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Impact of accumulating drifting macroalgae on a shallow-water sediment system: an experimental study

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ABSTRACT: Using an outdoor flow-through experimental set-up consisting of twelve 30 l containers, effect of accumulation of drifting filamentous macroalgae on a shallow-water sediment system was studied for 3 wk after the addition of 0.9 (low dose) and 1.8 kg fresh wt m^{-2} (high dose) of filamentous red algae. Estimates of structural changes were based on relationships between numbers and biomass of bacteria, autotrophic microflora, ciliates and meiofauna and their qualitative composition. Effects on the functional level were assessed by measuring primary productivity, changes in carbon pools, as well as oxygen and nutrient flux. The low-dose treatment did not significantly alter the composition or patterns of primary productivity and nutrient fluxes when compared with the control (no addition). The high-dose addition decreased the abundance of microalgae, ciliates and meiofauna, whereas no clear trend was seen for bacteria relative to the control. From the oxygen flux values it was apparent that the systems in control and low-dose containers were autotrophic ($P > R$), whereas in the high-dose treatments the oxygen concentration fell sharply, exhibiting a net oxygen consumption most of the time due to fast mineralization of the macroalgal biomass. The ammonium concentration increased significantly (maximum mean rate 1.4 mmol m^{-2} d^{-1}) and concomitantly with low oxygen values. The content of particulate organic carbon (POC) in the top 5 mm sediment increased by 2 g m^{-2} in both control and low-dose containers due to increased meiofaunal biomass, while in the high-dose treatments the POC content decreased by 2.3 g m^{-2}. From the results it appears that the influence of accumulating macroalgae on the sediment system depends on the amount and the physiological status of the macroalgae. With a high load of drifting macroalgae in a stagnant situation, the structure and function of the sediment community are strongly affected. No significant flow of organic material from the macroalgal mat to the sediment system could be proven. The macroalgal mat apparently constitutes an independent habitat, which influences the sediment community by shading and, when mineralization is fast, by creating unfavourable conditions via low oxygen values.

INTRODUCTION

During the last decade there has been a major re-evaluation of the general view of marine pelagic food webs. Through the use of new sampling techniques the importance of bacteria, flagellates and ciliates in the pelagic energy flow has been discovered. In benthic systems the importance of the microscopic food web has long been recognized. A large number of investigations have dealt with the different 'compartments' of benthic systems, i.e. bacteria, microscopic algae, protozoa and small metazoa, but few studies exist where most or all of these groups are assessed simultaneously. There is still a lack of studies on the relative importance of these groups in terms of numbers and biomass, let alone studies that deal with rates of energy flow (cf. Jansson & Wulff 1977, Montagna 1984, Admiraal et al. 1988, Bouvy 1988).

Twenty years ago the suggestion that large-scale man-induced eutrophication of the sea was in process would most probably have been met with suspicion by scientists, politicians and the public. Today eutrophication of the sea is a subject of intense public debate in Sweden (Larsson et al. 1985, Rosenberg 1985, Fleischer et al. 1987, Rosenberg & Loo 1988), and massive plankton blooms and large-scale bottom anoxia have been reported from other coastal areas as well (e.g. Nielsen & Ærtebjerg 1984, Weigelt & Rumohr 1986, Lancelot et al. 1987). One possible effect of eutrophication, easily

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seen by the public, is the accumulation of vast quantities of macroscopic algae in shallow sheltered bays and on sandy beaches (McComb et al. 1979, Nicholls et al. 1981, Reise 1983, Rosenberg 1985, Wennberg 1987). Little is known about the effect of this accumulation on the community of sandy sediments, in particular the lower trophic levels of the food web.

By using an outdoor experimental set-up we aimed at studying to what extent and how the accumulation of filamentous macroalgae, in quantities found in nature, affects the structure and function of a shallow-water sandy sediment community. Estimates of structural changes were based on relationships between numbers and biomass of bacteria, autotrophs, micro- and meiofauna and their qualitative composition. Effects on the functional level were assessed by measuring primary productivity, changes in carbon pools and oxygen and nutrient fluxes.

MATERIAL AND METHODS

Experimental set-up. The effect of accumulation of drifting macroalgae on a sediment community was studied in an outdoor flow-through system at Tjärnö Marine Biological Laboratory near Strömstad on the west coast of Sweden (58° 52′ N, 11° 09′ E). Twelve circular 30 l containers were placed in a frame of timber fixed between 2 rafts; a roof of transparent PVC prevented contamination by rain and seabird faeces (Fig. 1). Sandy sediment was collected from a nearby shallow bay (0.2 m water depth) in 2 layers (the top 1 cm was scraped off and kept separate) and sieved (mesh size 500 µm) to remove macrofauna [mainly juveniles of the polychaete *Hediste diversicolor* O. F. Müller and the bivalve *Cerastoderma edule* (L.)]. The sand was homogenized and spread out in 2 layers (2 cm of surface sediment on top of a 8 cm thick bottom layer) on the bottom (area 0.1 m^2) of each container. Seawater from 2 m depth was pumped up and filtered through 2 cotton-filter cartridges (50 and 1 µm; Vattenteknik, Malmö, Sweden) before it reached a 50 l cistern (Fig. 1). The water flow to each container was controlled by a rollerclamp on each tube (6 mm i.d.), so that a turnover time of roughly 10 h was established (1.5 l h^{-1}). To allow the vertical chemocline to stabilize, the containers were allowed to equilibrate for 11 d before the experiment was started. The experiment was run for 3 wk (9 to 31 August 1987). During this period the temperature of the overlying water varied between 14.5 and 19.5 °C.

Fresh filamentous red algae (mainly *Rhodomela, Polysiphonia* and *Ceramium* spp.) were collected by diving, and were then rinsed with seawater to remove fauna and epiphytes. We chose to use filamentous red algae because they tend to accumulate in sheltered shallow areas in late summer and autumn and have also been reported to form wracks on the shores of the west coast of Sweden (Wennberg 1987). An amount of 1.8 kg fresh weight (FW) per m^2, corresponding to the natural amount of drifting macroalgae in a nearby sandy bay, was added to 4 containers (referred to as high dose) and half the amount (0.9 kg FW m^{-2}) to 4 other containers (referred to as low dose). These additions initially reduced the light (photon flux density measured by Biosphere quantameter in sunlight at noon) at the sediment surface by about 90 % in the high-dose and by 70 % in the low-dose containers. Four containers without addition of macroalgae served as controls. At the end of the experiment the remaining macroalgae were collected, dried and weighed.

