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Effect of Sediment Load on the Microbenthic Community of a Shallow-Water Sandy Sediment

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ABSTRACT: Anthropogenic activities, such as construction work, dredging, and different kinds of recreation activities, can alter sediment loading in shallow coastal areas. The effect of increased load of fine sediment on the microbenthos (benthic microalgae, bacteria, and meiofauna) was studied in two experiments using undisturbed cores of a sandy sediment from a microtidal bay on the Swedish west coast. In each experiment, a total of 24 cores were incubated in an outdoor flow-through set-up. Twelve cores were treated with a 2.5-mm thick layer of autoclaved fine-grained, (silt) carbon-rich surface sediment. In the first experiment, estimates of the impact were based on measurements of chlorophyll *a*, biomass of microalgae, bacteria, and meiofauna, and bacterial production. The main purpose of the second experiment was to study the effect on sediment oxygen profiles using microsensors. Within a week, after being covered by fine sediment, benthic microalgae (particularly diatoms) had migrated upward and the oxygen profiles were restored at the sediment surface by photosynthesis. However, the oxygen-producing layer became thinner and the algal composition changed. Bacterial biomass was restored to the same level as in the sandy sediment. Meiofauna also appeared to move upward and the meiofaunal composition was re-established. The results suggest that the microbenthic community of sandy sediment has an inherent capacity to recover after a moderate deposition of fine-particle sediment. Active upward migration of benthic diatoms appears to be a key mechanism for restoring the oxygenation of the sediment surface. The altered sediment type also implies changed species composition, and hence altered benthic trophic interactions, which may affect, for example, flatfish recruitment.

Introduction

In the coastal zone, shallow-water sediments constitute highly productive areas providing foraging and breeding grounds for many commercial fish species and their prey (e.g., Pihl and Rosenberg 1982; Pihl 1989 and references therein). Where macroscopic vegetation is lacking, sediment-associated microalgae, such as diatoms, cyanobacteria, and various flagellates, are the only autochthonous primary producers, constituting an important carbon source for the local benthic food webs. This microalgal community, concentrated in a thin (few millimeters) photic zone, forms a highly active biofilm at the sediment-water interface. Hence, it has a substantial impact on the exchange of both dissolved and particulate matter between the sediment and the water column, influencing processes such as nutrient fluxes (Rizzo et al. 1992; Reay et al. 1995) and stabilization of the sediment (Yallop et al. 1994). Above all, the oxygenation of the sediment surface by algal photosynthesis is one important factor influencing most processes at the sediment surface (e.g., Glud et al. 1992).

Today, human influence on shallow coastal areas is huge. Anthropogenic impact not only implies eutrophication and contamination but also physical disturbance, which may lead to acute or chronic change, or even loss of productive habitats. For example, construction work, dredging, bottom trawling, extraction of sand, and various recreational activites may alter sediment loading (Jonge et al. 1993; North Sea Task Force 1993). For shallow-water areas, the main focus of impact studies has been on resuspension (Schaffer and Sullivan 1988; Delgado et al. 1991a; Jonge and Beusekom 1992), whereas the opposite process, sedimentation, has been less studied. Changes in the degree of shelter and current velocities as a consequence of building constructions, such as piers and moles,

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may increase natural sediment loading. Only few studies describe the effect of increased sediment loading on the microbial community of shallow-water sediments, which are characterized by the presence of autotrophic microorganisms (benthic microalgae) (Shaffer 1984; Plante-Cuny et al. 1993).

Development of biofilms on deposited material, for example after deposition of low-carbon material (e.g., drilling mud) has been previously studied (Findlay et al. 1992). Most studies concerning the relationship between sediment transport and benthic microorganisms have either been made in deeper waters or in tidal areas, where sediments are regularly resuspended and deposited. Hardly any information exists from virtually nontidal areas, such as the Swedish coasts. Also, little is known about the intrinsic capacity of the microbenthic community to recover, or adapt to such a physical change of the habitat. It may be hypothesized that benthic motile photosynthetic microorganisms, such as diatoms, can play an important role in the process of recovery from a moderate change in sediment loading.

