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Influence of microphytobenthos on the nutrient flux between sediment and water: a laboratory study

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ABSTRACT: The importance of microphytobenthos as a regulator of the flux of inorganic phosphorus and nitrogen between sediment and water was investigated in a laboratory study. Sediment from the SE Kattegat was incubated in nutrient-enriched seawater during exposure to varying light quantities (0, 5, 10, and 30 μE m^{-2} s^{-1}). Microphytobenthos growth was limited by both inorganic nutrients and light quantity. When exposed to no-light conditions, chlorophyll *a* content of the sediment decreased only slightly and remained at an almost constant level (50 to 55 mg m^{-2}) for several weeks, and increased rapidly when exposed to light. A relationship was observed between light quantity and the rate and direction of the flux of NH_4^+ and PO_4^{3-}, but not NO_3^-, between the sediment and overlying water The indirect influence of the microphytobenthos on the nutrient flux, i.e. by changes in the oxygen concentration, seemed more important than the direct effect by uptake by the algae. The rate of release of phosphate from the sediment exposed to darkness was up to 0.2 mmol PO_4 m^{-2} d^{-1} The maximum mean rate of ammonia release was 1.6 mmol m^{-2} d^{-1} in the dark and ca 0.1 mmol m^{-2} d^{-1} at 5 μE m^{-2} s^{-1}. When the amount of light was ≥ 10 μE m^{-2} s^{-1}, the microbenthic activity (oxygen production and increased nutrient requirements) prevented the release of PO_4 and NH_4 from the sediment.

INTRODUCTION

The role in coastal ecosystems of sublittoral microphytobenthos at depths greater than a few metres has rarely been discussed, probably because the benthic microflora has been considered to play a subordinate role in primary production compared with the phytoplankton. However, considerable primary production and biomass of sediment-associated microflora have been documented for depths greater than 10 m in both marine (Boucher 1977, Chassé 1983, Plante-Cuny 1984, Sundbäck 1986) and lacustrine temperate waters (Romagoux 1976, Björk-Ramberg 1984).

In coastal areas regeneration of nutrients from the sediment is important for primary production in the water column (Rowe et al. 1975, Blackburn & Henriksen 1983, Flint & Kamykowski 1984, de Vries & Hopstaken 1984). In shallow water, the sediment-associated microflora may compete for nutrients and thereby function as a 'filter' (Blackburn & Henriksen 1979, Hansson in press) influencing the inorganic nutrient flux between sediment and water (Henriksen et al. 1980, Blackburn & Henriksen 1983, Kelderman 1984, Granéli & Sundbäck 1985, Asmus 1986). The microphytobenthos also affects the oxygen conditions at the sediment-water interface (Revsbech & Jörgensen 1983, Baille 1986, Granéli & Sundbäck 1986) and this may, in turn, influence nitrogen turnover processes at the sediment surface (Andersen et al. 1984, Enoksson 1987) and desorption rates for PO_4 (e.g. Balzer et al. 1983).

To study the relationship between microphytobenthos and the inorganic nutrients in the bottom water, we designed an experiment in which sediment was exposed to a series of light quantities. As oxygen concentration may influence the nutrient fluxes, the O_2-levels in the overlying water were also measured (see Granéli & Sundbäck 1986).

MATERIAL AND METHODS

Experiments were conducted in aquaria containing natural sand sediment, collected on 28 October 1984 from grab samples (ca 10 cm deep) from a depth of 15 m

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in Laholm Bay, Sweden (56° 33' N, 12° 50' E) (in the SE Kattegat). Samples were divided into 2 layers (the top 1 cm was scraped away and kept separate). The sediment was sieved (mesh size 0.55 mm) to remove macrofauna and homogenized to minimize initial variability within and among experimental units caused by patchiness of the microflora and meio- and microfauna.

Because sampling was carried out late in the season when algae were not in abundance at 15 m, surficial sediment (top 1 cm) was collected on 30 October from the shallow (0.5 m) Salviken Bay in Öresund. This algae-rich sediment was sieved and mixed with the surficial sediment from Laholm Bay (proportions ca 3:1). The species constituting the microflora in the 2 sediments were not essentially different.

