eelgrass and macroalgal growth. In the combined N+P mesocosms, water column concentrations of chlorophyll *a*, PN, and particulate P, rates of total system and water column *NP* and night-time respiration, and growth rates of juvenile winter flounder and killifish were all increased relative to the N-alone mesocosms. Declines of eelgrass and macroalgae were also more severe.

KEY WORDS: Nutrients · Nitrogen · Phosphorus · Limitation · Coastal lagoons · Eelgrass

INTRODUCTION

In aquatic ecology the term 'nutrient limitation' is used most widely to refer to limitation of net production of key plant components (usually phytoplankton), or of total system net production (Hecky & Kilham 1988, Howarth 1988). The issue of whether aquatic systems or their individual plant components are limited by nutrients, and if so, by which nutrient, appears to differ between systems and remains controversial (Schindler 1981, Smith 1984, Nixon et al. 1986). Resolution of the issue is fundamental to understanding the functioning of aquatic systems and to predicting the effects of nutrient enrichment.

The general paradigm in the literature is that in temperate freshwater lakes P is the limiting nutrient (Schindler 1975, Vollenweider 1976), but in temperate coastal marine systems the limiting nutrient is N (Nixon & Pilson 1983, Oviatt et al. 1995). Exceptions include temperate estuaries and bays that receive large seasonal inflows of freshwater and which exhibit seasonal shifts in limitation (McComb et al. 1981, D'Elia et al. 1986). Other exceptions include marine bays with long residence times and minimal freshwater inflows, where P is apparently limiting (Smith & Atkinson 1984).

An array of direct and indirect approaches have been adopted to identify limiting nutrients in aquatic systems (reviewed by Hecky & Kilham 1988, Howarth 1988). Experiments involving enrichment of whole ecosystems or realistic models of ecosystems (mesocosms) have been identified as the most appropriate, because they best incorporate the complex interactions such as competition and recycling that occur within natural systems (Hecky & Kilham 1988, Howarth 1988). In such experiments, the systems have been enriched with individual and combinations of nutrients, and the limiting nutrient identified by comparing the size of the biomass and production changes.

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In temparate regions, such experiments have been conducted for freshwater lakes (Schindler 1975) and marine bays (Oviatt et al. 1995), but not for shallow coastal lagoons. Much of the evidence concerning nutrient limitation in lagoons has been derived from smaller-scale approaches, and is conflictory. Certain studies have suggested potential N limitation (Ryther & Dunstan 1971, Caraco et al. 1987), others potential P limitation (Nowicki & Nixon 1985), and in still others, the responses have been too variable to allow identification of the limiting nutrient (Harlin & Thorne-Miller 1981).

In the 'whole systems' enriched by Schindler (1975) and Oviatt et al. (1995), primary production was carried out almost exclusively by phytoplankton. In shallow lagoons, the plant communities can also include complex assemblages of macrophytes, drift macroalgae, and epiphytic and epibenthic microalgae (Thorne-Miller et al. 1983), each with different access to nutrient pools and light. Because of this greater complexity, and the closer coupling of water column and sediments in lagoons (Nixon 1982), the issue of nutrient limitation may be more complex than in phytoplankton-based systems.

This paper describes the results of a 'whole-system' experiment broadly equivalent to those of Schindler (1975) and Oviatt et al. (1995), but conducted for shallow coastal lagoons. The experiment involved enrichment of mesocosms designed as living models of the lagoons of southern Rhode Island, USA. The mesocosm approach was adopted to better constrain the nutrient inputs to the systems, to allow replication within treatments, and to allow us to capture at least some of the complex interactions of natural lagoons. The engineering of the mesocosms will be described in detail in S. Granger & S. Nixon (unpubl.). Descriptions of the field lagoons have been provided in Conover (1961), Boothroyd et al. (1985), and Lee & Olsen (1985).

MATERIALS AND METHODS

Experimental facility. The 10 mesocosms employed for the experiment were located outdoors adjacent to lower Narragansett Bay, Rhode Island, USA (Fig. 1). Each mesocosm had an area of 2.3×1.8 m^2, with 1.1 m of coastal water (28 to 33‰) overlying 0.3 m of intact sandy-silt sediments (Fig. 2). The depth of the mesocosms (1.1 m) was roughly equivalent to the average depth reported for the lagoons of southern Rhode Island (Nixon et al. 1982). The mesocosms were filled and flushed with water from Narragansett Bay at 5% volume d^{-1} This rate of flushing is within the range of estimated rates for the Rhode Island lagoons (3 to 10% for Ninigret-Green Hill Pond lagoon, Isaji & Spaulding 1981; <10% for Point Judith and Potter Pond lagoons, LaCotta 1981).

