Internat. Rev. Hydrobiol.	**85**	2000	2–3	359–375

B. Worm[1]*, T. B. H. Reusch[2] and H. K. Lotze[1]

[1] Institut für Meereskunde, Düsternbrooker Weg 20, D-24105 Kiel, Germany
[2] Max-Planck-Institut für Limnologie, August-Thienemann-Str. 2, 24306 Plön, Germany

In situ Nutrient Enrichment: Methods for Marine Benthic Ecology

key words: benthic communities, field experiment, nitrogen, nutrient limitation, phosphorus

Abstract

Nutrient enrichment of marine sediments or the water column has been used to study plant nutrient limitation and its cascading effects on community structure. Here we develop methodological recommendations for *in situ* enrichment. We review 18 published enrichment methods. Nutrient concentrations varied through time and among sites, with sediment depth, distance from the source, fertilizer type and load. Combining available data, we could predict an increase in sediment porewater phosphate ($r^2 = 0.48$) but not ammonium ($r^2 = 0.07$) concentrations in a multiple regression model. In three comparative field experiments we applied a coated slow-release fertilizer in the sediment and the water column and followed nutrient concentrations over time. We recommend coated fertilizer pellets, because they provide gradual nutrient release, allow for realistic nutrient gradients, and even application but we emphasize that nutrient concentrations need to be monitored through time.

1. Introduction

Nutrient supply sets the productivity potential of primary producers in aquatic ecosystems. When light and temperature are adequate and loss rates do not exceed gains, the availability of macronutrients (N and P) controls algal and seagrass productivity and biomass (reviewed by Short, 1987; Hecky and Kilham, 1988; Howarth, 1988). Competition for limiting nutrients determines algal community structure (Tilman, 1977; Fong *et al.*, 1993) with potential effects on higher trophic levels (bottom-up control, Menge, 1992). In turn, consumers can control species composition and abundance at lower trophic levels (top-down control, Menge, 1992; Worm and Chapman, 1998; Worm *et al.*, 1999). *In situ* enrichment experiments are considered a superior tool to analyze the causes and effects of nutrient limitation in ecosystems (Binkley and Vitousek, 1991). Most importantly, such experiments can be used to generate predictions about the effects of increasing coastal eutrophication, which is a rapidly-growing world-wide concern (Nixon, 1990, Carpenter *et al.*, 1998).

Like most field experiments, *in situ* enrichment studies combine advantages (realism, replication) with disadvantages (mostly small scale, low precision). Comparative studies at eutrophic versus oligotrophic sites (Hauxwell *et al.*, 1998; McGlathery, 1995) overcome the problem of scale, since large areas and the response of whole ecosystems to increasing nutrient availability can be investigated. However, like all "natural experiments" such studies risk confounding nutrient effects with other effects (e.g. exposure, water flow, McGlathery, 1995). This is even more severe when the factor "nutrients" is not replicated, i.e.

---

* present address: Biology Department, Dalhousie University

Halifax, Nova Scotia, Canada, B3H 4J1

when only one eutrophic and one oligotrophic site are compared. Laboratory or mesocosm (aquaria or tank) studies overcome the problem of low precision, but allow only limited inference on natural systems. Ideally, comparative and laboratory approaches should be combined with replicated field experiments (NIXON, 1990; LOTZE, 1998; WORM *et al.*, 1999).

All marine autotrophs derive nutrients directly from the water column. Seagrasses and some tropical macroalgae (Caulerpales) can use additional nutrient pools present in the sediment (SHORT and MCROY, 1984; WILLIAMS, 1984). A number of methods for nutrient enrichment of the water column and the sediment have been developed. However, there appears to be no consensus on the relative merits or constraints of available methods. The goal of this paper is to gather hitherto scattered comparative information on the effectiveness and limitations of methods for *in situ* nutrient enrichment and to develop recommendations for the use of these methods. First we review and analyze published data. Then we describe our own enrichment experiments of the sediment and water column in order to improve some of the reviewed methods.

2. Literature Review

In 33 studies we found 18 different techniques for benthic nutrient enrichment (Table 1). Six different types of fertilizer were applied and 13 different modes of application were developed. Nutrients were applied at a single time or at mostly irregular intervals throughout the experiment (ranging from 1 d to 1 yr). Fertilizer loads varied widely between approximately 20 g–2000 g N or P m^{-2}. Rationales for choosing a specific technique or loading were rarely clarified. Most studies tested for nutrient limitation of seagrass ($N = 15$) or macroalgae ($N = 5$) or the relative effects of nutrients and consumers on plant community structure ($N = 6$). Almost half of the studies ($N = 15$) did not monitor the treatment levels (nutrient concentrations on fertilized versus unfertilized plots) at all and only 6 studies report more than one measurement of nutrient concentrations through time. However, in all but one publication (DENNISON *et al.*, 1987) some nutrient effects on the plants or the community were reported, which was frequently used as evidence that the enrichment procedure was successful and plant growth is nutrient limited. In the following we compare the available evidence for the effectiveness of the various methods.

2.1. Sediment Enrichment

Sediment nutrient enrichment was most frequently attempted using coated slow-release fertilizer (studies 1–10, Table 1). Typically Osmocote (Sierra Chemical Company, Milpitas, CA, USA) was used. These fertilizer pellets (2–5 mm diameter) are made of various nutrients in variable combinations (N, P, N-P, N-P-K). Nutrients are coated with a semipermeable membrane to allow for gradual release. Coated fertilizers were applied plain by burying the pellets in the sediment or enclosed in bags or peat pots and then buried. Mean application depth varied between 0.75 cm (UDY and DENNISON, 1997) and 12 cm (ERFTEMEIJER *et al.*, 1994). Fertilizer loads typically ranged between 20–200 g N m^{-2} and 20–40 g P m^{-2}. Nitrogen concentrations in the sediment porewater were enriched up to factor 138, phosphate concentrations up to factor 18 compared with control plots (Table 1). In 4 out of 5 studies where enrichment effects on the porewater were quantified, nutrient concentrations were apparently not increased by the fertilizer treatment some of the experimental plots. However, this may be due to insufficient porewater sampling. If measurements of nutrient concentrations in experimental plots were obtained, this was done at only one date per experiment and typically at the end of the experiment. Increases in nutrient availability before or after this measurement were inevitably missed. In only one study (BULTHUIS *et al.*, 1992) were nutrient concentrations monitored over time (6 dates, monthly intervals). Porewater ammonium (one initial dose of 100 g m^{-2}) was enriched 60-fold (1080 μmol l^{-1} in fertilized plots) after 30 d, and gradually decreased thereafter. After 5 months a two-fold increase in porewater ammonium was still detectable. Phosphate (initial dose 20 g m^{-2}) only showed a 1.4-fold increase after 1 month (7 μmol l^{-1}) and a 9-fold increase over ambient concentrations after 4 months (47 μmol l^{-1}). At three additional sites ammmonium remained enriched 4- to 10-fold (46–177 μmol l^{-1}) 5 months after fertilization but was depleted at a fourth site. Phosphate was depleted at all sites after 5 months. This might not indicate problems with the fertilizer, rather it shows that nutrient enrichment levels can vary (1) among sites and (2) over time.