The aim of this study was to investigate the effect of fine-particle deposition on the microbiota (microalgae, bacteria, and meiofauna) of a shallow-water sandy sediment in a microtidal area, focusing in particular on the response of microalgae. The scenario simulated is one in which an originally sandy sediment is covered by a thin layer of finer sediment (e.g., as a result of construction work or dredging activities that have reduced the ambient flow and increased the natural sedimentation rate).

Materials and Methods

The effect of fine-particle sediment loading on benthic microbiota was studied in two experiments (expts. A and B) in which intact sediment cores were incubated in an outdoor flow-through set-up. The experiments were made at Tjärnö Marine Biological Laboratory on the west coast of Sweden (58°52′N, 11°09′E). The area is practically nontidal, with a maximum tidal amplitude of ≈30 cm. Expt. A was run for 30 d in June and expt. B was run for 11 d in August 1993. In expt. A, estimates of the impact were based on measurements of chlorophyll *a*, biomass of algae, bacteria, and meiofauna, and bacterial production. The main purpose of expt. B was to study the oxygen profiles in the sediment, which because of technical problems was not possible in the first experiment. The only other variable measured in this latter experiment, was chlorophyll *a* content of the sediment.

Experimental Set-up

The flow-through system consisted of a container, 1.0 m × 0.7 m × 0.2 m, with a transparent polyethene roof to protect the cores from bird feces and rainwater. Surface water (1 m depth) from Tjärnö Bay was pumped up and exchanged 10 times a day (about 240 l h^{-1}). Before entering the container, the water passed through two cotton-filter cartridges (50 μm and 1 μm; Vattenteknik, Malmö). Sediment for the experiments was collected from a shallow sandy bay at a water depth of about 0.3 m. Sediment cores were collected randomly using transparent PVC tubes (i.d. 67.8 mm, length 120 mm) so that the sediment surface was ≈0.5 cm below the rim of the tube. The cores were carefully carried in a insulated box to the nearby laboratory. For both experiments, 24 cores were numbered and immediately placed randomly in the flow-through container. Fine-grained surface sediment from a sheltered site was collected and sieved in three steps (mesh size 500 μm, 100 μm, and 60 μm) to produce a silty sediment with grains <60 μm. This sediment was autoclaved and added as a slurry to 12 randomly chosen cores (deposition cores), allowing it to settle to a 2.5-mm thick layer. Twelve cores were left untreated (controls).

Sampling

At each sampling, three deposition cores and three control cores were randomly chosen, subsamples taken, and the remainder discarded. In this way, repeated sampling was avoided. In expt. A, sediment samples were taken on days 1, 8, 14, and 30, and in expt. B on days 1 and 11. Oxygen profiles were measured in expt. B on days 1, 2, 3, 6, 8, and 11. Before subsampling, most of the overlying water was removed gently with a Pasteur pipette. The subsamples were taken with cut-off 2-ml plastic syringes (i.d. 8.7 mm). A larger syringe (i.d. 20 mm) was used for particulate organic carbon (POC) and particulate organic nitrogen (PON) samples. Samples for all variables were taken from each core and to avoid the effect of timing, samples were taken from the controls and deposition cores alternately.

Using a cut-off syringe, 5 mm of surface sediment from the control cores were divided into two layers, the upper 2.5 mm (U-layer) and the lower 2.5 mm (L-layer). These depths were the smallest that could be handled by the sampling technique used. From cores treated with sediment, 7.5 mm deep samples were divided into three layers—the 2.5 mm sediment on the top (D-layer), the middle 2.5 mm (U-layer) and the lower 2.5 mm (L-layer) (Fig.1)