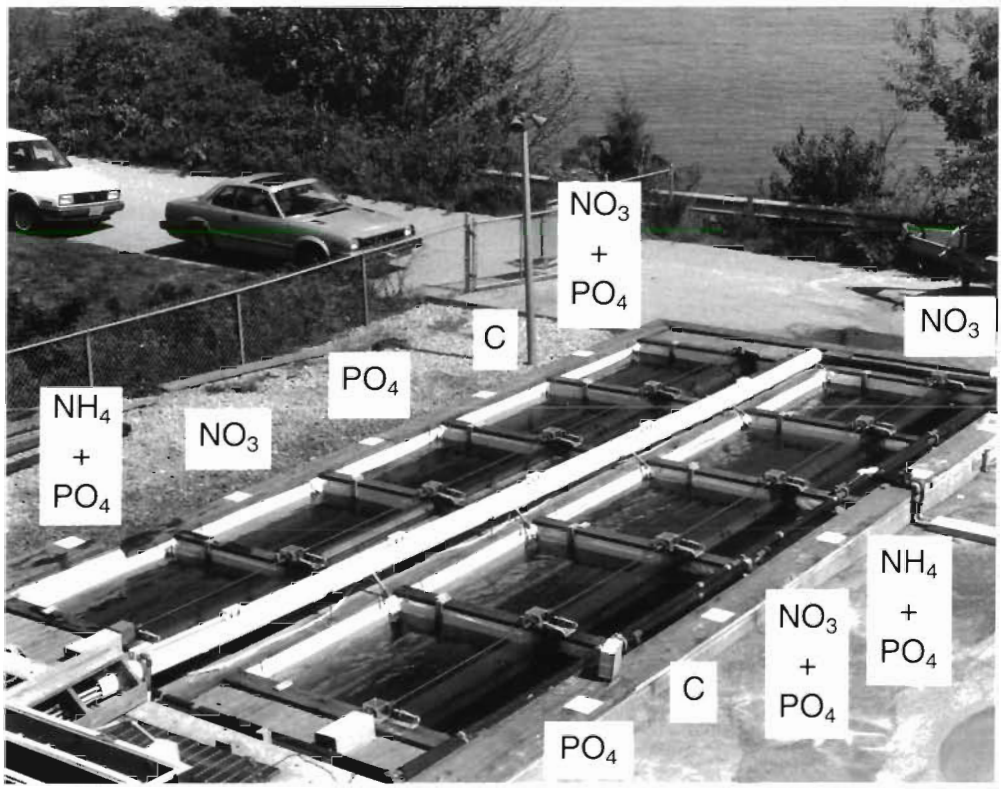

Fig. 1. Aerial view of the lagoon mesocosm facility showing the allocation of the experimental nutrient treatments

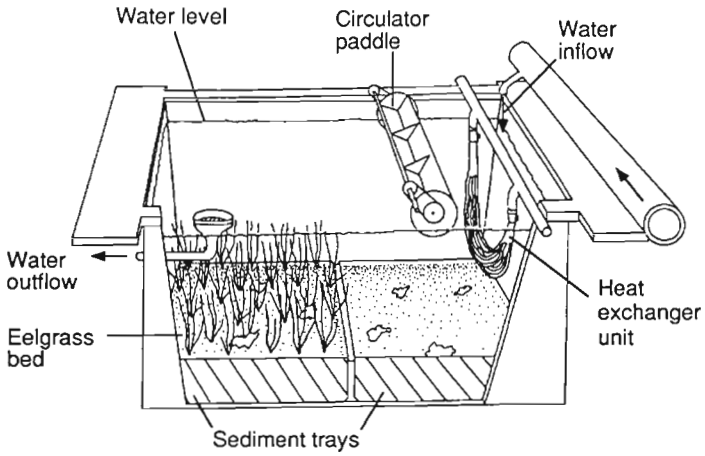

Fig. 2. Schematic side view into one of the 'lagoon' mesocosms

Before entering the mesocosms, the inflowing water was passed through macroalgal 'nutrient scrubbers' for 24 h to reduce dissolved nutrient concentrations to levels characteristic of Block Island Sound (off the coast of Rhode Island), the ocean-water source for the field lagoons. The macroalgal scrubbers were designed after Adey (1978) and reduced the incoming dissolved inorganic nitrogen (DIN) and phosphorus (DIP) loadings by 50%. Because nutrient removal by the scrubbers was most efficient at high incoming concentrations (Granger & Nixon unpubl.), the scrubbers not only reduced the overall loadings but also eliminated any possible pulsed inputs.

In each mesocosm, the water columns were kept well mixed using transparent paddle-wheel circulators which rotated in one direction for 6 h, and then, after a 15 min pause, rotated for 6 h in the other. The circulators generated near-surface and near-bottom currents of 15 to 20 cm s^{-1} and 5 to 10 cm s^{-1}, respectively. Under unenriched conditions, these currents were sufficient to maintain well-oxygenated (>4 mg O_2 l^{-1}) conditions throughout the water column (Granger & Nixon unpubl.). At present, anoxia rarely develops in the water columns of the Rhode Island lagoons (V. Lee pers. comm.).

During summer, water temperatures were maintained at field levels using a heat-exchanger cooling system. Temperatures were kept below 24°C, the temperature above which prolonged exposure has been shown to cause declines in eelgrass *Zostera marina* (Zimmerman et al. 1989). White acrylic panels were placed on the insides of each mesocosm to increase internal light levels. When the water was clear, as in the controls, light levels at the sediment surface exceeded the light compensation level (30 µE m^{-2} s^{-1}; Drew 1979) and daily photoperiod requirement (6 h; Dennison & Alberte 1985) for eelgrass.