Fertilizer stakes (typically Jobe Tree Spikes^{TM}, Lexington, KY, USA) were used as a second sediment enrichment method (studies 11–14, Table 1). Stakes were simply stuck into the sediment. The average loads which were chosen tended to be high, ranging around 30–600 g N m^{-2} and 30–130 g P m^{-2}. Porewater nutrient concentrations after enrichment with fertilizer stakes were in a similar range as those from coated fertilizers for nitrogen, but higher for phosphorus. Nitrogen was enriched by up to a factor of 144 and phosphate by up to a factor of 457 (Table 1). Variable or no responses of porewater nutrient concentrations to enrichment were found in 2 out of 4 studies. In one study, porewater sampling was done at four dates across a two-year period (WILLIAMS, 1990). Porewater ammonium concentrations increased steeply within 1 week after fertilization (6-fold, 300 μmol l^{-1}) and declined gradually over a 10-months period. In a mangrove study, fertilizer stakes lasted for about 1 year (FELLER 1995). This may indicate that fertilizer stakes allow for longer time lags between replacements than other methods.

There are only isolated observations on the effectiveness of other methods than the previously described (Table 1). In most cases, nutrients (e.g. NH_4NO_3) were enclosed in a semipermeable matrix. Nutrients enclosed in agar poured into petri dishes may elevate porewater concentrations when delivered at high loads (500 g N m^{-2}, 100 g P m^{-2}, MURRAY *et al.*, 1992). In another study, monthly loads of 100 g N and 20 g P m^{-2} were enclosed in Kleenex tissue and buried at 10 cm depth in a seagrass meadow. Porewater nutrients increased with increasing sediment depth (0–20 cm) up to 60-fold compared with controls (BULTHUIS and WOELKERLING, 1981). In an unusual approach, POWELL *et al.*, (1989) used natural nutrient sources to demonstrate seagrass nutrient limitation. Replicated stakes were installed which attracted seabirds defecating on experimental plots. Depending on sediment depth, NH_4 increased by 70% and PO_4 15-fold following 2 years of enrichment. In two other studies large sediment diffusers were used. In order to analyze sediment ammonium effects on seagrass, DENNISON *et al.*, (1987) used two-compartment plexiglas chambers. The outer reservoir compartment was flushed every 2 days with seawater of defined ammonium concentration, the inner chamber contained sediment and eelgrass and was connected to the outer chamber through diffusion ports. FLOTHMANN and WERNER (1992) analyzed nutrient limitation of soft-sediment microphytobenthos. They injected nutrient solutions into perforated PVC pipes, which were buried in the sediment. These two approaches provided good control of porewater nutrients but had the disadvantage that large artificial structures were introduced into the sediment.

2.2. *Water Column Enrichment*

Nutrient enrichment of the water column was attempted less often (11 studies) than sediment fertilization (22 studies) and information on the effectiveness of various methods is scarce. CHAPMAN and CRAIGIE (1977) introduced porous flower pots as nutrient diffusers in

Table 1. Overview of published methods for water column or sediment enrichment with nitrogen (N), phosphorus (P) or both (N+P).

Study no.	Method	Rationale of the experiment
	A. Sediment enrichment	
1	coated fertilizer pellets	nutrient limitation of seagrasses
2	coated fertilizer pellets	nutrient limitation of seagrasses
3	coated fertilizer pellets	nutrient limitation of seagrasses
4	coated fertilizer pellets	nutrient limitation of seagrasses
5	coated fertilizer pellets	nutrient limitation of seagrasses
6	coated fertilizer pellets	nutrient limitation of seagrasses
7	coated fertilizer pellets	nutrient limitation of seagrasses
8	coated fertilizer pellets in bags	nutrient limitation of seagrasses
9	coated fertilizer pellets in bags	nutrient limitation of seagrasses
10	coated fertilizer pellets in peat pots	nutrient limitation of seagrasses
11	fertilizer stakes	nutrient competition among seagrasses
12	fertilizer stakes	effects of nutrients and grazing on mangrove community
13	fertilizer stakes	effects of nutrients on seagrass-macroalgae interaction
14	fertilizer stakes	effects of nutrients on seagrass-macroalgae interaction
15	non-coated fertilizer dissolved	nutrient limitation of seagrasses
16	non-coated fertilizer in agar	nutrient limitation of seagrasses
5	non-coated fertilizer in agar	nutrient limitation of seagrasses
17	non-coated fertilizer in mesh bag and tube	effects of nutrients and grazing on seagrass community
18	non-coated fertilizer in Kleenex tissue	nutrient limitation of seagrasses
19	non-coated fertilizer in dialysis tubing	effects of nutrients and grazing on mangrove community
20	non-coated fertilizer in sediment diffusors	nutrient limitation of seagrasses
21	non-coated fertilizer in sediment diffusors	nutrient limitation of microphytobenthos
4	fish meal	nutrient limitation of seagrasses
22	bird faeces	nutrient limitation of seagrasses
	B. Water column enrichment	
23	dissolved nutrients in plastic bags	effects of nutrients and grazing on coral community
24	dissolved nutrients in plastic bags	nutrient limitation of macroalgae
25	non-coated fertilizer in porous flower pots	nutrient limitation of macroalgae
26	non-coated fertilizer in porous flower pots	nutrient limitation of seagrasses and macroalgae
27	non-coated fertilizer in porous flower pots	effects of nutrients and grazing on coral community
28	non-coated fertilizer in porous flower pots	effects of nutrients on seagrass epiphytes
17	non-coated fertilizer in mesh bag and tube	effects of nutrients and grazing on seagrass community
15	non-coated fertilizier in agar	nutrient limitation of macroalgae
29	non-coated fertilizer in agar in porous flower pots	effects of nutrients and grazing on intertidal community
30	dissolved bird faeces	nutrient limitation of macroalgae
31	dissolved nutrients plain	effects of nutrients on kelp bed
	C. Sediment and water column enrichment	
32	fertilizier stakes	effects of nutrients and grazing on seagrass community
33	fertilizier stakes	effects of nutrients and grazing on tideflat community
33	non-coated fertilizier dissolved	effects of nutrients and grazing on tideflat community
17	non-coated fertilizier in mesh bag and tube	effects of nutrients and grazing on seagrass community

Abbreviations: R = Response, N = No Response, VA = Variable response (sometimes no effect), Repl. = Replicate measurements through time.

Source	Nutrient effects on plants/community			Repl.	Response of nutrient conc.		Relative increse of nutrient concentrations	
	N+P	N	P		N	P	N	P
Orth (1977)	R							
van Lent (1995)		R		1	VA		3.0	
Erftemeijer *et al.* (1994)		R	N	1	VA	VA	1.1	1.7
Pulich Jr. (1985)	R							
Perez *et al.* (1991)		N	R					
Udy and Dennison (1997)		R	R	1	R	R	97.2–138.5	8.1–18.3
Short *et al.* (1990)		R	R					
Kenworthy and Fonseca (1992)		R	N		VA	N		
Bulthuis *et al.* (1992)		R	R	6	VA	VA	1–61.1	1–9.4
Fonseca *et al.* (1994)		R	R					
Williams (1987)	R			1	R	R	144.1	457.1
Feller (1995)	R			1	R	R	6.9	9.0
Williams (1990)	R			4	VA		1.4–3.6	
Ceccherelli and Cinelli (1997)	R			1	VA		8.6	2.8
Pedersen (1995)	R							
Perez *et al.* (1991)		N	R					
Murray *et al.* (1992)		N	R	1	VA	R	2.0	9.5
Williams and Ruckelshaus (1993)	R			1	R		7.5–14.7	
Bulthuis and Woelkerling (1981)		R	R	1	R	R	4.8–352	6.5–85.5
Feller (1995)		R	R	1	R	R	61.0	26.7
Dennison *et al.* (1987)		N		1	R		25–500	
Flothmann and Werner (1992)	R			7	R	R	2.0–10.0	1.3–2.3
Pulich Jr. (1985)	R							
Powell *et al.* 1989	R			1	R	R	1.7	15.4
Miller and Hay (1996)	R							
Lapointe (1989)	R			1	R	R	100–300	170–600
Chapman and Craigie (1977)	R							
Harlin and Thorne-Miller (1981)		R	R	1	R	R	1.4–9.4	5.0 –8.0
Hatcher and Larkum (1983)	R			1	R		8.0–11.2	
Coleman and Burkholder (1995)	R			4	R		2.7–25.2	
Williams and Ruckelshaus (1993)	R			5	R		1.9–150	
Pedersen (1995)		R	R					
Wooton *et al.* (1996)	R							
Bosman *et al.* (1986)	R							
North *et al.* (1980)	R							
McGlathery (1995)	R			6	R	R	0.5–12.2	2–3.4
Posey *et al.* (1995)	R							
Posey *et al.* (1995)	N							
Williams and Ruckelshaus (1993)	R			5	R		6.3–15.2	