A sample of the lower layer of the Laholm Bay sediment was spread to a depth of 2 cm over the base of cylindrical dark-grey 6 l PVC aquaria (346 cm^2). A 2 cm layer of the mixed surficial sediment was spread over the lower layer. Aquaria were completely filled with filtered (Whatman GF/F, retention 0.7 µm) water collected from a depth of 15 m in Laholm Bay (salinity 21 ‰), and then covered with PVC (dark aquaria) or glass lids of varying light transparencies (white paper was used as neutral filter). The joints between the aquaria and their lids were sealed with silicon grease to minimize exchange of oxygen with the atmosphere.

The experimental arrangement consisted of 10 aquaria (5 × 2 replicates) held at 14.5 ± 1 °C and the experiment was run for 81 d (9 Nov to 24 Jan) with a 16/8 h light/dark cycle. Duplicate aquaria were randomly chosen and exposed to 4 different light regimes (0, 5, 10 and 30 µE m^{-2} s^{-1}, equivalent to 0 to 1.7 E m^{-2} d^{-1}), a range that is similar to the range observed in the field at approximately 15 m (Sundbäck 1986). After 36 d, the light treatments were inverted (0 µE to 30 µE and vice versa; 5 µE to 10 µE and vice versa) to check that the differences between the aquaria were mainly a result of different light regimes and to determine how rapidly the microcosms reacted to changed light conditions.

At the beginning of the experiment, nutrients (700 µ*M* N as $NaNO_3$ and 8.9 µ*M* P as K_2HPO_4) were added to the water in all but 2 of the aquaria initially exposed to 30 µE m^{-2} s^{-1}. The amount of phosphate added was within the same order of magnitude as PO_4 concentrations normally encountered in the pore water, while an excess of nitrate was added to prevent nutrient limitation. The growth of benthic algae and phytoplankton in Laholm Bay is not limited by phosphate (Nyman & Granéli 1983).

Initially, the aquaria were sampled each week, and subsequently (towards the end of the experiment), samples were taken each fortnight. Samples were always taken 3 to 4 h after the beginning of the light period. For each sampling, 350 ml aliquots of the overlying water were collected for analyses from each aquarium and the volume replaced by filtered seawater. The following measurements were performed on these aliquots: inorganic nitrogen (NO_3^- + NO_2^-, NH_4^+), inorganic phosphorus (PO_4^{3-}) and O_2 and ^{14}C-assimilation (to check for phytoplankton growth). Nutrients were analysed according to methods described in Carlberg (1972), oxygen levels were determined using the Winkler technique and ^{14}C-assimilation was measured according to Aertebjerg Nielsen & Bresta (1984).

The response of the microphytobenthos was monitored by both the change in the chlorophyll *a* content and the ^{14}C-assimilation of samples taken from the top 3 mm of the sediment with a cut-off plastic syringe (0.64 cm^2). Six samples from each aquarium were pooled. Chlorophyll *a* was extracted for 24 h with 90 % acetone and measured according to Lorenzen (1967). The ^{14}C-assimilation was measured by incubating subsamples from the pooled sediment sample in glass flasks containing 25 ml filtered water from the aquaria. All samples were incubated for 2 h under the same conditions as the experimental system.

A semi-quantitative estimate of microfloral succession was obtained by microscopically examining fresh sediment samples.

RESULTS

The replicate aquaria for each treatment yielded comparable data and the deviation of the measured values was generally less than 10 % (Figs. 1 to 6).

For the first 36 d, the chlorophyll *a* content decreased only slightly from initial values (ca 70 mg m^{-2}) in aquaria exposed to no light, remained stable at 5 µE m^{-2} s^{-1} light quantity, increased for the first 2 wk in aquaria exposed to 10 µE and increased up to 100 mg m^{-2} within 2 wk in aquaria exposed to 30 µE m^{-2} s^{-1} (Fig. 1). In the aquaria without added nutrients the values decreased slightly after an initial rise.