The sediments for the base of each mesocosm were collected 1 mo prior to commencement of enrichment. The sediments were collected from Point Judith Pond lagoon using a crane-operated grab sampler, care being taken to maintain the vertical orientation of the sediments. One week prior to the experiment, young eelgrass shoots collected from the field adjacent to the site of sediment collection were transplanted into the sediments of one half of each mesocosm. The shoots were transplanted at a density of 252 shoots m^{-2} bed and a biomass of 93 g dry wt m^{-2} bed. These values approximate the lower range of values for the Rhode Island lagoons (Thorne-Miller et al. 1983).

Each mesocosm was 'inoculated' with living tissue of 3 macroalgal species equivalent to 2 g dry wt m^{-2} of *Ulva lactuca*, 3 g dry wt m^{-2} of *Gracilaria tikvahiae*, and 0.5 g dry wt m^{-2} of *Cladophora* sp. The *U. lactuca* and *G. tikvahiae* were added in mid April and the *Cladophora* spp. in late June, when populations became available in the field. The quantities added were within the range of values reported for spring through early summer for local lagoons and embayments (Thorne-Miller et al. 1983, French et al. 1989).

Juveniles of 4 fish and 4 macroinvertebrate species were added to each mesocosm. The fish included 8 juvenile winter flounder *Plueronectes americanus* [45 mm standard length (SL)], 8 sticklebacks *Gasterosteus aculeatus* (35 mm SL), 8 killifish *Fundulus heteroclitus* (48 mm SL), and 8 silversides *Menidia menidia* (25 mm SL). The invertebrates included 16 hard clams *Mercenaria mercenaria* (2 groups of 8 at 28 and 45 mm), 8 bay scallops *Argopecten irradians* (2 groups,

Table 1. Dissolved inorganic nitrogen and phosphorus (DIN and DIP) loadings to the 5 treatments. Inputs to controls include background inputs via bay water after partial nutrient removal by algal scrubbers plus atmospheric deposition. The atmospheric DIN inputs include wet ammonium and nitrate plus dry nitrate deposition (L. Zhuang unpubl.). The atmospheric DIP inputs are based on average wet precipitation TP concentration values from Nowicki & Oviatt (1990) multiplied by volume of wet precipitation over the experiment. Inputs to PO_4-alone, NO_3-alone, NO_3 + PO_4 and NH_4 + PO_4 treatments include background inputs as for controls, plus experimental additions

Treatment	Loading (µmol N or P m^{-2} d^{-1})				
	NO_3 + NO_2	NH_4	DIN	PO_4	Molar DIN:DIP
Control	101	27	128	33	4
PO_4 alone	101	27	128	718	0.2
NO_3 alone	8282	27	8309	33	252
NO_3 + PO_4	8282	27	8309	718	12
NH_4 + PO_4	101	8225	8326	718	12

35 and 38 mm), 45 periwinkle snails *Littorina littorea* (10 mm), and 8 grass shrimp *Palaemonetes pugio* (29 mm length).

Experimental design. The experiment involved 5 treatments, each conducted in duplicate (Table 1). The treatments were apportioned among the 10 mesocosms, insuring that the 2 replicates of each treatment were not located on the same side or at the same end of the facility (Fig. 1). Two mesocosms received no experimental nutrient additions and served as controls (C). Two mesocosms were enriched with phosphate alone (PO_4 alone) and 2 with nitrate alone (NO_3 alone). Comparison of these 2 'single nutrient' treatments was used to identify the primary limiting nutrient.

Two mesocosms were enriched with both nitrate and phosphate ($NO_3 + PO_4$) at the same loadings employed for the single nutrient treatments. Two additional mesocosms were enriched with ammonium plus phosphate ($NH_4 + PO_4$) at the same loadings as for the $NO_3 + PO_4$ mesocosms. Comparison of the 'single' and the 'combined N + P' treatments (NO_3, PO_4, $NO_3 + PO_4$ and $NH_4 + PO_4$) was used to detect evidence of secondary nutrient limitation. Comparison of the $NO_3 + PO_4$ and $NH_4 + PO_4$ treatments was used to determine the relative influence of the form of added DIN.

All treatments received background inputs from the atmosphere and via the throughflowing water. The background inputs of N and P averaged about 129 and 33 µmol m^{-2} d^{-1}, respectively, and were small compared to the experimental additions of 8219 µmol N m^{-2} d^{-1} and 685 µmol P m^{-2} d^{-1}. The experimental nutrient loadings were in the same order as those reported for highly enriched lagoons, such as Moriches Bay, Long Island, New York, USA (7000 µmol N m^{-2} d^{-1}; 1000 µmol P m^{-2} d^{-1}; Ryther 1989), and the Childs River and Quashnet River regions of Waquoit Bay, Massachusetts, USA (10 000 to 12 000 µmol N m^{-2} d^{-1}; K. Foreman pers. comm.).

The molar N:P ratio of the inputs to the combined N + P mesocosms was 12:1, which is equivalent to the molar N:P ratio of the dissolved inorganic nutrient inputs (13:1) via sewage to Narragansett Bay (Nixon & Pilson 1983). It is also in the same order as the molar N:P ratio of the inputs (7:1) to Moriches Bay (Ryther 1989). The nutrients added to the mesocosms were added daily (late afternoon) to the water column in dissolved form from stock solutions of $NaNO_3$, NH_4Cl, and KH_2PO_4. Enrichment lasted 6 mo from 25 March to 30 September 1991.