a kelp bed. Large quantities of $NaNO_3$ (12 kg wk^{-1}) dissolved rapidly (<1 wk) from the pots, but no water column nutrient data are reported. Yet plant growth increased following the enrichment treatment. This method was modified for nitrogen and phosphate enrichment and applied in seagrass beds (HARLIN and THORNE-MILLER, 1981) and coral reef "microatolls" (HATCHER and LARKUM, 1983). In the seagrass study total loads were also in the range of several kg m^{-2} $week^{-1}$. Water column nutrients were elevated 2 d after application at 2 of 3 sites, but were quite variable (Table 1). In the reef study a 2 kg batch of nitrogen fertilizer lasted several weeks, possibly because of limited water exchange in the microatolls. Twelve days after pot deployment nitrogen was enriched by 100–300 µmol l^{-1} (<20 cm distance from pots). However, there was a steep spatial gradient in nutrient concentration. At 1 m distance nutrients were diluted by >1 order of magnitude (HATCHER and LARKUM, 1983). Moreover, water column nutrient concentrations when elevated by flower pot diffusers decreased steeply through time (COLEMAN and BURKHOLDER, 1995), with very high concentrations shortly after pots were exchanged (731 µmol l^{-1}), decreasing to 30 µmol l^{-1} after 1–2 days, 8 µmol l^{-1} after 3 days and 1 µmol l^{-1} after 6 days. Similar steep declines over time were found by WILLIAMS and RUCKELSHAUS (1993), who used NH_4Cl held in a nylon mesh bag inside a perforated centrifuge tube (80–107 g N m^{-2}). Tubes were replaced every 1–4 d. In three successive experiments water column ammonium was enriched 30–50-fold after 0.5 h, but quickly declined to ambient concentrations 1–4 days after replacement.

Clearly, the application of non-coated fertilizer generally requires high nutrient input per unit area because of rapid dissolution. This can cause considerable pollution. NORTH *et al.*, (1980), added 1 ton NH_4SO_4 per day for 15 d periods on several experiments, but no information was provided on the effects on nutrient concentrations in the fertilized kelp bed. To study the interaction of nutrient and grazing effects on a coral community 170 g of NPK garden fertilizer were dissolved approximately weekly for 1–2 h into seawater-filled plastic bags that surrounded 0.25 m^{-2} caged plots (MILLER and HAY, 1996). Also, LAPOINTE (1989) incubated plants in plastic bags for 6 h every 3 d, but again pulse concentrations had to be unrealistically high to compensate for short incubation time (100–600-fold enrichment).

2.3. Combined Enrichment

In seagrasses and rhizomatous algae, combined enrichment of the sediment and the overlying water column may be of interest because these plants can use both nutrient pools. In a Bermuda seagrass meadow, MCGLATHERY (1995) placed fertilizer stakes halfway into the sediment, so that the upper part dissolved into the water column. Nutrients were added at 59 g N m^{-2} and 15 g P m^{-2} (refertilized every 2 weeks). Only water column nutrients were monitored and increased up to 10-fold. However, this effect was variable among 2 sites, possibly as a function of water motion. Enrichment effects were remarkably constant over time at the less exposed site (2.2–4-fold increase over 3 months, 6 measurements through time). WILLIAMS and RUCKELSHAUS (1993) fertilized eelgrass plots in a factorial design (water column alone, sediment alone, water column and sediment, control). They used NH_4Cl (80–107 g N m^{-2}) held in a nylon mesh bag inside a perforated centrifuge tube. Water column but not sediment tubes were replaced every 1–4 d. Water column results are reported above. The sediment was enriched with ammonium 7–15-fold compared with controls.

2.4. Regression Analysis

To summarize variables that may affect the nutrient concentrations in enrichment experiments, we combined measured nutrient data from 17 studies that provide information on initial load [g N or P m^{-2}], depth of application [cm sediment] or distance to the diffuser [cm water column] and time since enrichment [d]. Data from sediment enrichment studies ($N = 12$) and water column studies ($N = 5$) were treated in separate analyses, because of very different nutrient concentrations and experimental time frames: nutrient data were collected 6–1000 d after fertilization (mean 132 d) in sediment studies and 0.02–12 d (mean 4.3 d) after fertilization in water column studies. For each measurement through time we calculated absolute increase [μmol l^{-1} in fertilized plots – μmol l^{-1} in control plots] and relative increase [μmol l^{-1} in fertilized plots/μmol l^{-1} in control plots] as the dependent variables. Relative increase consistently showed better statistical fits than absolute increase, thus we only report the former. Because of an overall scarcity of nutrient data, we used multiple measurements through time were provided. Because such time-series data may not be independent measurements, the results of this analysis should to be interpreted with caution. In a separate analysis we investigated whether there were statistical differences among the different sediment enrichment methods (coated fertilizer pellets plain, in bags, fertilizer stakes, nutrients in agar, nutrients in dialysis tubing) or water column enrichment methods (flower pots, dialysis tubing, stakes). We used ANOVA with "enrichment method" as the main effect and absolute increase and relative increase as dependent variables. These analyses may be interpreted with caution because of low sample sizes and an unbalanced design ($n = 2$ to $n = 9$).

Data were log-transformed to fulfil the assumption of homogeneity of variances.

For sediment porewater data, none of the selected variables explained a significant part of the variance in porewater ammonium increase (multiple regression, overall $r^2 = 0.07$, $n = 34$, $P = 0.52$). However, phosphate load, time since application and depth of application had significant effects on porewater phosphate increase (multiple regression, overall $r^2 = 0.48$, $n = 22$, $P = 0.008$). The multiple regression model for porewater phosphate predicted:

Equation 1. $\text{Relative increase} = 4.011 + 0.073\ \text{load} + 0.024\ \text{time} - 0.498\ \text{depth}$

where "load" is initial phosphorus load in g P m^{-2} ($P = 0.015$), "time" is measured in days since fertilization ($P = 0.009$) and "depth" is depth of application in cm ($P = 0.195$). The positive slope for the time effect is somewhat unexpected and indicates rising phosphate concentrations over the time frame of most studies (mean 132 d from fertilizer application to nutrient sampling). Logarithmic transformation of the dependent variable resulted in a slightly better fit ($r^2 = 0.49$) and a significant effect of depth of application ($P = 0.038$). Differences among application methods were insignificant for ammonium ($F_{4,21} = 0.8$, $P = 0.56$) but significant for phosphate ($F_{4,17} = 3.7$, $P = 0.025$). Phosphate concentrations in experiments using fertilizer stakes (mean 154-fold increase) were significantly higher compared with experiments using fertilizer pellets (mean 3–7-fold increase using plain pellets or pellets in bags respectively. Similar analyses for water column nutrients revealed no significant relationships (multiple regression, $n = 15$, all $P > 0.15$, ANOVA, $P > 0.15$).