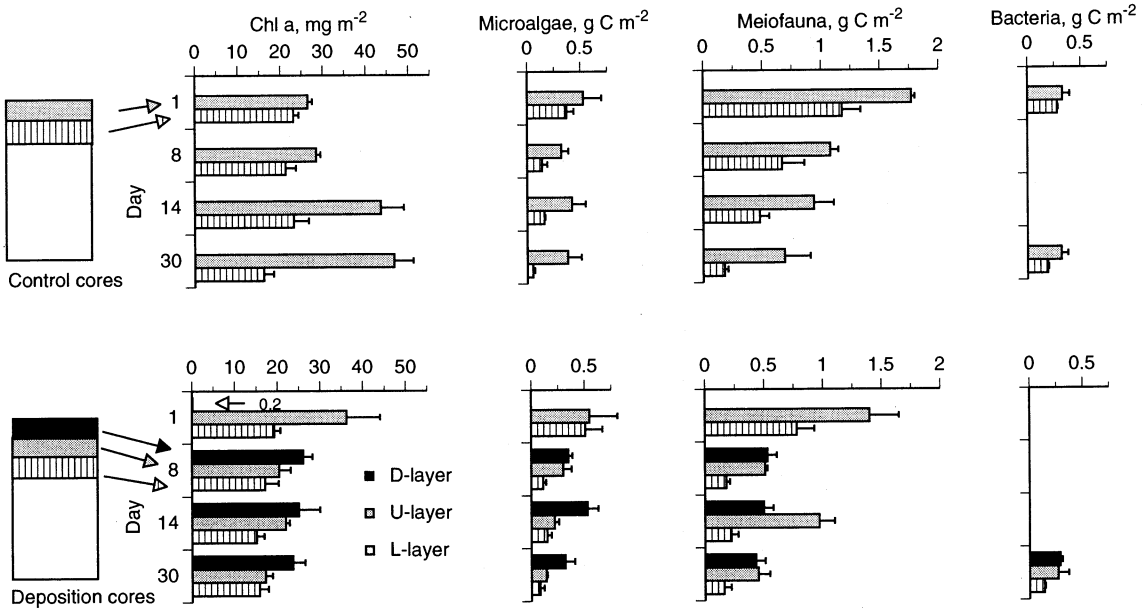

Fig. 1. Chlorophyll *a* and biomass content in the different layers of sandy sediment cores without (control cores) and with (deposition cores) deposition of 2.5 mm of silty sediment. Each bar shows mean (+ SE) of three replicate cores. Drawings to the left explain the different layers of control and deposition cores respectively. D-layer represents the deposition layer of 2.5 mm on the top, U-layer the original upper 2.5 mm, and L-layer the original lower 2.5 mm.

Analyses

POC and PON were analyzed in the silty sediment used for deposition and in the initial sandy sediment of expt. A. One sample was taken from each core. Dry sediment was homogenized in a ceramic mortar and the samples were packed in tin capsules. POC samples were treated with 2.5 M HCl for about 24 h to remove carbonates. Two replicate subsamples for each core were analyzed. POC and PON contents were analyzed using a Heraeus CHN-O-RAPID elemental analyser.

Chlorophyll *a* content was determined spectrophotometrically and corrected for pheopigments. Three subsamples from each core were pooled and extracted with 15 ml 95% acetone overnight in a refrigerator. After 5 min of ultrasonication, the analysis proceeded according to Lorenzen (1967).

For benthic microalgae, two subsamples from each core were pooled and diluted to 3 ml with filtered seawater (Whatman GF/F) and the algae were preserved with glutaraldehyde (final concentration 2.5 %). Algal cells were removed from sediment particles using a sonication bath (Sonorex RK 100, 35 kHz) for 4 × 3 min, during which the samples were continuously cooled with ice. Cells were counted in a Bürker counting chamber under an epifluorescence microscope (500 × magnification). All samples were counted within 48 h. Algal cells were grouped into six size classes: <7.5 µm, 7.5–11 µm, 12–15 µm, 16–22 µm, 23–30 µm, and >30 µm, corresponding to the divisions of the grid area in the eye piece of the microscope. The diatom *Cylindrotheca closterium* (Ehrenberg) was recorded as a separate group. Filamentous and coccoid cyanobacteria constituted two additional classes. Except for cyanobacteria, dimensions of at least 30 cells per size group were measured and the average cell volume for each group was calculated using geometric formulae according to Edler (1979). For cyanobacteria, the dimensions of each cell, filament or colony were measured. The factor for converting cell volume (µm³) to carbon (pg) was 0.089 for diatoms and 0.11 for cyanobacteria (Edler 1977, 1979).