Response measurements. The parameters monitored in the experiment were some of those most widely used to assess nutrient limitation of aquatic systems (Howarth 1988). These included changes in water column chlorophyll *a* concentrations, concentrations of dissolved inorganic and particulate N and P in the water column, dry biomass of various plant components, and rates of total system and water column net production. Since changes in primary production caused by enrichment should theoretically be transferred up the food web (Nixon et al. 1986), we also monitored changes in fish growth as an index to assess nutrient limitation.

Water column chlorophyll *a* concentrations were determined twice per week. Acetone extraction and pigment analysis followed Holm-Hanson et al. (1965). Dissolved nutrient analyses were conducted weekly. Duplicate analyses were conducted for nitrate plus nitrite (based on Bendschneider & Robinson 1952), ammonium (Fiore & O'Brien 1962), and phosphate (Murphy & Riley 1962). The analyses were performed using a Lachat Instruments Flow Injection Analyzer (Model Quickchem IV). Water column particulate nitrogen (PN) and particulate phosphorus (PP) concentrations were determined once every 3 wk from material collected on filters. The PN analysis was conducted using a Carlo-Erba Model 1500 CHN Elemental Analyzer. PP analysis followed Solarzano & Sharp (1980). Gelman A/E filters were employed for all filtration procedures.

Eelgrass biomass was measured at the start and end of the experiment. At the start, biomass was determined by randomly subsampling the eelgrass shoots selected for transplantation. At the end of the experiment, aboveground biomass was estimated by clipping all aboveground eelgrass. Belowground biomass was estimated by sieving the sediments (5 mm mesh). The eelgrass was oven dried (60°C) to constant weight prior to dry mass determination. Drift (or unattached) macroalgal biomass was estimated once every 2 wk using random quadrats of 0.4 × 0.4 m (6 per mesocosm) or by sampling the entire mesocosm. On each occasion, the macroalgae were patted dry using paper toweling, weighed to estimate wet weight, and then returned to the appropriate mesocosm. Small subsamples (<1 g) were retained and dried (60°C) for determination of wet wt:dry wt ratios.

Epiphytic material on the eelgrass leaves was sampled once per month. Samples were taken from the fourth or fifth youngest leaves on randomly selected shoots. On each occasion, each leaf was gently cut underwater into an inverted glass tube. In the laboratory, the epiphytic material was scraped from the leaf and mechanically blended to reduce subsampling variability. Duplicate subsamples were filtered, dried (at 60°C) and weighed to estimate dry wt cm^{-2} of leaf. Dry mass values were corrected for total suspended solid concentrations in the water column.

Rates of total system daytime net production (*NP*) and night-time respiration (*R*) were measured 15 times through the experiment. The method was based on that of Odum & Hoskin (1958) and Oviatt et al. (1986). On each occasion, dissolved oxygen concentrations were measured in the water column shortly after sunrise when concentrations were lowest, just before sunset when concentrations were highest, and then again shortly after the following sunrise. Concentrations were measured using an Orbisphere model 2714 oxygen meter. Daytime NP was estimated by subtracting the oxygen concentration at dawn from the concentrations in late afternoon and then correcting for diffusion with the atmosphere. Night-time *R* was estimated by subtracting the final dawn concentration from the late afternoon concentration and again correcting for diffusion.

The exchange coefficient used to correct for diffusion was determined prior to the experiment during the engineering design of the mesocosm facility. It was determined by depressing the dissolved oxygen concentration in one of the mesocosms containing only filtered seawater to about 2.0 mg l^{-1}, and then measuring the rate of reaeration of the water column with the paddle wheel circulators rotating as under experimental conditions. The dissolved oxygen concentrations in the water column were lowered through addition of 300 g of sodium bisulfite.

The metabolism of the water column was measured 7 times. This was achieved by using clear acrylic metabolic chambers filled with mesocosm water and deployed in a central location within each mesocosm. Each chamber isolated approximately 3% of the tank water column (and associated plankton) from the sediments and rest of the mesocosm. The water column in each chamber was kept well mixed by 2 revolving propellers (7 rpm). Each chamber extended from slightly above the water surface to the sediments, allowing the phytoplankton to circulate through the vertical light gradient within each mesocosm. In each chamber, a thin polycarbonate sheet was floated on the water surface to eliminate oxygen exchange with the atmosphere. Daytime *NP* and night-time *R* were calculated as for the total system, except there was no need to correct for diffusion with the atmosphere.

Growth of the winter flounder and mummichogs added to the mesocosms was estimated as the difference in mean SL between the time of addition to the mesocosms and retrieval at the end of the experiment. For all variables, Fisher's Least Significant Difference (LSD) tests (SAS/STAT 1985) were used to determine which of the treatment means were significantly different.