3. Method

We performed three *in situ* enrichment experiments in order to reveal whether coated fertilizer pellets are a useful tool for long-term nutrient enrichment of the sediment and the water column. Two experiments were located in the outer reaches of fjords in the Western Baltic. Both sites (Friedrichsort, Kiel Fjord 54°23′ N, 10°12′ E and Maasholm, Schlei Fjord, 54°41′ N, 10°0′ E) are strongly influenced by cultural eutrophication, with high nutrient concentrations in the winter (usually >100 μmol l^{-1}

$NO_3 + NH_4$, > 10 μmol l^{-1} PO_4), but low nutrient availability from May-August (usually all macronutrients <1 μmol l^{-1}). Both sites are protected and maximum wave height is 0.3–0.5 m. The third experiment was conducted at an exposed (maximum wave height 2.5 m) and less eutrophic site (Oehe, 54°42′ N, 10°0′ E, winter nutrient concentrations usually <30 μmol l^{-1} $NO_3 + NH_4$, <3 μmol l^{-1} PO_4), 3 km N of the mouth Schlei Fjord. Water temperature ranged between 0°C in winter and 25°C in summer. Salinity fluctuated from 12–20 PSU. Lunar tides are negligible in the Baltic compared to irregular wind-driven sea level changes with an amplitude of ± 50 cm around mean water level.

3.1. *Sediment Enrichment*

We followed porewater nutrient dynamics after sediment enrichment with a coated slow-release fertilizer. The experiment was run from May-October 1994 at Friedrichsort, Kiel Fjord. The sediment consisted of medium-grained silicate sand which is low in organic content. For a detailed description of the site refer to Reusch *et al.* (1994).

The experiment was established at 2 m depth. Sixteen circular plots (80 cm across) were established within 3 m of each other. Prior to the experiment the area was cleared of rare mussel clumps and seagrass shoots, then replanted with seagrass (*Zostera marina*) at defined densities (7–18 plants per plot). Seagrass density had no effect on sediment nutrient concentrations and is not further considered here. For nutrient enrichment we used a coated slow release fertilizer (Plantacote Depot, Urania Agrochem, Hamburg, Germany) that is very similar to the Osmocote fertilizer commonly described in the literature. It consists of 14% N (5.7% NO_3 and 8.3% NH_4), 9%P (P_2O_5) and 15% K_2O, the latter which we assumed to have no effect due to the high K-level of seawater. The fertilizer is enclosed in 3–5 mm pellets coated with a polyurethane membrane. Different coatings allow for different release periods (4 months, 6 months or 8 months, in soil at 20°C). We first applied a 4-month (hereafter 4-M) and later in the year a 8-month (8-M) release time fertilizer, both at 150 g N and 110g P m^{-2} On 12 May, the 4-M fertilizer was evenly distributed across enrichment plots (n = 8) and gently massaged into the upper sediment layer (0–10 cm depth). On 5 August, when nitrogen enrichment from the first fertilization had ceased, the procedure was repeated with 8-M fertilizer. Control plots (n = 8) were mechanically treated in the same way as a procedural control. Control and enrichment treatments were spatially arranged in 4 blocks following a randomized block design. All plots were located within 3 m distance to each other in order to avoid interaction.

Sediment porewater was sampled monthly in triplicate in all experimental plots using 10 ml plastic syringes. A plastic tip was perforated and wrapped with 20 μm mesh gauze. At 3 randomly chosen points within a plot tips were inserted 5 cm into the substratum using a new syringe for each subsample. Samples were cooled on board the dive boat and deep frozen 1–2 h afterwards. Since the concentration of ammonium in the porewater is generally >20 μmol l^{-1}, changes in concentration due to freezing were considered non-significant. In the laboratory samples were diluted 1 : 5 with distilled water and analyzed for dissolved ammonium and soluble reactive phosphate (Grasshoff, 1976). We did not analyze for nitrate because it is reduced to ammonium in largely anoxic sediments and was always near the detection limit at this site (Reusch *et al.*, 1994).

We analyzed porewater concentrations by ANOVA for randomized blocks with enrichment (enriched vs control) as the independent variable. Subsamples within plots were pooled for the analysis. Where it was necessary data were log- or square-root-transformed to meet the assumption of homogeneity of variances (Cochran's Test).

3.2. *Water Column Enrichment*

We applied a coated fertilizer for water column enrichment. This novel method was developed as part of a recent attempt to analyze the relative influence of nutrients and grazers on macro- and microalgal community structure in the Baltic (Lotze *et al.*, 1999, Worm *et al.*, 1999, H. Hillebrand *et al.*, unpublished manuscript). Because previous methods gave variable results at different sites and seasons (see review above) we ran the experiment from February-October 1998 at two sites that differed in exposure and nutrient regime (Maasholm and Oehe, see description above). Average water depth in the experiment was 0.8–1 m. Plantacote Depot^{TM} 6-M slow release fertilizer was applied using diffuser bags made from polyethylene mesh with 1 mm mesh size. Diffuser bags of variable length (2.5, 5, 10, 20, 40, 80 cm length × 2.5 cm width) were filled with coated fertilizer. Fertilizer mass increased proportionally with increasing diffuser length (fertilizer mass [g] = 4* diffuser length [cm]). Nutrient diffusers were placed inside and outside of cages (25 × 25 × 25 cm), covered with 1 mm polyethylene mesh. The presence of these cages had no effect on water column nutrient availability (ANOVA, $P > 0.2$ for all nutrients) and is not further discussed. Six replicates for each enrichment treatment and a control treatment were run and arranged in a randomized block design. Plots were separated by 2 m. Diffusers were exchanged every 6–8 week because a pilot experiment had revealed that nutrient release drops after this period.

To monitor nutrient release through time we collected water samples 10–15 cm above 5 control plots with intermediate fertilizer mass (80 g) and above control plots without enrichment every 3 weeks ($n = 5$ at each site). In August we sampled all 42 plots at Maasholm to reveal how increasing fertilizer mass changes nutrient availability. Water samples were obtained with 30-ml plastic syringes, immediately filtered through GFF filters and analyzed within 3 h for dissolved ammonium, nitrate, nitrite and phosphate on a Technicon^{TM} autoanalyzer. Nutrient data were analyzed by repeated-measures ANOVA (comparison between fertilized and unfertilized plots and between sites over time) or by linear regression (increase of nutrient availability with fertilizer mass) for each nutrient separately. Where it was necessary data were log-transformed to meet the assumption of homogeneity of variances.

4. Results

In all our experiments, coated fertilizers increased nutrient availability for dissolved nitrogen compounds and soluble reactive phosphorus over several weeks. Nutrients were increased by a factor relative to fluctuating ambient concentrations and not as a fixed amount added to ambient concentrations (Fig. 1, 2).

4.1. Sediment Enrichment

Throughout the experiment, nutrient concentrations were increased by at least 50% (NH_4) or 150% (PO_4) compared to control plots, although these differences were not always statistically significant (Fig. 1). The 4-M fertilizer doubled porewater ammonium concentrations within 2 d after application. This increased steeply to 18-fold enrichment after 1 month (Fig. 1) and declined again to 4-fold enrichment after 2 months. The 8-M fertilizer released nutrients more gradually, with only 8-fold increase after one month. Over the experimental period control plots had almost constant ammonium concentrations (21–24 μmol l^{-1}) but fertilized plots varied 10-fold (35 μmol l^{-1} to 385 μmol l^{-1}). Phosphate concentrations in the porewater increased 12-fold (4-M) and 5-fold (8-M fertilizer) following enrichment (total range of 1.4–8 μmol l^{-1} in control plots vs. 2.5–65 μmol l^{-1} in fertilized plots). Ammonium enrichment ceased after 2 months, while phosphate concentrations were still significantly elevated (4-fold). This pattern was similar subsequent to the second enrichment in August.