The ^{14}C-assimilation of the sediment exposed to no light was < 1 to 3 mg C m^{-2} h^{-1} (Fig. 2). The primary production at 5 and 10 µE varied between 5 and 10 mg C m^{-2} h^{-1} and between 12 and 19 mg C m^{-2} h^{-1}, respectively (Fig. 2). At 30 µE the production rate increased to between 90 and 100 mg C m^{-2} h^{-1} within 4 wk (Fig. 2). In the aquaria exposed to 30 µE m^{-2} s^{-1} without added nutrients the values decreased slowly (Fig. 2). The ^{14}C-assimilation of the overlying water was low (< 1 mg m^{-2} h^{-1}) and, consequently, interference by phytoplankton production during the experiment could be ignored.

After 36 d, when the light quantity was changed from

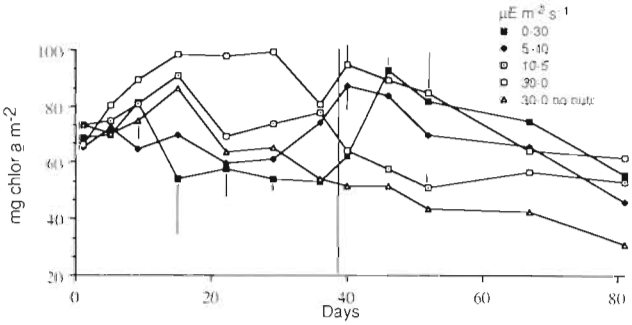

Fig. 1 Chlorophyll *a* content of the sediment in aquaria exposed to 4 different light regimes. Vertical line denotes inversion of light treatments (0 to 30, 5 to 10 µE m^{-2} s^{-1} etc.). Range of values of duplicate aquaria appear only above or below mean values and are shown only when the deviation from the mean was greater than 10 %

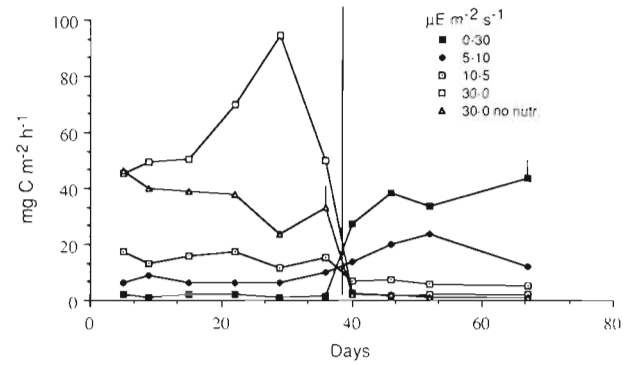

Fig. 2. ^{14}C-assimilation of the sediment in aquaria exposed to 4 different light regimes. For further explanation see Fig. 1

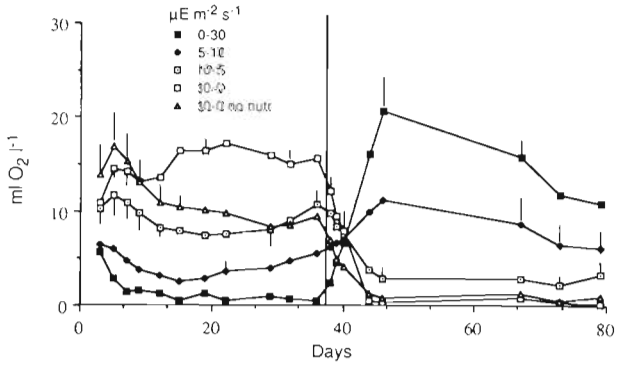

Fig. 3. Oxygen concentration of the overlying water in aquaria exposed to 4 different light regimes. For further explanation see Fig. 1