Oxygen profiles were measured using a microsensor with a guard cathode (Revsbech 1989). The measurements were made indoors at constant light (≈720 µmol m^{-2} s^{-1}) with three halogene lamps the light source. The starting position of the microsensor was set with a micromanipulator and a stereomicroscope. The profile was then run automatically by a computer-controlled stepping motor using a program developed in Lab-VIEW (National Instruments). Measurements were made at intervals of 200 µm. Whenever possible, three cores from each treatment and three profiles per core were measured.

Samples for bacterial biomass were preserved in 4% borax buffered 0.2 µm filtered formalin. Bacteria were extracted by homogenization (Ultra-Turrax, 60 s) of diluted samples and counted using acridin-orange epifluorescence microscopy (Hob-

bie et al. 1977). Bacterial cell volumes were determined from photographs by measuring 20 cells per sample. Volumes were converted to carbon using the conversion factor 2.42×10^{-13} g C μm^{-3} (Moriarty 1990a).

Bacterial productivity in the sediment was assessed by measuring incorporation of ^{3}H-thymidine in a sediment slurry (cf. van Duyl et al. 1993). By using small volumes of sediment slurries, dilution and recirculation of added ^{3}H-thymidine can be avoided and slurrying does not appear to influence thymidine incorporation when incubation time is kept short (Moriarty (1990b). Sediment samples (≈87 µl) for bacterial productivity were taken with a cut-off plastic syringe (i.d. 4.7 mm) and transferred to test tubes. To each test tube, 49 µCi [methyl-^{3}H]-thymidine (specific activity: 5–6.7 Ci $mmol^{-1}$) were added. Two tubes per core and sediment layer were incubated for 15–20 min in the dark in the flow-through container. Ethanol-killed sediment served as controls (one tube per treatment and each sediment layer). DNA was extracted according to Wicks and Robarts (1987), Moriarty (1988), and Moriarty (1990a). For further details and isotope dilution tests, see Nilsson et al. (1991). Incorporation of isotope was converted to bacterial production according to Moriarty (1990b), except that a conversion factor of 5×10^{17} cells produced per incorporated mole thymidine was used (Moriarty 1988). Production rates were converted to daily values assuming a similar rate for 24 h.

For meiofauna, three subsamples from each core were pooled and preserved in 4% borax-buffered formalin. Meiofauna was extracted, sieved, sorted, and counted as described in Sundbäck et al. (1990). Biomass was calculated by assigning animals to different size classes as described by Widbom (1984), this value converted to carbon by multiplying ash-free dry weight (AFDW) × 0.45.

Statistical Tests

Cochran's test was used to check homogeneity of variance (Winer et al. 1991). Treatment effects were tested using a 1-way ANOVA for each sampling occasion. The same test was used when the biomass of the different algal groups was compared. A nested ANOVA was calculated for the oxygen profiles at each occasion using maximum oxygen content of each profile and the corresponding depth of the profile curves as variables. Only days 6, 8, and 11 could be included in the statistical analysis because of too few measurements on the other occasions. Differences at 5% level were accepted as significant.

Results

Visual Observations

Initially the colour of the sediment surface in the deposition and control cores was different, but, after about a week, they showed a growing resemblance. In both control and deposition cores the sediment surface was sometimes flaky and at least on one occasion the flakes tended to float away. Flaking was probably due to stimulated photosynthetic activity where oxygen bubbles can be entrapped in the topmost layer, lifting it off (cf. Lassen et al. 1992).

POC and PON

In expt. A, the initial load of POC in the deposition layer was ca 25 g C m^{-2}, corresponding to three times the content of the original upper layer (5.7 g C m^{-2}). The PON content was 2.9 g C m^{-2} and 0.9 g C m^{-2}, respectively. In expt. B, the deposition layer contained 19.4 g C m^{-2} and 2.4 g N m^{-2}.