RESULTS

N limitation

Comparison of the PO_4-alone and NO_3-alone mesocosms with the controls indicates that, under unenriched conditions, the systems and especially their phytoplankton were limited by N. Enrichment with NO_3 alone caused phytoplankton blooms (Fig. 3). During June and July mean chlorophyll *a* concentrations were 12 times greater than in the controls, and 3 times greater than in the mesocosms enriched with PO_4 alone (Fisher's LSD test, $p < 0.010$). The phytoplankton blooms apparently shaded out the under-

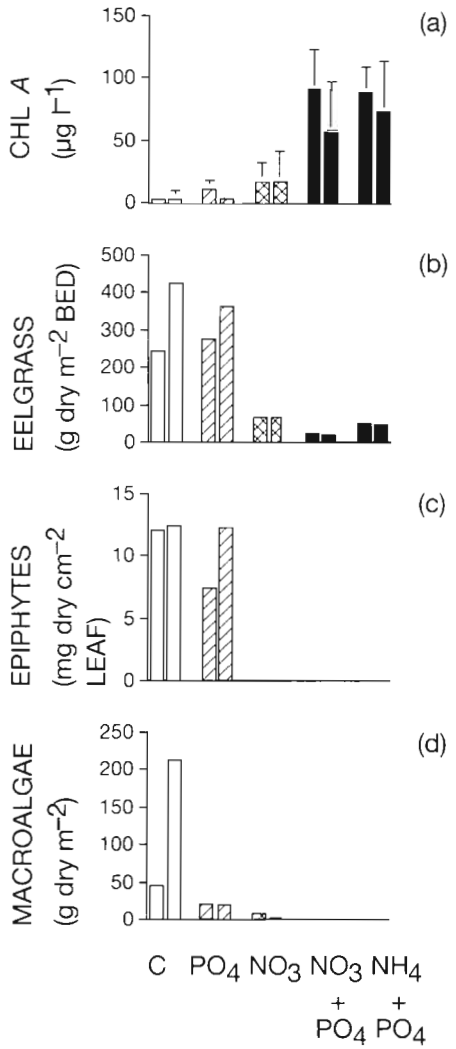

Fig. 3. Plant community shifts in the mesocosms of the 5 duplicate treatments; C: control. Chlorophyll *a* values are mean concentrations (+ SD) for 5 May to 30 September 1991 (n = 21). Eelgrass values are total (above- plus belowground) biomasses at the end of the experiment. Epiphyte values are final biomass values. Macroalgal values are peak biomass values in mid summer

lying eelgrass, macroalgae and epiphytes. In the PO_4-alone mesocosms, as in the controls, water column chlorophyll *a* concentrations remained low, the eelgrass beds survived and grew, and the biomasses of epiphytes and macroalgae (mainly *Cladophora* spp.) were high.

For both the NO_3-alone and the PO_4-alone treatments, concentrations of the added nutrient built up to levels greater than in the controls (Fig. 4). The build up was less for DIN in the NO_3-alone mesocosms, suggesting preferential utilization of DIN. In the PO_4-alone mesocosms, the concentrations of DIP averaged 7.2 µM, which is not significantly different from the value of 7 µM predicted assuming zero biological activity and 5% volume d^{-1} flushing (Table 2). In the NO_3-alone mesocosms, the average DIN concentrations (36 µM) were between 4 and 6 times lower than predicted.

This preferential utilization of DIN, and the apparent N limitation of the systems, is confirmed if the concentrations of the particulate forms of each of the nutrients are compared with the concentrations of the dissolved inorganic forms (Table 3). In the mesocosms enriched with PO_4 alone, the PP:DIP ratios were low (between 0.1:1 and 0.2:1), confirming minimal transformation of the added DIP. In the NO_3-alone mesocosms the opposite applied, with concentrations of PN exceeding those of DIN by factors of between 1.3:1 and 1.9:1

The metabolic responses of the systems were also indicative of N limitation, especially in the water column. In the mesocosms enriched with PO_4 alone, the rates of *NP*, both for the water column and the total system, were as in the controls (Fig. 5). In the mesocosms enriched with NO_3 alone, the rates of *NP* of the water column were significantly increased (Fisher's LSD test, $p < 0.010$). For total system *NP*, the mean rates in both NO_3-alone replicates were greater than in the controls, but the difference was not significant at $p = 0.05$ (Fisher's LSD test). The increase in water column *NP* was compensated for by increased benthic *R* as a result of sediment shading and the decay of eelgrass and macroalgae (Fig. 6).

For winter flounder *Plueronectes americanus* the rates of growth in the NO_3-alone and PO_4-alone mesocosms were higher than in the controls (Fisher's LSD test, $p < 0.0001$), but the rates of growth between the 2 single treatments were not significantly different (Fisher's LSD test, $p < 0.0001$; Fig. 7). Because of the large variation in growth among individuals within treatments, sampling of only 8 fish per mesocosm may have been insufficient to detect the probably greater growth of winter flounder in the NO_3-alone mesocosms.