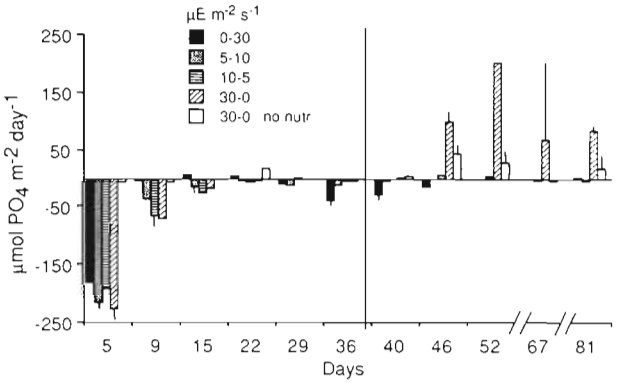

Fig. 4. Rates of decrease and increase of PO_4^{3-} in the overlying water in aquaria exposed to 4 different light regimes. Ranges of values appear only above the mean values. For further explanation see Fig. 1

0 to 30 and from 5 to 10 µE m^{-2} s^{-1}, both chlorophyll *a* content and ^{14}C-assimilation of the sediment initially increased (Figs. 1 and 2). There was no marked decrease in chlorophyll *a* content when the light was reduced from 30 to 0 and from 10 to 5 µE m^{-2} s^{-1} (Fig. 1).

The change in the O_2-concentration of the overlying water was correlated with light quantity (Fig. 3). Although the peaks of the curves did not always coincide, the values exhibit a similar trend to those obtained for chlorophyll *a* content and primary production of the sediment. The change from 30 to 0 µE m^{-2} s^{-1} induced the oxygen concentration in the nutrient-enriched aquaria to fall to zero within 1 wk, and after an additional 20 d, a smell of H_2S appeared. In the aquaria without added nutrients, the values decreased more slowly and stabilized at 2 ml O_2 l^{-1}. Additional data regarding oxygen concentrations are presented in Granéli & Sundbäck (1986).

During the first 5 d, the concentration of PO_4 decreased rapidly in all aquaria with added nutrients (maximum rate was ca 250 µmol m^{-2} d^{-1} at 30 µE) (Fig. 4). After an additional 1 wk the uptake rate decreased with decreased light exposure (70 µmol m^{-2} d^{-1} at 30 µE and 35 µmol m^{-2} d^{-1} at 5 µE). In the dark aquaria, the concentration of P remained almost unchanged (ca 0.5 mmol m^{-2}) from Day 5 to 29.

Changing the light quantity from 30 to 0 µE m^{-2} s^{-1} induced a marked flux of PO_4 out of the sediment in aquaria containing added nutrients as the O_2 concentration decreased (the maximum rate of increase was 200 µmol m^{-2} d^{-1}) (Fig. 4). The concentrations of PO_4 also increased in the aquaria without added nutrients (maximum rate of increase was approximately 80 µmol m^{-2} d^{-1}). Conversely, only a slight increase in P was noted in the aquaria initially kept in the dark (6 to 8 µmol m^{-2} d^{-1} during Weeks 2 and 3) (Fig. 4).

The NH_4 concentration in the overlying water was initially low (150 to 250 µmol m^{-2}) in all aquaria (N was added as NO_3). Concentrations increased in the aquaria that were kept in the dark and at 5 µE m^{-2} s^{-1} for the first 36 d. In the aquaria kept in the dark the NH_4 concentration increased about 100 times, i.e. to between 15 and 20 mmol m^{-2} (which is equivalent to a mean rate of 0.6 to 0.7 mmol m^{-2} d^{-1}) (Fig. 5). Inverting light treatments changed the direction of the NH_4 flux

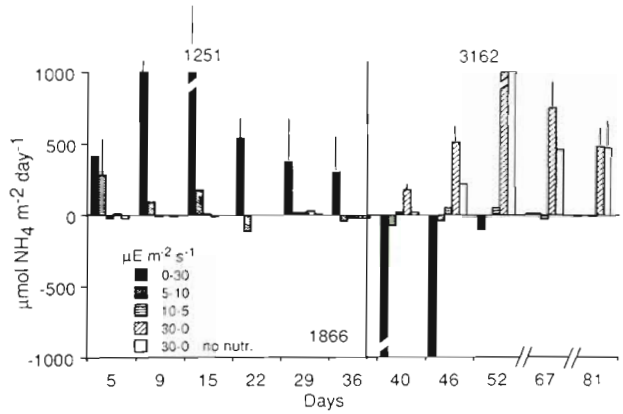

Fig. 5. Rates of decrease and increase of NH_4^+ in the overlying water in aquaria exposed to 4 different light regimes. For further explanation see Figs. 1 and 4