4.2. Water Column Enrichment

Nutrient diffusers increased water column nutrient concentrations relative to background concentrations across a wide range of ambient conditions (Fig. 2, Table 2). Although nutrient concentrations were lower at Oehe (significant effect of site, Table 2), enrichment patterns were similar among the two sites (insignificant S × E interaction, Table 2). This indicates that relative enrichment levels can be compared among the two sites, despite different

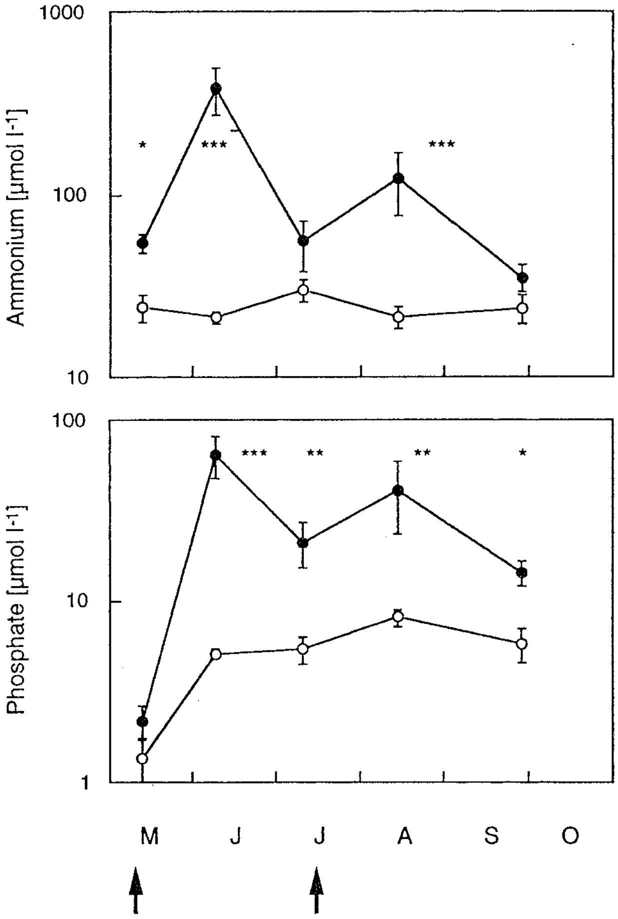
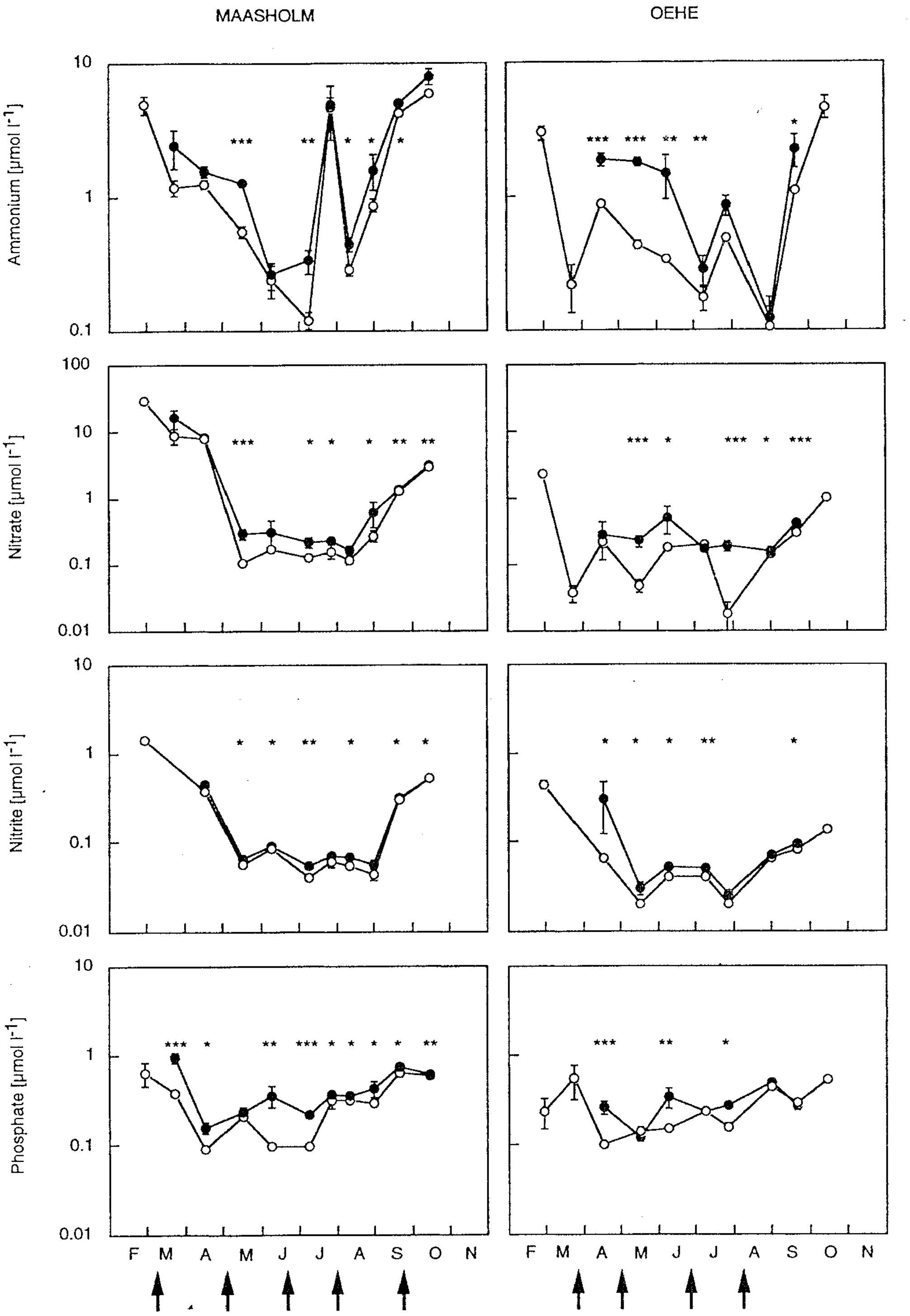


Figure 1. Effects of a coated fertilizer on sediment porewater nutrients. Mean (±1SE, n = 8) ammonium and phosphate concentrations in the porewater (0–5 cm depth) are shown for fertilized plots (dark symbols), and unfertilized control plots (open symbols). Arrows indicate dates of fertilizer application (500 g 4-M fertilizer in May, 500 g 8-M fertilizer in August). Significance of differences between fertilized and control plots was tested by ANOVA and is indicated by asterisks, with $P < 0.05$ = *, $P < 0.01$ = **, $P < 0.001$ = ***.

Figure 2. Effects of nutrient diffusers filled with a coated fertilizer (20 cm diffuser length = 80 g fertilizer) on water column nutrients (15 cm above plots) at a sheltered (Maasholm) and an exposed site (Oehe). Dark symbols indicate fertilized plots, open symbols control plots (mean ±1 SE, n = 16). Arrows indicate dates when fertilizer pellets were replaced. Water samples were taken at 3-week intervals. Significance of differences as tested by ANOVA is indicated by asterisks as in Fig. 1. For statistical comparison of sites refer to Table 2.