Chlorophyll a

After a week, the chlorophyll content of the deposition layer (D-layer) had reached the values of the U-layer in the controls (Fig. 1). Thereafter the values in the D-layer did not increase further, whereas there was an increasing trend in the U-layer of the controls. However, no significant differences between the U-layer of the controls and the D-layer were found except for day 30. In the deposition cores, the chlorophyll content of the U-layer and L-layer did not change during the experiment. No significant differences were found between the L-layer of the controls and the U-layer of the deposition cores. Expt. B showed the same general trends as expt. A (expt. B not shown).

Microalgal Biomass and Composition

Microalgal biomass is based on conversion of biovolume to carbon. The biomass consisted initially of cyanobacteria and diatoms in equal proportions. Initially, the number of diatom cells in all cores was within the range $2.5–3 \times 10^{10}$ m^{-2}, corresponding to a biomass of 0.22–0.27 g C m^{-2}. As for chlorophyll *a*, the algal biomass in the D-layer rose within a week to the same level (about 0.3 g C m^{-2}) as in the U-layer of the control cores (Fig. 1). In both treatments and controls, there was an initial decrease in all layers except the D-layer. In terms of total algal biomass there was no significant difference between the D-layer and the U-layer except for day 1. However, the biomass of diatoms was significantly higher in the D-layer on day 8. No significant differences were found between the U-layers.