Sampling. On each sampling occasion 2 to 3 cores were taken for each organism group from each container, using a cut-off plastic syringe (diameter 22 mm for meiofauna, chlorophyll *a* and primary productivity; diameter 9 mm for autotrophic microflora, bacteria and ciliates). The top 5 mm of the sediment was used for analyses. A test showed that 90 % of the meiofauna occurred in this layer. Samples (600 ml) from the overlying water were taken for analyses of dissolved inorganic nutrients [NH_4^+, NO_3^- + NO_2^-, PO_4^{3-} and $Si(OH)_4$]. Samples were taken once a week, though oxygen concentration was measured more frequently (see Fig. 10).

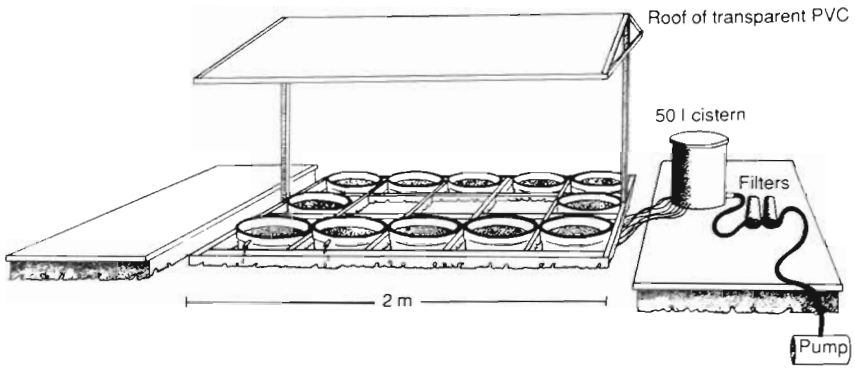

Fig. 1. The outdoor experimental set-up

Primary productivity and chlorophyll *a*. For microphytobenthic productivity and chlorophyll *a* content, 3 sediment cores were taken from each container; 2 cores were pooled and treated as one sample and one was kept separate. Chlorophyll *a* content was analysed according to Lorenzen (1967) after extraction with 90 % acetone overnight and 5 min of ultrasonication. The benthic primary production was measured as ^{14}C uptake in subsamples taken with a glass tube (5.8 mm i.d.) from the homogenized pooled sample. The sediment was spread out in glass vials, and 25 ml of filtered seawater and 0.15 ml of $H^{14}CO_3$ solution (3 µCi) were added. The vials were placed upside down on the bottom of each container and incubated for 2 h (10:00 to 12:00 h). The samples were filtered on 0.2 µm PC-filters (Nuclepore®), put into scintillation vials, 2 drops of 0.1 M HCl were added and the filters were dried at 60°C. The organic matter and filters were dissolved with 1 ml of Soluene®-350 and then, after 8 h, 15 ml of scintillation mixture (Hionic-Fluor™) were added. The samples were counted in a LKB-Wallac 1217 liquid scintillation counter. Total carbon dioxide concentration in the water and carbon assimilated were calculated using equations in Ærtebjerg Nielsen & Bresta (1984). All values were corrected for dark fixation and converted to daily production using insolation values obtained by a Kipp and Zonen solarimeter placed on the laboratory roof. Since incubations were made with the sediment spread out in the incubation bottles, productivity values were corrected to 'intact core' using a factor of 0.4 (Cadée & Hegeman 1974).

Although the inflowing seawater was filtered, we measured ^{14}C uptake in the overlying water to check for phytoplankton growth, by incubating one light and one dark vial from one container of each treatment.

Algal cells. The number of living autotrophic cells was counted using epifluorescence microscopy. Two sediment samples from each container were pooled, diluted with filtered seawater to a volume of 6 ml, and ultrasonicated (Sonorex RK 100) for 10 min. This treatment detached most of the epipsammic cells, but apparently did not break cells, since motile cells could be seen in sonicated samples. Fluorescent cells were counted in a Bürker counting chamber. Cells were grouped into size and shape classes and identified as far as possible to genus level. Average cell volume and carbon content for each group were calculated according to Edler (1977, 1979). The factor to convert cell volume to carbon varied between 0.085 and 0.11.

Ciliates. Ciliates were extracted by a modified version of the seawater-ice method (Fenchel 1967). The samples were transferred to plastic test tubes (15 mm i.d.) with a bottom of nylon gauze (mesh size 100 µm), and covered with cotton and seawater ice. The nylon gauze was brought into contact with 0.2 µm-filtered seawater in a Nunc M24 multivial (Nunc AS, Denmark) for 1 h, which probably extracted ca 80 % of the ciliates (own preliminary testing; Fenchel 1967). The ciliates were preserved in Lugol's solution and counted within 12 h in an inverted microscope at × 250, differentiating into 3 size classes (length < 50, 50–150, > 150 µm). The biovolume of 30 individuals from the medium and large size classes were measured in the microscope by squeezing them between glass slides as described by Fenchel (1967). Ciliates smaller than 50 µm were assigned a volume of 10 000 μm^3 (Jonsson 1987). Biovolume was converted to carbon using conversion factors AFDW = 0.15 × volume (Finlay & Uhlig 1981) and carbon = 0.43 × AFDW (Fenchel & Finlay 1983).

Meiofauna. Sediment cores were preserved in 4 % borax buffered formalin containing rose bengal. The organisms were extracted by decantation (Uhlig et al. 1973). The supernatant was poured through a set of sieves with mesh sizes 0.5, 0.2, 0.1 and 0.04 mm. The remaining heavy residue was checked for dense organisms (mainly foraminiferans, ostracodes and bivalves). The number of organisms in each size fraction was sorted into major taxa and counted under a low power microscope at × 25 to 50. The number of organisms in each size fraction was used for conversion into AFDW, as given in Widbom (1984). AFDW was converted to carbon using a factor of 0.45 (Båmstedt 1986).

Bacteria. Samples were preserved in 4 % borax-buffered 0.2 µm-filtered formalin. The number of bacterial cells was counted using acridine orange epifluorescence microscopy (Hobbie et al. 1977). Samples were shaken with 1 M KCl for 1 h to break electrostatic interactions (M.-O. Samuelsson pers. comm.) and homogenized for 30 s. Two filters were prepared from each core and the number of bacteria on 10 microscopic fields were counted on each filter. The biovolume of 20 bacterial cells from each core was measured, assuming a spherical shape for cocci and a cylindrical shape for rods. Volume was converted to carbon using the same conversion factors as for ciliates.

Particulate organic carbon (POC) and nitrogen (PON). The contents of POC and PON of dried and homogenized sediment and macroalgal samples were measured using a Heraeus CHN-O-RAPID elemental analyser. For POC analyses, the sediment samples were treated with 2.5 M HCl for 30 min at 40°C to remove inorganic carbon. Sediment samples were taken on Days 1, 16 and 23, and macroalgal samples were taken on Days 1 and 23.