▶


MAASHOLM
OEHE
Ammonium [µmol l-1]
10
1
0.1
*** ** * * *
*** *** ** **
*
Nitrate [µmol l-1]
100
10
1
0.1
0.01
*** * * * ** **
*** * *** * ***
Nitrite [µmol l-1]
10
1
0.1
0.01
* * ** * * *
* * * ** *
Phosphate [µmol l-1]
10
1
0.1
0.01
*** * ** *** * * * * **
*** ** *
F M A M J J A S O N
F M A M J J A S O N

background concentrations. Significant effects of "Time" and T × S interactions (Table 2) indicate strong seasonal patterns in nutrient supply, which differed among sites. The pattern of enrichment changed significantly through time for phosphate but not for nitrogen (T × E interaction, Table 2), but this was not different among sites (T × S × E interaction, Table 2). Averaged over all dates increases in inorganic nitrogen ($DIN = NO_3 + NH_4 + NO_2$) due to enrichment were 50% (± 17.6% SE, n = 10 dates) at Maasholm and 130.5% (± 35.6%, n = 7 dates) at Oehe. Average increases in inorganic phosphate (PO_4) were 68.8 ± 27.5% at Maasholm and 49.6 ± 26% at Oehe.

Nutrient availability increased linearly with diffuser length and fertilizer mass (Fig. 3). For Maasholm in August, linear regression models (Fig. 3) predicted DIN availability to increase by 51% at intermediate fertilizer mass (80 g), which was almost exactly the value we obtained when we averaged relative increases across the experimental period (50%, see above). This value doubled with every doubling of fertilizer mass (100% increase at 160 g fertilizer, 200% at 320 g). Phosphate availability was predicted to increase by 9% at intermediate fertilizer mass, which did not correspond well with the measured average increase of 68.8%.

5. Discussion

Nutrient enrichment experiments in the field provide the only tool for assessing nutrient limitation *in situ* and allow for realistic conclusions about nutrient effects within marine ecosystems. In order to compare results from various studies and to derive valid generalizations, experimental nutrient enrichment levels need to be quantified. Almost half of the reviewed studies did not quantify nutrient enrichment levels but inferred enrichment effectiveness indirectly from the response of the plant (e.g. increased tissue nutrients, growth rate) or plant consumers (increase in herbivores). Only 1 out of 33 studies reported no plant or community response to all enrichment treatments (DENNISON *et al.*, 1987). DENNISON *et al.* (1987)

Table 2. Repeated-measures ANOVA on the effects of site (Maasholm vs Oehe) and nutrient enrichment on dissolved inorganic nitrogen (DIN) and Phosphorus (DIP).

Dependent	Source	df	MS	*F*	*P*
DIN	Site (S)	1	189.62	121.331	0.0001
	Enrichment (E)	1	19.9	12.734	0.0031
	S × E	1	0.37	0.237	0.634
	Error	16	1.563		
	Time (T)	6	72.373	57.301	0.0001
	T × S	6	45.596	36.1	0.0001
	T × E	6	0.531	0.42	0.6366
	T × S × E	6	0.723	0.572	0.5507
	Error	96	1.263		
DIP	Site (S)	1	0.10	24.06	0.0002
	Enrichment (E)	1	0.20	48.38	0.0001
	S × E	1	0.00	0.45	0.511
	Error	16	0.00		
	Time (T)	6	0.31	51.73	0.0001
	T × S	6	0.16	25.78	0.0001
	T × E	6	0.04	6.69	0.0011
	T × S × E	6	0.01	1.63	0.1995
	Error	96	0.01		

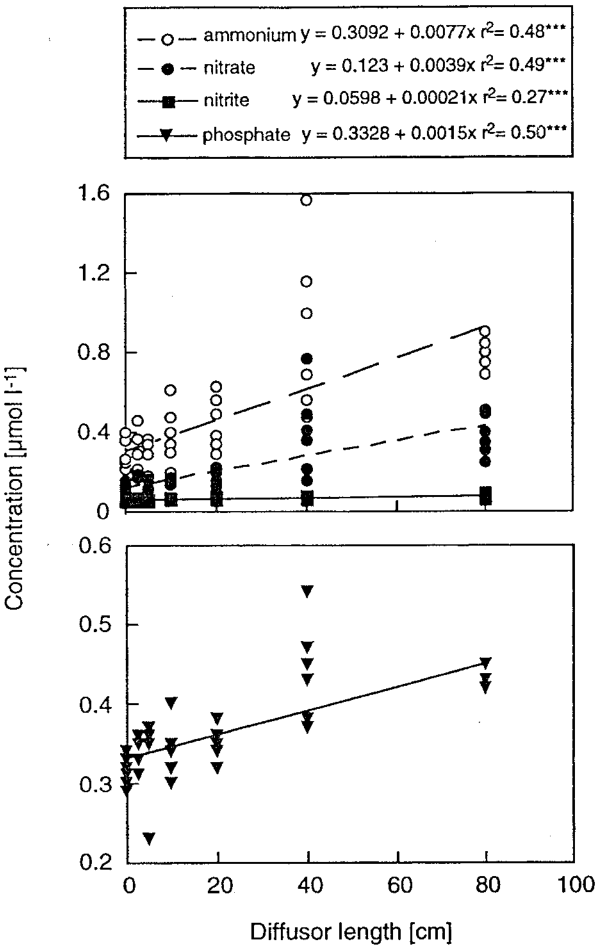


Figure 3. Manipulation of water column nutrient levels with nutrient diffusers filled with a coated fertilizer. Nutrient levels increase linearly with increasing diffuser length and fertilizer mass (fertilizer mass [g] = 4 * diffuser length [cm]). Significance of linear regression models is indicated by asterisks as in Fig. 1.

applied nutrients through tightly controlled diffusion chambers, which allowed precise quantification of nutrient availability. Therefore, they could rule out "unsuccessful" enrichment as a reason for absence of plant response. In contrast, when the level of nutrient enrichment is unknown, then there are two explanations if results show no effect of nutrient treatments on plant communities. (1) It is possible that elevated nutrients have no effects (community not nutrient limited) or (2) that enrichment did not work (communities may or may not be nutrient limited). Because these alternative hypotheses cannot be distinguished, negative results may be under-reported in the literature, which would challenge current generalizations about ubiquitous nutrient limitation in benthic plant communities.

Less than 20% of reviewed studies followed nutrient concentrations through time. These studies and the primary data supplied in this paper indicate that nutrient concentrations obtained by fertilization vary strongly over time (>70-fold, BULTHUIS and WOELKERLING, 1981). Hence, measurements at only one point in time may greatly over- or underestimate average nutrient availability on control or fertilized plots. Thus, it cannot be judged whether treatment concentrations were close to realistic or desired concentrations. Moreover, it can be important to know whether nutrients were available in short pulses (hours to days) or over a longer period since variations in pulse length and frequency can cause very different responses in plants (PICKERING *et al.*, 1993). For all these reasons we propose that careful monitoring of nutrient availability through time is indispensable for the interpretation of nutrient enrichment studies.