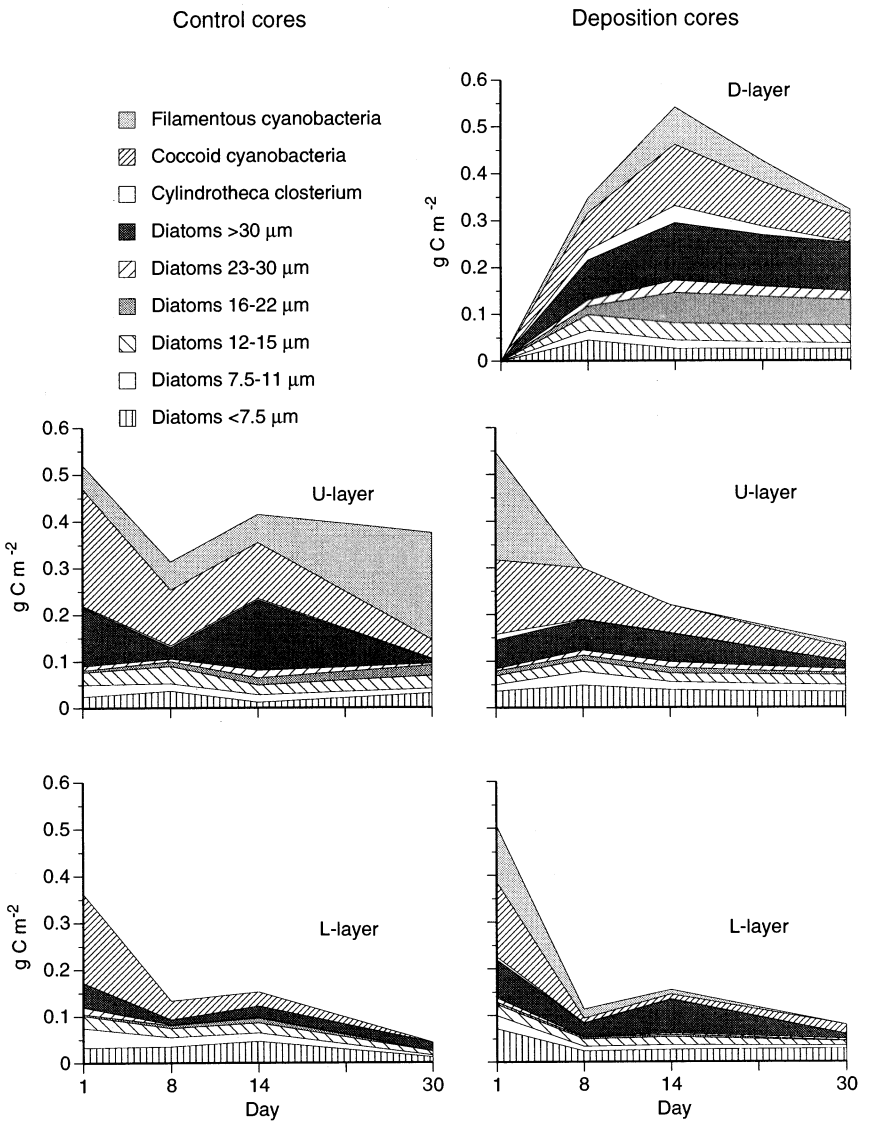

Fig. 2. Biomass and composition of benthic microalge in the different layers of control and deposition cores. Cores were untreated (control cores) or treated (deposition cores) with deposition of 2.5 mm of silty sediment. D-layer represents the deposition layer of 2.5 mm sediment on the top, U-layer the original upper 2.5 mm, and L-layer the original lower 2.5 mm.

If only diatoms are considered, motile species >16 µm seemed to become more abundant in the D-layer than the other layers (Fig. 2), although this was not supported by the ANOVA. The individual size group that appeared to increase most was the 16–22 µm group. When time was included as a factor, significant treatment effects were found for the size classes 16–22 µm and >30 µm (ANOVA, $p < 0.01$).

Oxygen Profiles

Oxygen profiles were measured only in expt. B. An immediate effect of the sediment load was a decrease in the oxygen concentration of the sediment; profiles measured within half an hour after the deposition revealed no oxygen below the sediment surface (Fig. 3). Thus, there were initially great differences in the shape of the profiles between the controls and deposition cores. However, already on the following day (day 2), oxygen appeared at 1 mm depth in the deposition cores and the profiles started slowly to resemble those of the control cores. The peak of the oxygen profile always appeared at greater depth in the controls than in the deposition cores, giving significant differences for day 6, day 8, and day 11. The maximum values of oxygen were higher in the controls compared to the deposition cores, showing signif-