Oxygen. The oxygen concentration in the inflowing water (in the cistern) and in the unstirred overlying water in the experimental containers was measured

with a YSI Model 58 oxygen electrode. During the measurements the electrode was kept 1 to 2 cm above the sediment surface.

Inorganic nutrients. Samples for analyses of NH_4^+, $NO_3^- + NO_2^-$, PO_4^{3-} and $Si(OH)_4$ were taken from the water cistern and, after stirring, from the overlying water of each experimental container. The samples were immediately filtered (Whatman GF/F, retension capacity 0.7 µm) and nutrients were analysed according to methods described by Carlberg (1972).

Statistical analysis. Visual inspection of data-plots and variance-ratio tests indicated that data were not normally distributed and that variances were non-homogeneous. Application of Taylor's power law (Green 1979) suggested a $\sqrt{x+1}$ transformation. Inspection of transformed data showed that the transformation was successful in reducing non-normality and heterogeneity of variances. The effect of treatments on different variables was tested by a 2-way nested ANOVA (Underwood 1981, p. 585). Further comparisons between different means were tested by using Newman-Keuls multiple comparison test (NK), with differences accepted as significant when $p < 0.05$.

RESULTS

Visual observations

The containers within each treatment behaved very similarly with one exception (see below). In the control containers the sediment surface kept a light-brownish colour during the entire experiment. In the low-dose containers the macroalgae floated at the water surface throughout the experiment (bubbles, most likely oxygen, were formed in the algal mat). In the high-dose containers, the macroalgae soon turned into a greyish mat floating just above the sediment surface, which turned black within 2 wk, and a smell of H_2S was noted. At the end of the experiment, the sediment surface in these containers turned more light-coloured as a result of improved oxygen conditions. One of the 4 high-dose containers, however, behaved more like a low-dose container (cf. oxygen flux values below). We did not exclude this container from the statistical data sets, but in order to clarify differences between treatments, we give 2 means where n = 4 or 3.

Autotrophic microflora

There was no consistent difference between treatments in the biomass of sediment-associated microalgae (ANOVA, $p > 0.05$), but there was a significant difference between days (ANOVA, $p \leq 0.01$). The number and biomass of the microalgae did not change significantly in the control containers during the course of the experiment (NK, $p > 0.05$), being about 70 to 80 $\times 10^9$ cells m^{-2} corresponding to 650 to 700 mg C m^{-2} (Fig. 2). In the low-dose containers, the microalgal biomass first increased (by 200 mg m^{-2} during the first week), mainly due to the growth of filamentous cyanophytes, and then declined slightly, but was qualitatively similar to the control containers: small (5 to 20 µm) naviculoid diatoms and plate-shaped cyanophyte colonies (*Merismopedia* and *Microcrocis* spp.) together with filamentous cyanophytes (*Oscillatoria* and *Phormidium* spp.) made up most of the biomass (Fig. 2). In the high-dose containers the biomass of viable microalgae grew qualitatively differently (plate-shaped cyanophyte colonies dominated over thread-like

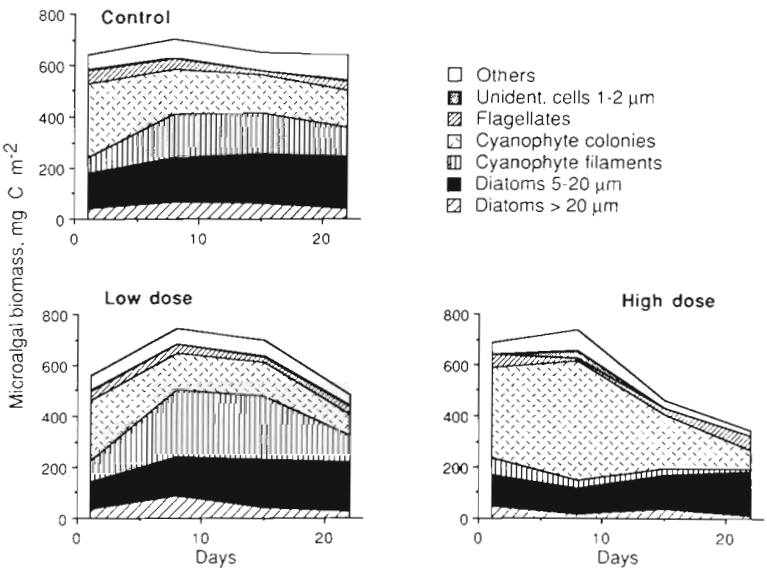

Fig. 2. Biomass and composition of autotrophic benthic microflora in the top 5 mm sediment. Curves are based on means of 4 replicate containers. Control = containers with no addition of macroalgae; low dose = addition of 0.9 kg FW m^{-2} of filamentous red algae; high dose = addition of 1.8 kg FW m^{-2} of filamentous red algae

cyanophytes) and at the end of the experiment the total biomass had significantly decreased (by 50 %) from the initial value (NK, $p \leq 0.05$), whereas the biomass of diatoms remained unchanged (Fig. 2).

Chlorophyll *a*

The mean chlorophyll *a* content of the sediment varied between 40 and 90 mg m^{-2} (Fig. 3), but there was no significant difference between the treatments until Day 23, when values in the control containers were significantly higher than in the low- and high-dose treatments (NK, $p \leq 0.05$).

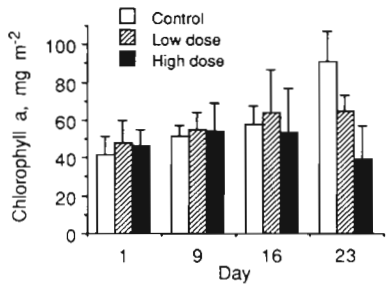

Fig. 3. Chlorophyll *a* content in the top 5 mm sediment. Each bar shows mean + SD (n = 4). For explanation of treatments see Fig. 2

Ciliates

Ciliate numbers and biomass decreased in all treatments as the experiment continued (Fig. 4). There was a significant difference between treatments (ANOVA, $p \leq 0.05$) and between dates (ANOVA, $p \leq 0.001$). There was no significant difference between containers at the start of the experiment (mean values 1.1×10^7 individuals m^{-2} corresponding to about 60 mg C m^{-2}), but with time ciliate numbers and biomass in the high-dose containers decreased most and from Day 9 onwards they were significantly lower than in the control and low dose containers (NK, $p \leq 0.05$) (Fig. 4).