The selection of an enrichment method will depend in part on the context of the study. For sediment enrichment, coated fertilizer pellets and fertilizer stakes have been used most widely. The general advantage of fertilizer stakes seems to be their long-term effectiveness (up to 1 year) in contrast to coated fertilizer pellets (1–5 months, depending on coating and sediment depth). A disadvantage of stakes may be that they generally represent a highly localized point source of nutrients which is likely to produce strong, potentially unrealistic gradients, especially for phosphorus. In contrast, coated fertilizer pellets allow more even application over larger areas (if used plain), as well as localized application (in bags). When we applied a coated fertilizer in sediment we found that enrichment levels were initially high (8–18-fold for ammonium, 5–12-fold for phosphate), but declined over time. Another finding was that release is faster in ammonium than in phosphate. This closely mirrors results from South Australia (BULTHUIS *et al.*, 1992). However, when we compared nutrient response among 13 sediment enrichment studies we found no general pattern for nitrogen enrichment, which seems to be less predictable than phosphate enrichment. This underlines our general conclusion that good monitoring and adjustment of enrichment levels is needed in order to generate realistic experimental conditions that meet the requirements of the study.

Coated fertilizers had not previously been applied for water column fertilization. Our results (Fig. 2, 3) demonstrate that such fertilizer pellets can provide relatively good control of water column nutrient availability over a range of conditions (different nutrient background concentrations, sites, seasons and exposure). Importantly, we found a linear increase in nutrient availability with increasing fertilizer mass. This allows establishment of well-defined gradients in nutrient availability, which is highly preferable over having only one enriched vs. control treatment. For example, nutrient gradients can be very useful experimental systems in order to model the effects of increasing coastal eutrophication. Moreover, the coated fertilizer worked similarly at a wave exposed and a wave protected site, giving further support to the reliability of this method. Furthermore, within the range of concentrations encountered at our sites, coated fertilizers increased nutrient availability in proportion to background concentrations, rather than by an absolute concentration. Enrichment concentrations therefore remained largely unaffected by seasonal or spatial fluctuations of background concentrations (Fig. 2, Table 2). We can only speculate on the reason for this interesting release pattern. Possibly nutrients become diluted more rapidly, when concentrations are lower, leading to decreased absolute enrichment. As a further advantage, intermediate release times of coated fertilizers (6–8 weeks) allow for long-term enrichment without frequent fertilizer replacement. In contrast, application of non-coated fertilizers in flower pots requires very frequent replacement of fertilizer (5–15 days) and involves high nutrient loads, which can cause environmental problems when replication and duration of the experiment are increased. Similarly, the application of non-coated fertilizer in plastic bags involves very frequent visits to the site and artificially high nutrient input, which may be unrealistic and can have detrimental effects on some seagrasses and macroalgae (BURKHOLDER *et al.*, 1992; SCHAFFELKE and KLUMPP, 1998). This again compromises opportunities to infer from the experimental results to field conditions.

In conclusion, coated slow-release fertilizers allowed for a range of mostly realistic enrichment concentrations, gradual release, and good long-term control of enrichment levels. Their dynamic release pattern may facilitate comparative experiments among different sites and seasons. Using slow-release fertilizer pellets we found that relative enrichment levels are largely independent of fluctuations of background nutrient concentrations, plant density, presence of experimental cages, and wave exposure. We recommend the use of coated slow-release fertilizers for both water column and sediment enrichment.

6. Acknowledgments

This research was supported by a grant from the German Ministry of Science and Education to B.W. We are grateful for helpful comments by A. BOCKELMANN, H. HILLEBRAND, R. KAREZ, B. SCHAFFELKE, U. SOMMER and two anonymous reviewers.

7. References

BINKLEY, D. and P. M. VITOUSEK, 1992: Soil nutrient availability. – pp. 75–96 – *In*: R.W. PEARCY (Ed.): Plant physiological ecology. Field methods and instrumentation. Chapman and Hall, New York.

BOSMAN, A. L., J. T. DUTOIT, P. A. R. HOCKEY and G. M. BRANCH, 1986: A field experiment demonstrating the influence of seabird guano on intertidal primary production. – Est. Coast. Shelf Sci. **23**: 283–294.

BULTHUIS, D. A., D. M. AXELRAD and M. J. MICKELSON, 1992: Growth of the seagrass *Heterozostera tasmanica* limited by nitrogen in Port Phillip Bay, Australia. – Mar. Ecol. Prog. Ser. **89**: 269–275.

BULTHUIS, D. A. and W. J. WOELKERLING, 1981: Effects of *in situ* nitrogen and phosphorus enrichment on the seagrass *Heterozostera tasmanica* (MARTENS ex ASCHERS.) den Hartog in Western Port, Victoria, Australia. – J. Exp. Mar. Biol. Ecol. **53**: 193–207.

BURKHOLDER, J. M., K. M. MASON and H. B. GLASGOW Jr., 1992: Water-column nitrate enrichment promotes decline of eelgrass *Zostera marina*: evidence from seasonal mesocosm eperiments. – Mar. Ecol. Prog. Ser. **81**: 163–178.

CARPENTER, S. R., N. F. CARACAO, D. L. CORRELL, R. W. HOWARTH, A. N. SHARPLEY and V. H. SMITH, 1998: Nonpoint pollution of surface waters with phosphorus and nitrogen. – Ecol. Appl. **8**: 559–568.

CECCHERELLI, G. and F. CINELLI, 1997: Short-term efects of nutrient enrichment of the sediment and interactions between the seagrass *Cymodocea nodosa* and the introduced green alga *Caulerpa taxifolia* in a Mediterranean bay. – J. Exp. Mar. Biol. Ecol. **217**: 165–177.

CHAPMAN, A. R. O. and J. S. CRAIGIE, 1977: Seasonal growth in in *Laminaria longicruris*: relations with dissolved inorganic nutrients and internal reserves of nitrogen. – Mar. Biol. **40**: 197–205.

COLEMAN, V.L. and J. M. BURKHOLDER, 1995: Response of microalgal epiphyte communities to nitrate enrichment in an eelgrass (*Zostera marina*) meadow. – J. Phycol. **31**: 36–43.

DENNISON, W. C., R. C. ALLER and R. S. ALBERTE, 1987: Sediment ammonium availability and eelgrass (*Zostera marina*) growth. – Mar. Biol. **94**: 469–477.

ERFTEMEIJER, P. L. A., J. STAPEL, M. J. E. SMEKENS and W. M. E. DROSSAERT, 1994: The limited effects of *in situ* phosphorus and nitrogen additions to seagrass beds on carbonate and terrigenous sediments in South Sulawesi, Indonesia. – J. Exp. Mar. Biol. Ecol. **182**: 123–140.

FELLER, I. C., 1995: Effects of nutrient enrichment on growth and herbivory of dwarf red mangrove (*Rhizophora mangle*). – Ecol. Monogr. **65**: 477–505.

FLOTHMANN, S. and I. WERNER, 1992. Experimental eutrophication of an intertidal sandflat: effects on microphytobenthos, meio- and macrofauna. – pp. 93–100 *In*: G. COLOMBO (Ed.): Marine Eutrophication and population dynamics. Proceedings of the 25th EMBS. Olson and Olson, Fredensborg, Denmark.

FONG, P., J. B. ZEDLER and R. M. DONOHOE, 1993: Nitrogen vs. phosphorus limitation of algal biomass in shallow coastal lagoons. – Limnol. Oceanogr. **38**: 906–923.

FONSECA, M. S., W. J. KENWORTHY, F. X. COURTNEY and M. O. HALL, 1994: Seagrass planting in the Southeastern United States: methods for accelerating habitat development. – Restorat. Ecol. **2**: 198–212.

GRASSHOFF, K, 1976: Methods of seawater analysis. – Verlag Chemie. Weinheim, Germany.

HARLIN, M. M. and B. THORNE-MILLER, 1981: Nutrient enrichment of seagrass beds in a Rhode Island coastal lagoon. – Mar. Biol. **65**: 221–229.