(Fig. 5). After switching from 0 to 30 µE m^{-2} s^{-1} the NH_4 concentrations decreased rapidly (mean rate 1.5 mmol m^{-2} d^{-1}). Altering the light regime from 30 to 0 µE m^{-2} s^{-1} increased the NH_4 levels at a mean rate of 1.6 mmol m^{-2} d^{-1}. The increase was less in the control aquaria (approximately 0.5 mmol m^{-2} d^{-1}) (Fig. 5). The mean release of NH_4 at 5 µE m^{-2} s^{-1} was 0.1 (range 0.02 to 0.28) mmol m^{-2} d^{-1}.

The concentration of NO_3 + NO_2 varied less than the amounts of PO_4 and NH_4 at the different light levels (Fig. 6). The uptake rate was highest during the first

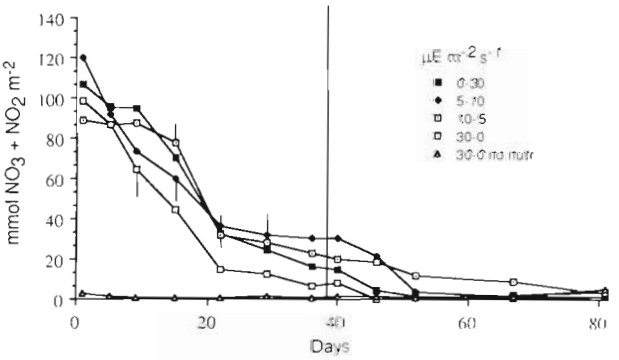

Fig. 6. Concentrations of NO_3^- + NO_2^- in the overlying water in aquaria exposed to 4 different light regimes. For further explanation see Figs. 1 and 4

3 wk and varied between 1.8 and 5 mmol m^{-2} d^{-1}. No increase in nitrate concentration was observed during the experiment.

Initially the benthic microflora was dominated by diatoms (mainly epipsammic forms e.g. *Opephora olsenii* Möller and small *Navicula* species). This dominance of diatoms persisted throughout in the aquaria without added nutrients, but motile diatoms became more abundant during the experiment. Towards the end of the period of light exposure, however, a dinoflagellate (*Amphidinium* sp.) became abundant. In the nutrient-enriched aquaria kept at a light quantity of 30 µE m^{-2} s^{-1}, a thick carpet of filamentous cyanobacteria (*Spirulina* cf. *subsalsa* and *Lyngbya* spp.) developed. Removal of the light resulted in disappearance of the cyanobacteria while a vital diatom flora remained, even after the presence of H_2S was noted. When the dark aquaria were exposed to 30 µE light after 36 d, a thick dark brown carpet of motile diatoms (mainly *Amphora* spp.) rapidly developed.

DISCUSSION

The chlorophyll *a* and ^{14}C-uptake curves indicated that light was a limiting factor during the experiment. The light saturation range for microflora from 15 m depth in Laholm Bay is 50 to 100 µE m^{-2} s^{-1} (Sundbäck 1986). Admiraal et al. (1984) found that intertidal diatom species were able to grow in the range 0.2 to 40 E m^{-2} d^{-1}. In our experiment, 0.6 E m^{-2} d^{-1} (10 µE m^{-2} s^{-1} × 16 h) was sufficient to support an autotrophically dominated system (P/R >1; see also Granéli & Sundbäck 1986). This level of irradiance is reached at 15 m between May and August (0.7 to 1 E m^{-2} d^{-1}). In Laholm Bay considerable microphytobenthic production takes place even as deep as 15 to 16 m (Sundbäck 1986).