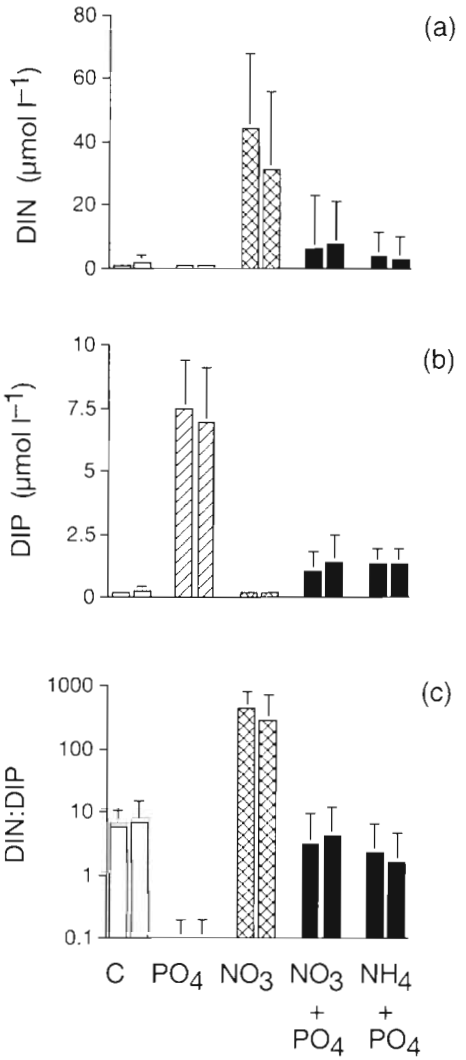

Fig. 4. Mean (+ SD) dissolved inorganic N and P (DIN and DIP) and molar DIN:DIP concentrations in the 5 duplicate treatments; C: control. Means calculated from 5 May to 30 September 1991. Note scale for ratios is logarithmic

Secondary P limitation

Comparison of all 4 of the combined N+P mesocosms with the mesocosms enriched with NO_3 alone suggests that the biomass and *NP* of the phytoplankton, and the *NP* of the total system, became secondarily P limited after enrichment with NO_3 alone. When this P was supplied, as in our combined N+P mesocosms, the secondary limitation by P was avoided and the effects of enrichment exacerbated.

Combined N+P enrichment led to phytoplankton blooms (*Nannochloropsis* spp.) that were on average 4 times more intense than in the mesocosms enriched with NO_3 alone (Fig. 3). The declines of the underlying eelgrass beds and macroalgal communities were also

Table 2. Comparison of observed and predicted water column concentrations (µM) of dissolved inorganic N and P (DIN and DIP) in the 2 replicates of the 5 treatments. Values are means for the period when concentrations would have reached equilibrium assuming no biological activity in the mesocosms and 5% volume d^{-1} flushing

Treatment	Predicted		Observed			
			Rep. 1		Rep. 2	
	DIN	DIP	DIN	DIP	DIN	DIP
Control	4.5	0.5	0.7	0.2	1.1	0.3
PO_4 Alone	4.5	7.0	0.5	7.4	1.0	6.9
NO_3 Alone	179	0.5	44	0.2	28	0.2
$NO_3 + PO_4$	179	7.0	0.8	0.9	6.8	1.3
$NH_4 + PO_4$	179	7.0	1.4	1.3	0.9	1.4

more severe. Despite the release of nutrients that probably accompanied the declines, the water column DIN and DIP concentrations were drawn down (presumably by phytoplankton) to levels only slightly higher than those in the controls (Fig. 4). The concentrations of DIN were less than 2% of those predicted in the absence of biological uptake, and the concentrations of DIP less than 20% (Table 2).

With combined N+P enrichment, and the increased transformation of the added nutrients, the water column concentrations of both PN and PP were increased (Table 3). Concentrations of PN were 1.7 times greater than in the NO_3-alone mesocosms, and PP concentrations 7.1 times greater than in the mesocosms enriched with PO_4 alone. The ratios of PN:DIN and PP:DIP were also much higher, confirming the increased efficiency of transformation of the added nutrients when N and P were added in combination.

The patterns of metabolic responses are also indicative of the development of secondary P limitation. The combined N+P mesocosms showed larger increases in water column and total system *NP* and *R* than in the mesocosms enriched with NO_3 alone (Fisher's LSD test, $p = 0.001$). The increased rates were seen mainly in the water column (Figs. 5 & 6), suggesting this was the site of development of the P limitation. Water column *NP* accounted for between 90 to 140% of total system *NP* in the NO_3-alone mesocosms, compared to 190 to 230% in the combined N + P mesocosms.

For winter flounder, the average rates of growth were significantly greater in the N + P systems than in the NO_3-alone mesocosms (Fig. 7; Fisher's LSD test, $p = 0.001$). For mummichogs, the rates of growth were not significantly greater than in the NO_3-alone mesocosms, but were greater than in the controls (Fisher's LSD test, $p = 0.04$). Evidence is available that suggests combined N + P enrichment led to larger populations of filter-feeding amphipods (*Corophium* spp.) and that these populations may have supported the increased growth of winter flounder and mummichogs (S. Nixon unpubl.).

Secondary light limitation of benthic plants

The responses of the eelgrass and macroalgae in the NO_3-alone and combined N+P treatments suggest these benthic plant components became secondarily light limited when the systems were supplied with N, especially in combination with P. In both, but especially the combined N+P treatments, the phytoplankton blooms reduced light levels at the sediment surface to below the light saturation levels for both eelgrass (100 µE m^{-2} s^{-1}; Dennison & Alberte 1982) and *Cladophora* sp. (30 to 40 µE m^{-2} s^{-1}; Hodgkin & Birch 1982).

As a consequence, the eelgrass beds declined and the *Cladophora* sp. mats that were observed in the controls and PO_4-alone mesocosms failed to develop. In the NO_3-alone mesocosms, the average eelgrass biomass at the end of the experiment was one-fifth of that in the controls. In the combined N+P mesocosms, the final eelgrass biomass was a factor of 2.0 lower than in the NO_3-alone mesocosms.