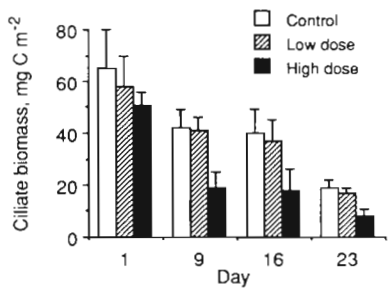

Fig. 4. Biomass of ciliates in the top 5 mm sediment. Each bar shows mean + SD (n = 4). For explanation of treatments see Fig. 2

Meiofauna

The meiofauna populations were strongly affected by the high-dose addition of organic material. The biomass of total meiofauna differed between treatments (ANOVA, $p \leq 0.025$) and between days (ANOVA, $p \leq 0.01$), and a significant treatments × time interaction term (ANOVA, $p \leq 0.001$) shows that treatments developed differently with time. The biomass of the total meiofauna in the control and low-dose containers increased (from 250 mg C m^{-2} on Day 1 to 560 mg C m^{-2} on Day 23 for control and from 220 to 570 mg C m^{-2} for low-dose), while it decreased in the high-dose containers (from 260 mg C m^{-2} on Day 1 to 150 mg C m^{-2} on Day 23) (Fig. 5). On Days 16 and 23 the biomass in the high-dose containers was significantly lower than in the control and low-dose containers (NK, $p \leq 0.05$). The composition of meiofauna also differed between treatments (Fig. 5). The control and low-dose containers developed towards a diverse community, where harpacticoid copepods, rotifers and foraminiferans occurred in large numbers and where ostracodes and bivalves were important in terms of biomass (Fig. 5). The high-dose containers developed in the same way at first, but after Day 9 these groups declined and a community dominated by nematodes began developing.

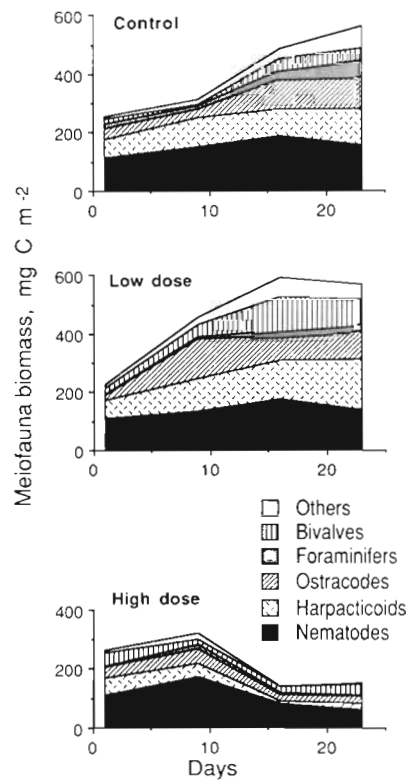

Fig. 5. Biomass and composition of meiofauna in the top 5 mm sediment. Curves are based on means of 4 replicate containers. For explanation of treatments see Fig. 2

Bacteria

We could not detect any clear trend in the number and biomass of bacteria. The biomass of bacteria varied only slightly in this experiment (between 90 and 190 mg C m^{-2}) (Fig. 6), and no significant differences between times and treatments could be found (ANOVA, $p > 0.05$). The average biovolume per individual cell did not differ significantly between treatments, and varied between 0.2 and 0.5 μm^3 during the experiment.

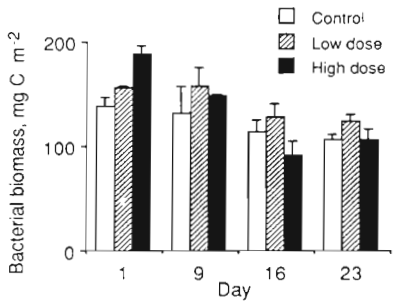

Fig. 6. Biomass of bacteria in the top 5 mm sediment. Each bar shows mean + SD (n = 4). For explanation of treatments see Fig. 2

Proportions of organism groups

Initially, living autotrophic microalgae constituted 58 % of the carbon associated with living biota (Fig. 7). This proportion decreased to 46 % in the control and 40 % in the low-dose treatment at the end of the experiment, but did not change significantly in the high-dose containers. The most obvious change in the control and low-dose containers was that the proportion of meiofauna increased from an initial 23 % to a final 42 % (their biomass had already doubled after 2 wk), while in the high-dose containers the proportion of meiofauna did not change, although its composition and biomass were altered (see above). Ciliates initially accounted for the least part of the living biota (5 %), and decreased to about 1 % in all treatments. The proportion of bacteria was 15 % in control and low-dose and increased to 20 % in the high-dose treatment.

POC and PON

Addition of filamentous algae initially corresponded to 71.2 g m^{-2} (high dose) and 35.6 g m^{-2} (low dose) of organic carbon (C/N mole ratio 9.7). The POC in the macroalgal mat decreased by 13.2 g C m^{-2} (mean rate 0.6 mg m^{-2} d^{-1}) in the low-dose containers and by 51.7 g C m^{-2} (mean rate 2.4 mg m^{-2} d^{-1}) in the high-dose containers, corresponding to a decrease of 37 and 73 %,

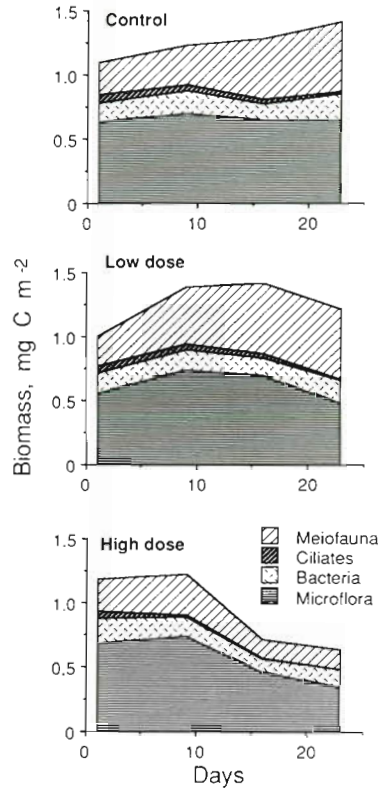

Fig. 7 Total biomass of living organisms and proportions between organism groups in the top 5 mm sediment. Curves are based on means of 4 replicate containers. For explanation of treatments see Fig. 2

respectively. The PON values decreased by 45 and 61 %, respectively and thus, at the end of the experiment there was a significant difference between the C/N mole ratio of the macroalgal biomass in the low-dose (C/N 11.2) and the high-dose (C/N 6.8) treatments. The mean initial POC content of the sand was 10.9 g m^{-2}. At the end of the experiment the carbon contents in both the control and low-dose containers had increased, though not significantly (NK, $p > 0.05$), by 2 g m^{-2} (Fig. 8), corresponding to a mean rate of 95 mg C m^{-2} d^{-1}. The increase rate was highest (200 mg C m^{-2} d^{-1}) during the first 2 wk in the control containers (Fig. 8). In the high-dose containers, the carbon content decreased significantly by 2.3 g (NK, $p \leq 0.05$), corresponding to a mineralization rate of 110 to 126 mg C m^{-2} d^{-1} The initial content of PON in the sediment (1.6 mg m^{-2}) did not change significantly in the control containers, and increased, though not significantly, by 0.4 mg m^{-2} (25 %) in the low-dose treatment. In high-dose containers the N-content decreased significantly by 0.6 mg m^{-2} or 38 % (NK, $p \leq 0.05$). The initial C/N mole ratio of the sediment was 8.0 (CV = 7.5 %) and no significant change could be seen at the end of the experiment nor between the treatments.