In the dark, chlorophyll *a* content of the sediment remained at a constant level for weeks. Subsequent exposure to light induced a rapid initiation of photosynthesis. Despite slightly increasing values of ^{14}C-uptake, the decrease in chlorophyll *a* values towards the end of the experiment (Fig. 1) most probably reflects an adaptation of the algae to increased light levels by decreased chlorophyll content of the cells. Functional chlorophyll *a* is usually found in the sediment at least down to a depth of 10 cm (e.g. Cadée & Hegeman 1974, Gargas & Gargas 1982). Gargas & Gargas (1982) found no change in the photosynthetic capacity of microphytobenthos kept in the dark for 4 mo and Admiraal et al. (1984) found that benthic diatom species survived more than 40 d in dark on sterilized sand and that during light limitation a mixed type of growth (photoheterotrophic) occurs. For diatoms capable of heterotrophic growth, Hellebust & Lewin (1977) demonstrated chlorophyll *a* synthesis in the absence of light.

Changes in the species composition of the benthic microflora with nutrient enrichment have been observed (e.g. van Raalte et al. 1976, Pringle & Bowers 1984). Kennett & Hargraves (1985) observed that seasonal anoxia affected the species composition of the benthic diatoms and that some species appeared to be adapted to the presence of sulfide ions.

The microphytobenthos influences the nutrient flux both directly through nutrient uptake from water and sediment, and indirectly by affecting the oxygen concentration at the sediment-water interface by photosynthesis and respiration. The latter effect seemed to be more important in our experiment. Microbial nitrogen transformation as well as phosphate adsorption and precipitation are redox sensitive. The uptake of nutrients by the sediment is also affected by bioturbation (e.g. Kristensen & Blackburn 1987). Although bioturbation (and grazing) by the macrofauna (but not meio- and microfauna) was initially suppressed by sieving the sediment, bioturbation may have occurred later during the experiment.

Decreasing values for both primary production and chlorophyll *a* content in aquaria without nutrient addition demonstrate that the microflora was nutrient limited (Figs. 1 and 2). Although the interstitial water often contains concentrations of inorganic nutrients orders of magnitude higher than the overlying water, the marine microphytobenthos appear to be nutrient limited (mainly by N) and hence compete for nutrients in the overlying water (Henriksen et al. 1980, Connor et al. 1982, Blackburn & Henriksen 1983, Wonnerberger & Höpner 1984, de Vries & Hopstaken 1984, Granéli & Sundbäck 1985, Asmus 1986, Sundbäck 1986). In the Dutch Wadden Sea the microbenthic primary production has increased concomitant with the increase in nutrient loading (Cadée 1984).

The rapid initial uptake of added P was approximately the same for all aquaria (even those not exposed to light) and may be due to adsorption to sediment particles during oxic conditions (Watanabe & Tsugonai 1984). By comparing the decrease of P-concentration of the overlying water in the dark and the light in our experiment, and assuming that non-biological P-adsorption equals the decrease in the dark from Day 1 to Day 5, adsorption would account for approximately 60 % of the sediment uptake in the light during the first week.

Provided the light level facilitated adequate oxygen production, no P was released from the sediment. The fact that P-release in the dark was more rapid after an initial 5 wk period of light exposure, than without an initial light period, suggests that the increased production of organic material by the algae, combined with increased respiration, enhances the P-release. The maximum rate at which P was released during anoxic conditions (200 μmol P m^{-2} d^{-1}) was the same as previously found for a N-rich bay in SW Sweden (Granéli & Sundbäck 1985). Granéli (1984) measured phosphate release rates during anoxic conditions between 60 and 150 μmol P m^{-2} d^{-1} for silty sediments from a depth of 20 m in the outer part of Laholm Bay, but during oxic conditions, no phosphate was released. Blackburn & Henriksen (1983) found rates of approximately 50 μmol P m^{-2} d^{-1} for sediment taken from a depth of 14 to 25 m in the Kattegat. These rates lie well within the range measured for aquaria without added nutrients in the work presented here (max. 80 μmol P m^{-2} d^{-1}).