Form of DIN

For none of the variables monitored were we able to detect a significant difference between the com-

Table 3. Mean concentrations (µM) of suspended particulate nitrogen (PN) and phosphorus (PP) in the water columns of the 5 replicated treatments. Values are means for 6 May to 30 September 1991. n = 4 per mesocosm

	Control		PO_4 alone		NO_3 alone		$NO_3 + PO_4$		$NH_4 + PO_4$	
	Rep. 1	Rep. 2	Rep. 1	Rep. 2	Rep. 1	Rep. 2	Rep. 1	Rep. 2	Rep. 1	Rep. 2
Particulate										
PN	10 ± 8	9 ± 6	18 ± 10	24 ± 27	58 ± 56	52 ± 36	94 ± 39	100 ± 19	77 ± 46	111 ± 63
PP	0.6 ± 0.4	0.4 ± 0.4	1.2 ± 0.7	0.8 ± 0.5	1.7 ± 0.9	1.0 ± 0.5	7.3 ± 2.3	5.3 ± 2.8	8.4 ± 2.4	7.5 ± 2.0
Particulate:dissolved inorganic										
PN:DIN	14	8	36	24	1.3	1.9	118	15	55	123
PP:DIP	3	1.3	0.2	0.1	9	5	8	4	6	5

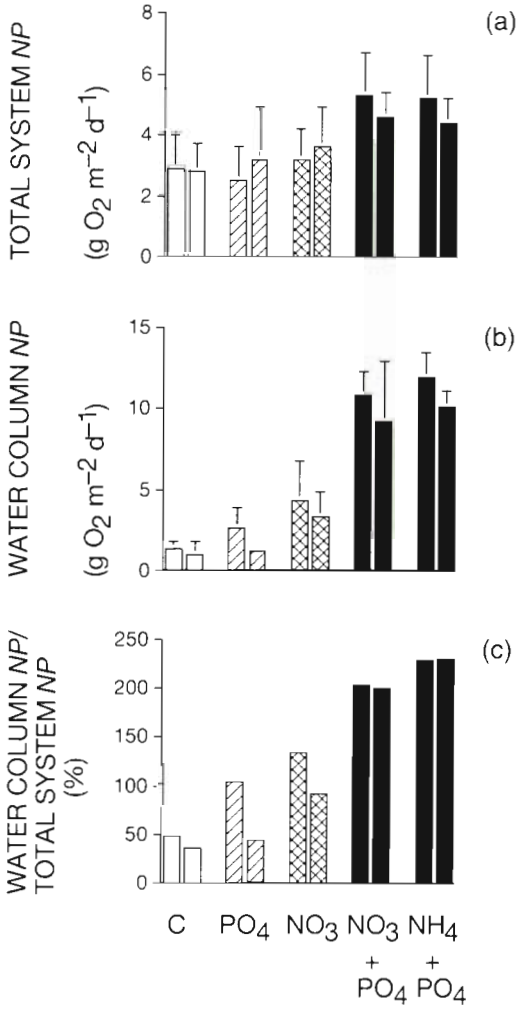

Fig. 5. Mean (+ SD) total system daytime net production (*NP*), water column *NP* and percentage contribution of water column *NP* to total system *NP* in the 5 duplicate treatments; C: control

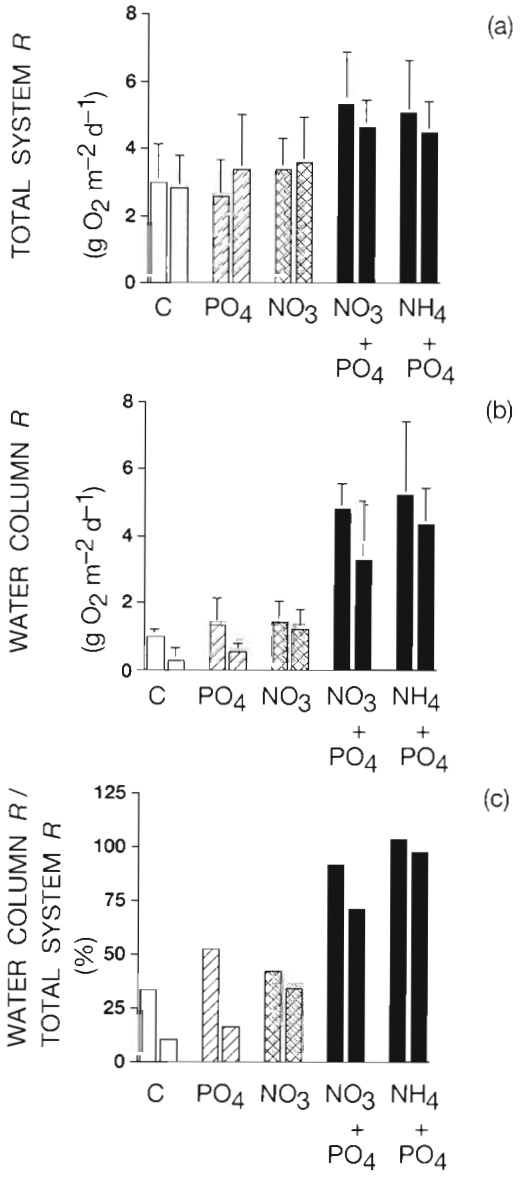

Fig. 6. Mean (+ SD) total system daytime respiration (*R*), water column *R* and percentage contribution of water column *R* to total system *R* in the 5 duplicate treatments; C: control

bined N + P mesocosms enriched with NO_3 and the combined N + P mesocosms enriched with NH_4. The absence of a difference indicates that the form of DIN is less important in limiting biomass and production in these systems than is the elemental composition of the nutrients.