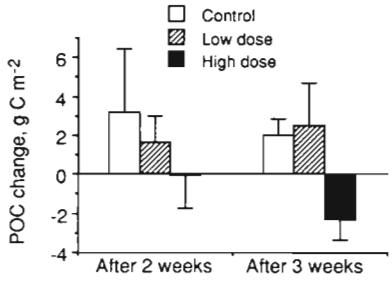

Fig. 8. Changes in the content of particulate organic carbon in the top 5 mm sediment. Each bar shows mean + SD (n = 4). For explanation of treatments see Fig. 2

Primary productivity in the sediment

Microphytobenthic primary productivity in the low-dose containers (160 to 310 mg C m^{-2} d^{-1}) did not differ significantly from the control (190 to 270 mg C m^{-2} d^{-1}) (Fig. 9), whereas the values for the high-dose treatment decreased significantly (NK, $p \leq 0.05$). After about 2 wk these values were only one-third (80 mg C m^{-2} d^{-1}) of the control values, but there was a slight increase at the end of the experiment (Fig. 9). Primary productivity in the overlying water varied between 0 and 10 mg C m^{-2} d^{-1}, which is at most 6% (mean 2.3%) of the sediment primary productivity.

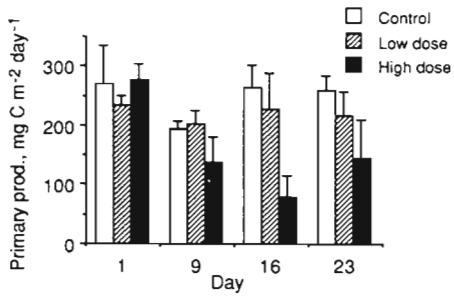

Fig. 9. Microbenthic primary productivity in the top 5 mm sediment. Each bar shows mean + SD (n = 4). For explanation of treatments see Fig. 2

Oxygen flux

Oxygen concentrations in the low-dose containers varied between 5 and >20 mg l^{-1} and did not differ significantly from those in the control containers (NK, $p > 0.05$). Calculation of oxygen fluxes indicated that the system in these containers was autotrophic ($P > R$) most of the time, with the mean maximum net rate of oxygen production being 140 mg in the control and 170 mg O_2 m^{-2} h^{-1} in the low-dose treatment (Fig. 10). Occasional diurnal measurements showed that the oxygen concentrations were highest in the late afternoon and early evening and lowest in early morning. Since we normally measured oxygen concentrations at 09:00 h, our values are likely to represent rather low values. In the high-dose containers oxygen concentrations fell sharply to values close to 0 mg l^{-1} within a week (except in one container), thus exhibiting a net oxygen consumption most of the time (maximum mean rate 110 mg if n = 4 and 135 mg O_2 m^{-2} h^{-1} if n = 3) (Fig. 10). Towards the end of the experiment (Days 20 and 22) a net production of oxygen was observed in the high-dose containers.

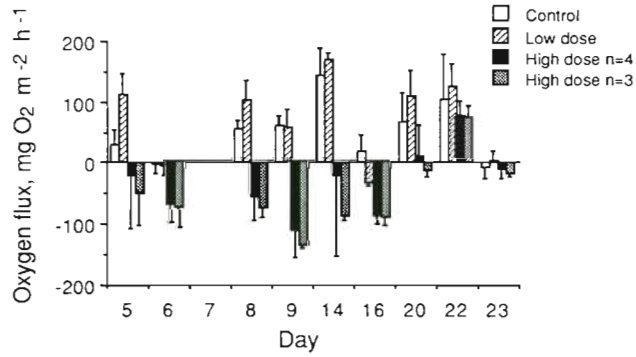

Fig. 10. Oxygen flux in the overlying water. Positive values = net production, negative values = net consumption. Each bar shows mean + SD (n = 3 and 4). For explanation of treatments see Fig. 2

Inorganic nutrients

Concentrations of inorganic N and P in the surface water (= inflow) were low during the entire experiment ($NH_4^+ < 2$ µM, $NO_3^- + NO_2^- < 0.5$ µM, and $PO_4^{3-} < 0.1$ µM). The ammonium flux differed between treatments and days as shown by a significant interaction term in the ANOVA ($p \leq 0.005$). There was no significant difference between the ammonium flux in the control and the low-dose containers; NH_4^+ was released in the beginning of the experiment (mean rate of 170 µmol m^{-2} d^{-1}), but was later taken up at a maximum rate of 530 µmol m^{-2} d^{-1} (Fig. 11a). In the high-dose containers NH_4^+ values increased significantly (NK, $p \leq 0.05$) in connection with low oxygen values at a mean rate of up to 1.4 (2.1 when n = 3) mmol m^{-2} d^{-1} (Fig. 11a), except in one container in which oxygen values did not drop and NH_4^+ was instead taken up at the same rate as in the control and low-dose treatments.

The flux of $NO_3^- + NO_2^-$ (mainly uptake varying between 10 and 150 µmol m^{-2} d^{-1}) did not differ significantly between treatments (ANOVA, $p > 0.05$) but between days (ANOVA, $p \leq 0.001$) (Fig. 11b). From Day 9 to Day 16, however, there was a significant increase in the disappearance rate of $NO_3^- + NO_2^-$ in the high-dose treatment (NK, $p \leq 0.05$) (Fig. 11b).

Phosphate concentrations in the overlying water

were close to the limit of detection and thus the calculated flux rates should be interpreted with caution. The PO_4^{3-} flux rates were low (+30 to −30 µmol m^{-2} d^{-1}) (Fig. 11). The variation among replicate treatments was high and no significant difference was observed between treatments (ANOVA, $p > 0.05$). With time, however, there was a significant change in the direction of fluxes, from efflux on Day 1 to uptake on Day 23 (ANOVA, $p \leq 0.001$).

Silicate concentration of the inflowing surface water varied between 4 and 8 µM during the experiment. The ANOVA showed that treatments developed differently with time (treatments × time interaction term $p \leq 0.01$). An uptake of silicate was observed in all containers, mean values of treatments varying between 250 and 2050 µmol m^{-2} d^{-1} with no significant difference between treatments except once: silicate was released at a maximum rate of 400 µmol m^{-2} d^{-1} in the high-dose containers in connection with low oxygen values (NK, $p < 0.05$) (Fig. 11d).