While nitrate fluxes are often directed towards the sediment because of denitrification, at least when there are high nitrate concentrations in bottom-near waters (as in our experiment), there is usually a net outflow of ammonia from sediments (Florek & Rowe 1983, Boynton & Kemp 1985, Nowicki & Nixon 1985).

We found an inverse relation between the amount of light and the release of NH_4 from the sediment. Henriksen et al. (1980) found a marked difference in ammonium flux for light (day) and dark (night) conditions, indicating that the microflora prevents ammonium from leaving the sediment surface during daytime (cf. Kelderman 1984). Our values for ammonia release in the dark (0.5 mmol NH_4 m^{-2} d^{-1} in aquaria without added nutrients) lie well within the range of those reported by Boynton & Kemp (1985) and Nowicki & Nixon (1985), but are somewhat lower than rates reported by Florek & Rowe (1983). Boynton & Kemp found that in Chesapeake Bay the ammonia release was highest in summer, max. 0.7 mmol m^{-2} d^{-1}. Nowicki & Nixon (1985) found that at 15°C (as in our experiment), less than 0.1 mmol NH_4 m^{-2} d^{-1} was released during darkness and less than 0.05 mmol m^{-2} d^{-1} during exposure to light in a shallow lagoon on Rhode Island, USA. This is comparable to the release rate at 5 μE m^{-2} s^{-1} obtained in our study.

Although the rate of denitrification in our experiment was not estimated, the low N:P ratio (6 to 7) of the flux out of the sediment indicates general denitrification (see Blackburn & Henriksen 1983).

It is difficult to distinguish the amount of nitrogen assimilated from the water by the benthic microflora from other N-turnover processes in the sediment. In addition, the microflora assimilates N from the interstitial water. Although we did not analyse the interstitial water, the theoretical N-uptake by the microphytobenthos can be estimated using the amount of assimilated carbon and the C:N ratio 10:1 for benthic microflora (Whitaker & Richardson 1980, Hunter & Russel-Hunter 1983, Brzezinski 1985). The calculated N-uptake (as NO_3) for the period Day 5 to Day 29 in aquaria with added nutrients and exposed to 30 μE m^{-2} s^{-1} is 3.3 mmol m^{-2} d^{-1}. The calculated value is equivalent to 106 % of the measured decrease in the overlying water. In the calculations, the amount of assimilated carbon was corrected by a factor of 0.4 to allow for C-uptake measured in flasks where the algae received more light than they would in intact sediment (Cadée & Hegeman 1974). If the Redfield ratio (6.6:1) is used, the N-uptake, 4.9 mmol m^{-2} d^{-1}, would be equivalent to

158 % of the N-decrease in the overlying water, which indicates that a large part of the N needed must be supplied from the interstitial water. Based on data from a 3 wk experiment, Granéli & Sundbäck (1985) calculated that the benthic microalgae accounted for ca 20 % of the disappearance of N from the *overlying water* and took up 40 to 60 % of the *total pool* of nitrogen (interstitial water + overlying water).

Our results confirm the hypothesis that a correlation exists between light intensity, microphytobenthic activity and nutrient flux (Blackburn & Henriksen 1979, Henriksen et al. 1980). The indirect influence of microphytobenthos on the flux, by changes in the O_2 concentration at the sediment-water interface, was more important in our experiment than the direct uptake of nutrients by the algae. In light, oxygen production by photosynthesis prevented the release of PO_4 and NH_4 from the sediment. The effect of the microphytobenthic 'filter' depends on the amount and duration of the exposure to light. In our experiment, 10 $\mu E\ m^{-2}\ s^{-1}$ (equivalent to 0.6 $E\ m^{-2}\ d^{-1}$) was sufficient to maintain both an autotrophically dominated system and to prevent the outflux of NH_4 and PO_4. The stable chlorophyll *a* values during weeks of darkness indicate the survival of a potential 'filter effect' during temporary shading during the growing season.

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