Hatcher, B. G. and A. W. D. Larkum, 1983: An experimental analysis of factors controlling the standing crop of the epilithic algal community on a coral reef. – J. Exp. Mar. Biol. Ecol. **69**: 61–84.

Hauxwell, J., J. McClelland, P. J. Behr and I. Valiela, 1998: Relative importance of grazing and nutrient controls of macroalgal biomass in three temperate shallow estuaries. – Estuaries **21**: 347–360.

Hecky, R. E. and P. Kilham, 1988: Nutrient limitation of phytoplankton in freshwater and marine environments: a review of recent evidence on the effect of enrichment. – Limnol. Oceanogr. **33**: 796–822.

Howarth, R. W., 1988: Nurient limitation of net primary production in marine ecosystems. – Ann. Rev. Ecol. Syst. **19**: 89–110.

Kenworthy, W. J. and M. S. Fonseca, 1992: The use of fertilizer to enhance growth of transplanted seagrasses *Zostera marina* L. and *Halodule wrightii* Aschers. – J. Exp. Mar. Biol. Ecol. **163**: 141–161.

Lapointe, B. E., 1989: Macroalgal production and nutrient relations in oligotrophic areas of Florida Bay. – Bull. Mar. Sci. **44**: 312–323.

Lotze, H. K., 1998: Population dynamics and species interactions in macroalgal blooms: abiotic versus biotic control at different life-cycle stages. – Dissertation. Ber Inst Meeresk Kiel 303, 134.

Lotze, H.K., B. Worm, and U. Sommer, 1999: Propagule banks, herbivory and nutrient supply control population development and dominance patterns in macroalgal blooms. – Oikos, in press.

McGlathery, K., 1995: Nutrient and grazing influences on a subtropical seagrass community. – Mar. Ecol. Prog. Ser. **122**: 239–252.

Menge, B. A., 1992: Community regulation: under what conditions are bottom-up factors important on rocky shores? – Ecology **73**: 755–765.

Miller, M. W. and M. E. Hay, 1996: Coral-seaweed-grazer-nutrient interactions on temperate reefs. – Ecol. Monogr. **66**: 323–344.

Murray, L., W. C. Dennison and W. M. Kempf, 1992: Nitrogen versus phosphorus limitation for growth of an estuarine population of eelgrass (*Zostera marina* L.). – Aquat. Bot. **44**: 83–100.

Nixon, S., 1990: Marine eutrophication: a growing international problem. – Ambio **19**: 101.

North, W. J., V. A. Gerard and R. H. McPeak, 1980. Experimental fertilizing of coastal *Macrocystis* beds. – *In*: Proceedings of the 10th International Seaweed Symposium. Walter de Gruyter, Den Haag, The Netherlands.

Orth, R. J., 1977: Effect of nutrient enrichment on growth of the eelgrass *Zostera marina* in the Chesapeake Bay, Virginia, USA. – Mar. Biol. **44**: 187–194.

Pedersen, M. F., 1995: Nitrogen limitation of photosynthesis and growth: comparison across aquatic plant communities in a danish estuary. – Ophelia **41**: 261–272.

Perez, M., J. Romero, C. M. Duarte and K. Sand-Jensen, 1991: Phosphorus limitation of *Cymodocea nodosa* growth. – Mar. Biol. **109**: 129–133.

Pickering, T. D., M. E. Gordona and L. J. Tong, 1993: Effects of nutrient pulse concentration and frequency on growth of *Gracilaria chilensis* plants and levels of epiphytic algae. – J. Appl. Phycol. **5**: 525–533.

Posey, M., C. Powell, L. Cahoon and D. Lindquist, 1995: Top down vs. bottom up control of benthic community composition on an intertidal tideflat. – J. Exp. Mar. Biol. Ecol. **185**: 19–31.

Powell, G. V. N., W. J. Kenworthy and J. W. Fourqurean, 1989: Experimental evidence for nutrient limitation of seagrass growth in a tropical estuary with restricted circulation. – Bull. Mar. Sci., **44**: 324–340.

Pulich Jr., W. M., 1985: Seasonal growth dynamics of *Ruppia maritima* L. and *Halodule wrightii* Aschers. in southern Texas and evaluation of sediment fertility status. – Aquat. Bot. **23**: 53–66.

Reusch, T. R., A. R. O. Chapman and J. P. Gröger, 1994: Blue mussels *Mytilus edulis* do not interfere with eelgrass *Zostera marina* but fertilize shoot growth through biodeposition. – Mar. Ecol. Prog. Ser. **108**: 265–282.

Schaffelke, B. and D. W. Klumpp, 1998: Nutrient-limited growth of the coral reef macroalga *Sargassum baccularia* and experimental growth enhancement by nutrient addition in continuous flow culture. – Mar. Ecol. Prog. Ser. **164**: 199–211.

Short, F. T., 1987: Effects of sediment nutrients on seagrass: literature review and mesocosm experiments. – Aquat. Bot. **27**: 41–57.

Short, F. T., W. C. Dennison and D. G. Capone, 1990: Phosphorus-limited growth of the tropical seagrass *Syringodium filiforme* in carbonate sediments. – Mar. Ecol. Prog. Ser. **62**: 169–174.

Short, F. T. and C. P. McRoy, 1984: Nitrogen uptake by leaves and roots of the seagrass *Zostera mari-*

na L. – Bot. Mar. **27**: 547–555.

TILMAN, D., 1977: Resource competition between planktonic algae: and experimental and theoretical approach. – Ecology **58**: 338–348.

UDY, J. W. and W. C. DENNISON, 1997: Growth and physiological responses of three seagrass species to elevated sediment nutrients in Moreton Bay, Australia. – J. Exp. Mar. Biol. Ecol. **217**: 253–277.

VAN LENT, F. and J. M. VERSCHUURE, 1995: Comparative study on populations of *Zostera marina* L. (eelgrass): *in situ* nitrogen enrichment and light manipulation. – J. Exp. Mar. Biol. Ecol. **185**: 55–76.

WILLIAMS, S. L., 1984: Uptake of sediment ammonium and translocation in a marine green macroalga *Caulerpa cupressoides*. – Limnol. Oceanogr. **29**: 374–379.

WILLIAMS, S. L., 1987: Competition between the seagrasses *Thalassia testudinum* and *Syringodium filiforme* in a Carribean lagoon. – Mar. Ecol. Prog. Ser. **35**: 91–98.

WILLIAMS, S. L., 1990: Experimental studies of Carribean seagrass bed development. – Ecol. Monogr. **60**: 449–469.

WILLIAMS, S. L. and M. H. RUCKELSHAUS, 1993: Effects of nitrogen availability and herbivory on eelgrass (*Zostera marina*) and epiphytes. – Ecology **74**: 904–918.

WOOTTON, J. T., M. E. POWER, R. T. PAINE and C. A. PFISTER, 1996: Effects of productivity, consumers, competitors, El Nino events and food chain patterns in a rocky intertidal community. – Proc. Natl. Acad. Sci. USA **93**: 13855–13858.

WORM, B. and A. R. O. CHAPMAN, 1998: Relative effects of elevated grazing pressure and competition by a red algal turf on two post-settlement stages of *Fucus evanescens* C. Ag. – J. Exp. Mar. Biol. Ecol. **220**: 247–268.

WORM, B., H. K. LOTZE, C. BOSTRÖM, R. ENGKVIST, V. LABANAUSKAS and U. SOMMER, 1999: Marine diversity shift linked to interactions among grazers, nutrients and dormant propagules. – Mar. Ecol. Prog. Ser. **185**: 309–314.

Manuscript received April 12th, 1999; revised November 2nd, 1999; accepted November 4th, 1999