DISCUSSION

Experimental set-up

The advantages and disadvantages of enclosures such as micro- and mesocosms, as compared with field experiments, have previously been discussed (Bloesch 1988 and references therein). The greater precision of measurements, gained by easier sampling and replication and adequate control treatments, is achieved at the price of creating a more or less artificial situation. In our experiment we sieved the sediment, excluded epifauna, prevented immigration and emigration, and altered the wave impact. In order to measure the flux of nutrients, it was also necessary to maintain a controlled low rate of water exchange. The 'healthy' look of control containers, however, indicated that we had not decreased this rate below that necessary to sustain a normal community. Since microfauna and bioturbation (e.g. Kristensen & Blackburn 1987) as well as water exchange and wave forces tend to prevent anoxia in sediments, our set-up probably amplified the effect of the treatments. Stagnant situations, where detached macroalgae or detritus can remain in the same place, are however not uncommon in sheltered bays and on sublittoral sediments (e.g. Hylleberg & Henriksen 1980, own obs.).

We can use the estimated population densities of the control containers to see how natural our experimental set-up was. The number and biomass of benthic microflora, as well as chlorophyll *a* content, of the sediment was within the range of values reported for sandy sediment in temperate areas (Plante et al. 1986 and references therein). Since microphytobenthos and diatoms are commonly regarded as synonyms (with the exception of salt marshes, where cyanophytes are common; e.g. Kaas 1987), it is noteworthy that initially only about one-third of the living microfloral biomass consisted of diatoms, the rest being mainly cyanophytes and various flagellates. This was probably due to the time of the year and the type of sediment used, i.e. sand from a brackish non-tidal area, which lacks the dense, vertically migrating epipelic diatom flora typical of tidal flats (Admiraal 1984, Paterson 1986), a habitat from which hitherto most investigations on marine and brackish-water microphytobenthos originate.

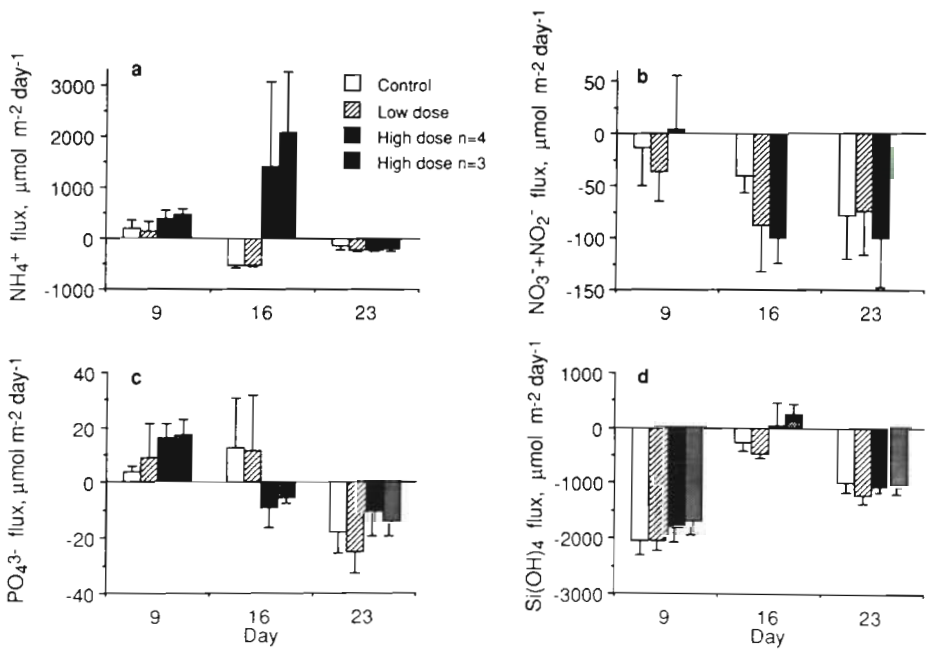

Fig. 11. Rates of decrease and increase of (a) NH_4^+, (b) NO_3^- + NO_2^-, (c) PO_4^{3-} and (d) $Si(OH)_4$ in the overlying water. Each bar shows mean + SD ($n = 3$ and 4). For explanation of treatments see Fig. 2

Our values for total meiofauna (1 to 2 × 10^6 individuals m^{-2}) and AFDW (around 0.5 to 1 g m^{-2}) are typical values for this kind of sediment and sampling methods (Rudnick et al. 1985). From being dominated mainly by nematodes and harpacticoids on Day 1, the control containers developed a more diverse community. The ciliate populations declined most likely as a consequence of our experimental arrangement; the decrease of water movement over the sediment resulted in the blocking of interstitia by detritus and autotrophs. Fenchel (1969, 1978) showed that benthic ciliates can be very specific in their requirements of food, sediment particle sizes and oxygen profile, and they are in general least numerous in non-capillary sediments. The number and biomass found for the controls in our experiment (5 × 10^6 to 1.25 × 10^7 individuals m^{-2} and 0.3 to 1.1 g wet wt m^{-2}) are typical values for ciliates in fine sand (Fenchel 1969).

Bacterial numbers and biomass found in control containers at the beginning and during the experiment are similar to those normally found in silty sand (Cammen 1982, Montagna 1982, Branch & Pringle 1987, Bianchi 1988).

Considered as a total – the biomass, density and proportions of organisms in control containers – the system does not indicate an unnatural structure, but approximately mimics a situation where a sandy sediment under stagnant conditions is gradually converted to a less capillary sediment.

Effect of macroalgal addition on the structure of the sand ecosystem

The addition of organic material either did not change the community composition to any significant degree (low dose) or changed the composition completely (high dose). We had expected that a moderate amount (low dose) of macroalgae would stimulate bacterial activity and in the end also increase the pool of nutrients available to the microphytobenthos (Owens & Stewart 1983, Levinton 1985). This would have led to an increased amount of food available for ciliates and meiofauna. If they were limited by the amount of food, a greater increase in populations in low-dose containers than in control containers would have been expected. But neither bacteria nor microphytobenthos increased significantly more in low-dose containers compared with control containers. This means that we do not know if the meiofauna and ciliates were food-limited in this experiment. Since they were not significantly fewer in the low-dose containers than in control containers, the low-dose treatment did not deteriorate the conditions either (at least not until the last date), which is also supported by the oxygen values. The lack of response might have been due to a lag time, which was not revealed by our 3 wk experiment. In a field experiment, Levinton (1985) found that detritus derived from *Ulva*, which was blended, dried and mixed with the sediment, subsidized diatom growth only after a 2 to 3 wk lag time.