DISCUSSION

The results of the experiment indicate that the issue of nutrient limitation of lagoons is complex. The limiting factor apparently depends on whether it is the entire system, or its phytoplankton or benthic plant components that are being considered. Under unenriched conditions, the *NP* of the total system and especially of its phytoplankton were limited by, and therefore most sensitive to, inputs of N. The experiment indicates that the limiting factor apparently also shifts depending on the loading of N to the lagoon. When our mesocosms were enriched with N alone, the phytoplankton blooms that resulted induced 2 forms of secondary limitation — P limitation of total system *NP* and of phytoplankton biomass and production, and light limitation of benthic plants. When P was supplied with this N, the secondary P limitation of the phytoplankton was ameliorated, and the light limitation of the benthic plants exacerbated.

Based on the responses of our mesocosms, we envisage that, as N loadings to the natural lagoons increase, the systems will pass through successive shifts in limi-

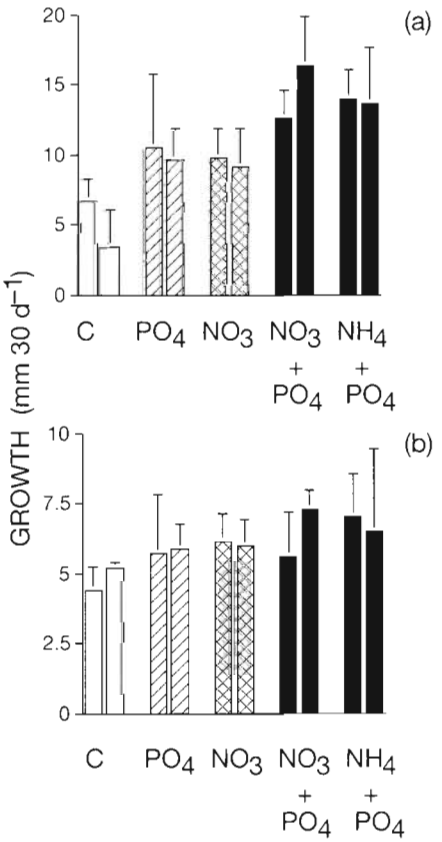

Fig. 7. Mean (+ SD) rates of growth of (a) winter flounder *Pleuronectes americanus*, and (b) killifish *Fundulus heteroclitus* in the 5 duplicate treatments; C: control

tation. Critical N loadings will be reached where total system *NP* and phytoplankton biomass and *NP* will become limited by P. Equivalent, but likely different, critical loadings will exist where the eelgrass and macroalgae will shift from nutrient to light limitation. Further experimentation is required to identify the specific loadings at which these shifts occur, but the responses in our NO_3-alone mesocosms suggest that for both the nutrient and light limitation shifts the critical loadings lie between the loadings to our controls (130 µmol N m^{-2} d^{-1}) and the loadings to our NO_3-alone mesocosms (8300 µmol N m^{-2} d^{-1}).

Nowicki & Nixon (1985) have provided evidence of P limitation of the phytoplankton in Potter Pond lagoon, Rhode Island. This lagoon, like the other Rhode Island lagoons, is currently enriched with DIN, but not DIP (Nixon et al. 1982), suggesting its P limitation represents a secondary phenomenon analogous to the condition in our NO_3-alone mesocosms. If this applies, this would suggest that the critical loading demarcating the shift from N to P limitation, for lagoons enriched with NO_3 alone, lies between 130 µmol N m^{-2} d^{-1}, the loading to our controls, and 960 to 2550 µmol N m^{-2} d^{-1}, the current loadings to the Rhode Island lagoons (Lee & Olsen 1985).

Our demonstration of N limitation in unenriched lagoons is similar to the demonstration of N limitation in temperate marine bays by Oviatt et al. (1995) using the Marine Ecosystems Research Laboratory (MERL) mesocosms. In the MERL mesocosms, as in ours, enrichment with N alone increased phytoplankton biomass and *NP* and total system *NP*, but these variables were unaltered by enrichment with PO_4 alone. The synergistic effects of combined N+P enrichment were not, however, observed in the MERL mesocosms, suggesting they were not secondarily limited by P. The MERL mesocosms were almost 5 times deeper than ours, and it may have been that when enriched with N alone, phytoplankton biomass and total system *NP* in the MERL mesocosms became secondarily limited by light rather than by P.

Thus, while both types of marine systems appear to be N limited when unenriched and to exhibit shifts in limitation when N loadings are increased, the nature of the shifts and the critical loadings at which they occur appear to be different. For both types of systems, the extent of limitation by any of the factors will likely depend not only on the loadings of N, but also on the relative loadings of P. In the present experiment, the N and P were added at single relatively high loadings at three N:P ratios (Table 1; 0.2:1, 12:1, and 250:1). Because the shifts in limitation determine the sensitivity of the systems to different forms and levels of enrichment, it may be informative to better quantify, for both types of systems, the shifts through a greater number and combination of N loadings and N:P ratios.

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