The high-dose community, on the other hand, did soon deteriorate, which quickly showed in microalgal, meiofauna and ciliate abundances. In the microalgal assemblage, a change in the species composition preceeded a decrease in the biomass. Levinton (1985) found that detritus addition initially depressed diatom standing stock. Despite the 50% decrease of the total microalgal biomass in our experiment, the diatom biomass was unaltered, which most likely demonstrates the capacity of benthic diatoms to tolerate anoxic conditions and sulfides (Admiraal 1984, Kennett & Hargraves 1985, Sundbäck & Granéli 1988). Low oxygen values during the middle of the experiment probably caused death of ciliates and most meiofauna groups. Nematodes did survive, although only in low numbers, which agrees with what has been found in several pollution studies (e.g. Widbom & Elmgren 1988). Ciliates were almost eradicated, which is puzzling since many ciliate species have the ability to tolerate anoxia and high levels of H_2S (Fenchel 1969). All the sediment that we put into the containers was oxygenated, so it is possible that no strictly anaerobic ciliates initially occurred in the containers, and also our experimental set-up prevented immigration from underlying anoxic sediments. Since the anaerobic ciliate community can be very diverse and abundant (Fenchel 1969), our set-up might have underestimated the ciliate activity that would occur in these sediments in nature.

The experiment was run for 3 wk and we do not know for certain whether the difference between low-dose and high-dose containers would have persisted, or if the low-dose containers after a time lag would have developed in a similar way as did the high-dose containers. However, since the amount of carbon added in the low-dose containers was 50% of the amount added in the high-dose containers, the deteriorating, if any, would most certainly be less drastic than in the high-dose containers.

Effect of macroalgal addition on the carbon pool

The addition of drifting macroalgal biomass could theoretically mean 2 alternative impacts on the function of the sediment ecosystem. (1) The productivity in the sediment would increase because of the extra source of energy and nutrients derived from allochthonous organic matter (see discussion above), an effect that is in accordance with the view that marine

sandy shallow areas are dependent on the import of organic carbon (e.g. Postma 1988). However, recent investigations from tidal sandy areas have also shown that autochthonous primary production may cover the food requirements of the benthos (Asmus & Asmus 1985, Reise 1985, Biological Research Ems-Dollard Estuary 1985). (2) Alternatively, the sediment below a (decomposing) macroalgal mat would turn into an unfavorable habitat with low oxygen concentrations (cf. Nicholls et al. 1981); even the oxygen-producing microphytobenthic photosynthesis would be eliminated through lack of light. The floating algal mat would then, at least temporarily, be a more favourable habitat for organisms, if they were capable of taking advantage of this new habitat (cf. Reise 1983), and the local biological activity would then move from the sediment up to the algal mat. Emigration to uncovered refuges, as found by Reise (1983), was not allowed in our experimental set-up. The new habitat would also favour epibenthic animals (Nicholls et al. 1981). We did not investigate the floating macroalgal mat separately (except for POC and PON content), and thus we could only get indirect information of processes in this habitat. A microscopic examination showed that the macroalgal mat in the low-dose containers sustained a dense epiphytic and microfaunal community, indicating a diverse and high biological activity.

The input of organic carbon in the form of filamentous algae was about 6 times (high dose) and 3 times (low dose) the initial amount of sediment POC, i.e. a considerable potential carbon source. The fact that the carbon content of the sediment in the high-dose containers decreased indicates that there was no significant direct input of POC from the macroalgal mat to the sediment. The number of bacteria in the sediment did not increase either. This agrees with the results of Levinton (1985), who suggested that bacterial productivity rather than abundance would respond to a detritus addition. Apparently most of the macroalgal carbon was mineralized in the algal mat itself, and was released as CO_2 and as dissolved organic matter (DOM), which we did not measure. The difference between the final C/N mole ratio of the macroalgae in low and high doses (11.2 and 6.8, respectively) may be due to a qualitative change in the algal mat with time, e.g. by the addition of new material in the low-dose containers through production (cf. Kristensen & Blackburn 1987). The mineralization was fast: in high dose treatments >70% carbon disappeared within 3 wk. Schmidt (1978) found that the mineralization rate of macroalgae was highly dependent on temperature and that under aerobic conditions 40% of the red algal carbon disappeared at 15°C during a 14 d decomposition experiment. Koop et al. (1982), who investigated mineralization of kelp on a beach, found that 70% of the carbon was lost as CO_2 to the atmosphere, while 28% passed to bacteria. They also found high DOM concentrations beneath decomposing kelp. The increase of sediment carbon in the low-dose treatment (equal to the increase in the controls) was likely due to sediment primary production, since the magnitude of increase in living microalgal biomass, ^{14}C-uptake and POC were about the same in the control and low-dose containers. Furthermore, the increase of pheopigments was the same in the control and low-dose containers, indicating that pheopigments too were mainly of microphytobenthic origin. Thus the overstory of decomposing macroalgae seems to have constituted an independent system that influenced the energy flow of the sand ecosystem only indirectly through shading and changing the oxygen (and possibly nutrient) conditions. The lack of coupling between the sediment and the algal mat can perhaps be partly a result of the fact that the macroalgal filaments were floating above the sediment surface and not buried into the sediment, as has been shown to be the case for, for example, detached green algae in other studies (Hylleberg & Henriksen 1980, Owens & Stewart 1983). An other reason might be the initial absence of epifaunal grazing and fragmentation in the algal mat.

Only about 10% of the initial POC of the sediment originated from living organisms, according to our calculations based on biovolumes. This agrees with the results of Cammen (1982), who found a large unidentified POC pool with a C/N weight ratio near 7 (= 8.2 mole ratio), i.e. close to our mean C/N ratio (8.0). Initially the microalgae made up 5.8%, bacteria 1.5%, ciliates 0.5% and meiofauna 2.3% of the total sediment POC. These values agree well with those found by others in similar sediments. Cammen (1982) found that bacteria always accounted for less than 2% and according to Bianchi (1988) benthic diatoms made up 3 to 6% of the total POC, while bacteria only accounted for 0.01 to 0.03%. There is, however, one group of organisms that we were not able to include in our calculations of the living biomass, i.e. heterotrophic flagellates. For example, more than half of the dinoflagellate species found on sandy substrates in the Danish Wadden Sea are confined to heterotrophic nutrition (Larsen 1985).

Our methods for calculating biomass from biovolumes may include several sources of error that lead to underestimations of the carbon content. Since a large part of microalgal carbon can be associated with dead (not fluorescent) cells, counting living (= fluorescent) algal cells underestimated the total microalgal carbon. Increasing pheopigment values during the experiment indicated increase of dead algal cells, most probably through grazing. If the microalgal biomass is instead calculated from chlorophyll *a* values using a

mean C/chl *a* ratio of 40 (de Jonge 1980, Cammen and Walker 1986), we obtain an initial value of 1.8 g C m^{-2}, which is 3 times higher than our mean value calculated from biovolumes (0.63 g C m^{-2}). Our initial C/chl *a* ratios (calculated from carbon values based on biovolumes) varied between 12 and 15, but decreased during the experiment to final values of 7 to 8. However, we do not know if these low ratios reflect natural highly variable ratios (de Jonge 1980) or methodological problems. In containers with macroalgal addition the lowered ratio might also reflect shade adaptation by the microalgae, i.e. an increase of the chlorophyll *a* content per cell.

The increase of sediment carbon between Day 1 and Day 23 (2 g m^{-2} based on elemental analyses) in the top 0.5 cm sediment of the control and low-dose containers could only to a minor part (16 and 10 %, respectively) be traced as increased biomass of living organisms (smaller than 0.5 mm) and was mainly due to increased meiofaunal biomass. This indicates that processes turning living biomass into accumulating detritus are rapid and agrees with what Asmus & Asmus (1985) found for the grazing food chain on a sandy tidal flat. In the high-dose containers 24 % of the POC decrease could be traced to decreased biomass of living organisms.

In the control containers the only source of increase in sediment carbon was the microphytobenthic primary production, calculated to be 5.2 g C m^{-2} for the whole experimental period based on ^{14}C-uptake. About 40 % of this value was observed as an increase of the sediment POC at the end of the experiment, and thus about 60 % of the assimilated carbon was probably lost via respiration and as DOM. This indicates that in the control containers the autochthonous primary productivity was high enough to support the energy demand of the benthos and in the end also explain the increase of the meiofaunal biomass.

An addition of 0.9 kg FW m^{-2} of macroalgae hardly changed the flows of oxygen when compared with the controls. The benthic primary productivity was not significantly lowered either, which would have been expected from the shading of the algal mat, thus suggesting shade adaptation of the benthic microalgae. The increased respiration and mineralization caused by the macroalgal addition were apparently balanced by primary production by the macroalgae and their epiphytes (diatoms and cyanophytes), since the oxygen production in the low-dose containers corresponded to that of the control containers. When the amount of drifting macroalgae was doubled a threshold was passed and both the structure and the functioning of the ecosystem was altered.

Although the rapid decomposition of macroalgae in the high-dose containers created a low-oxygen situation, which led to dark coloured sediment with H_2S production, the microphytobenthos did partly retain their photosynthetic capacity. The ability of the sediment microflora to recover fast was demonstrated by both increased microbenthic primary productivity and oxygen production at the end of the experiment, which has also been shown in previous experiments (Admiraal 1984, Sundbäck & Granéli 1988).

Inorganic nutrients

The experiment was run during August, a period with low concentrations of inorganic nutrients in the surface water (caused by dinoflagellate blooms) characteristic for late-summer situations. Several recent investigations have demonstrated the influence of microphytobenthos on the nutrient flux between sediment and water (Carlton & Wetzel 1988, Hansson 1988, Kelderman et al. 1988, Sundbäck & Granéli 1988). The microflora controls flux both by uptake from the overlying water and by regulating redox-sensitive processes, such as adsorption/desorption of phosphorus and ammonium flux, by photosynthetical oxygen production (Carlton & Wetzel 1988, Sundbäck & Granéli 1988).

Assuming a C/N mole ratio of 10 (Brzezinski 1985) and a mean daily primary production of 250 mg C m^{-2} for the control containers (Fig. 9), the sediment microflora would have needed 2.1 mmol N m^{-2} d^{-1}, i.e. 3.5 times the recorded maximum disappearance of inorganic N ($NH_4^+ + NO_3^- + NO_2^-$) from the overlying water. To this is added the requirements of bacteria (Wheeler & Kirchman 1986). This indicates either that the microphytobenthos was nitrogen-limited or that the main part was taken up from the pore water, which usually contains an order of magnitude higher concentrations than the overlying water (cf. Granéli & Sundbäck 1985). Regenerated ammonium might also have been rapidly recirculated within the benthic system. We do not know either to what extent the benthic microalgae may have used DON, such as free amino acids, as nitrogen source (Flynn & Butler 1986 and references therein). If we assume that 30 to 40 % of the primary production in the control containers was accounted for by diatoms, then the silicate uptake would be in the range 2.1 to 2.8 mmol m^{-2} d^{-1} (Si/C mole ratio 0.34; Marker & Casey 1982), which is of the same magnitude as the maximum uptake we measured.

It is difficult to interpret the role of the macroalgal mat for the nutrient fluxes from our data on inorganic nutrients. There was in most cases no significant difference between treatments. The macroalgae and associated bacteria could be expected either to compete for nutrients or release nutrients through mineralization. At least in the high-dose containers, where mineralization was fast, it would have been reasonable to expect a

raised level of inorganic nutrients. Both processes were probably operating simultaneously, in particular in the low-dose containers where the macroalgae were covered by a dense assemblage of epiphytes. Thus, during the experiment the nutrients seem to have been circulated within the algal mat itself (cf. McComb et al. 1979, Owens & Stewart 1983).

In the high-dose containers ammonium was released concomitantly with the low oxygen values. Microphytobenthic photosynthesis was not able to balance the high rate of oxygen consumption, thus accelerating the release of ammonium, which may have originated from the macroalgal mat as well as from the sediment. However, in this study phosphorus was not released, which is in contrast to what has previously been found in oxygen-depleted situations (e.g. Enoksson 1987, Carlton & Wetzel 1988, Sundbäck & Granéli 1988). On the other hand the simultaneous release of silicate was probably caused by a decreased Si-uptake by benthic diatoms (cf. Kelderman et al. 1988), since silicate flux is not considered to be redox-sensitive.

In conclusion, our experiment suggests that the impact of the accumulation of drifting macroalgae on the sediment community involves a threshold effect, which depends on the amount and the physiological status of the algae. With a large load of drifting macroalgae in a stagnant situation, the structure, and consequently the functioning, of the sediment community is strongly affected. We could not prove any significant flow of organic material from the algal mat to the sediment during the course of our 3 wk experiment. Inorganic nutrients (mainly ammonium) were released only when oxygen values were very low, and must therefore have been circulated within the macroalgal cover. The algal mat apparently constitutes an independent habitat, which influences the sediment community by shading and, when mineralization is fast, by creating unfavourable conditions via low oxygen values. Since our experimental set-up excluded factors such as wave impact and changes in the direction of currents, which may remove the algal mat, as well as emigration and immigration of organisms, our conclusions need to be verified by in situ investigations where both the sediment and the algal mat are studied.

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