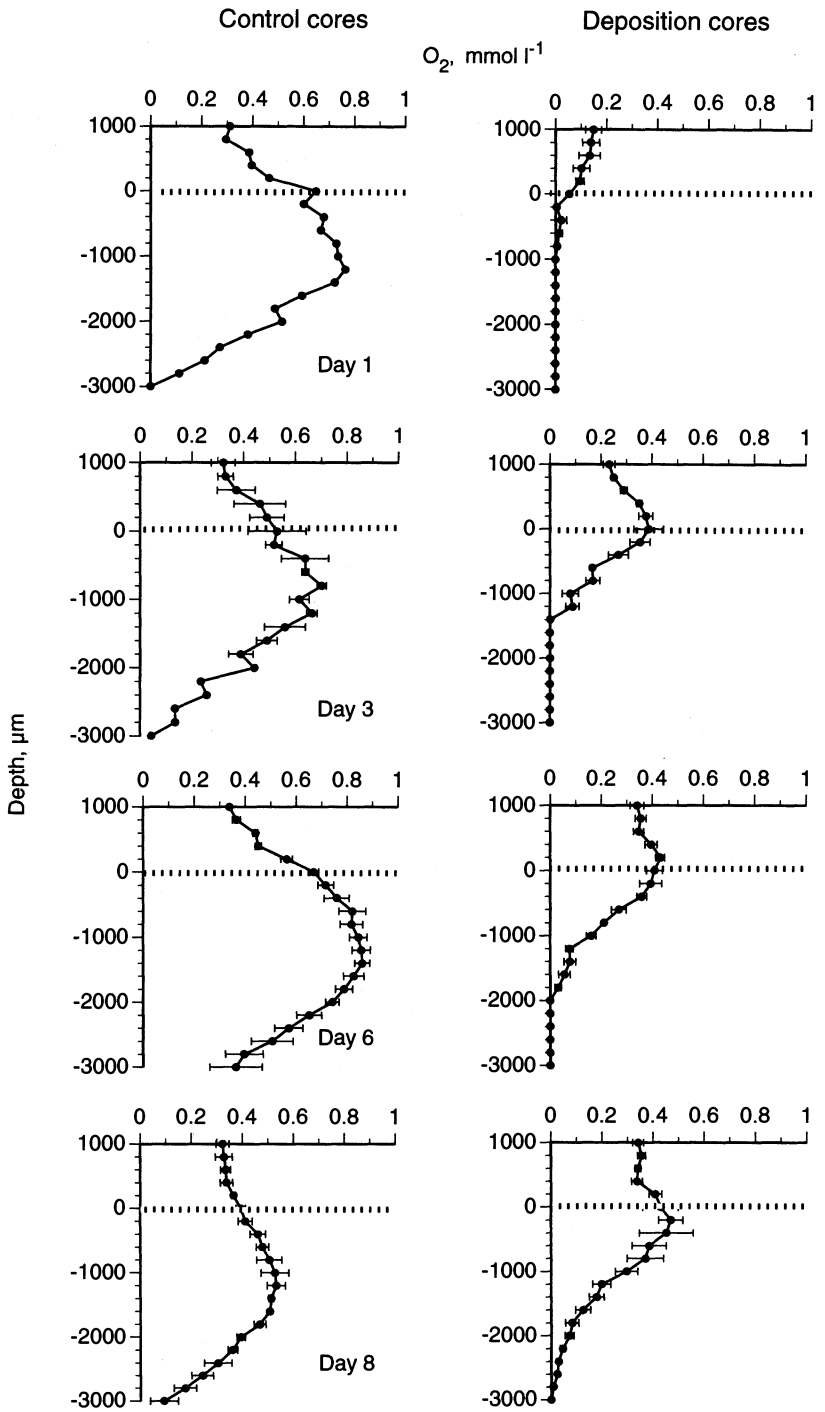

Fig. 3. Oxygen profiles of control and deposition cores showing oxygen concentrations at different levels above (+) and below (−) the sediment surface. Values on days 1 and 3 are based on means of two cores (horizontal lines show range). Values on days 6 and 8 are based on means of three replicate cores (horizontal lines show SE).

icant differences on day 6 and day 11. At the end of the experiment, the oxygen content decreased in both controls and deposition cores, particularly in the deposition cores.

Bacteria

Bacteria were quantified only at the beginning and end of expt. A. Bacterial numbers in the various layers in all cores ranged from 6.7 to 15 × 10^{12}, corresponding to a biomass of 0.14 g C m^{-2} to 0.33 g C m^{-2} (Fig. 1). The mean carbon content per bacterium was estimated to be 21.7 fg C. At the end of the experiment, there was no significant difference between the deposited layer and the U-layer of the controls, indicating that bacterial biomass was restored to the same level as in the sandy sediment. Neither was there any difference between the U-layers of the control and deposition cores.

Bacterial productivity was measured on two occasions in expt. A (days 8 and 14). In the control cores, bacterial activity was concentrated to the topmost 2.5 mm sediment. On both occasions, there were no significant differences between the D-layer and the U-layer of the controls and on Day 14, the bacterial productivity of the deposited layer had reached the same value as in the top layer of the control cores (≈60 mg C m^{-2}). This together with the fact that the productivity in the layer below the deposited sediment decreased significantly, implies that bacterial activity moved upwards when new sediment was added.

Meiofauna

The initial meiofaunal biomass in the U-layers was on an average 2.6 g C m^{-2} for the top 5 mm of sediment (1.6 g C m^{-2} and 1.0 g C m^{-2} in the U-layer and L-layer, respectively), and showed a declining trend through the experiment (Fig. 1). Intially, and therafter in the control cores, ca 60–80% of the meiofaunal biomass was found in the top 2.5 mm of sediment. After a week, the new deposited sediment layer had been colonized, but there was still a significant difference when compared with the U-layer of the control cores. Thereafter, the biomass did not increase further in the D-layer, but, because of declining biomass in the control cores, no significant as differences existed later in the experiment. This fact and a significantly lower biomass in the U-layer after a week apparently reflected upward migration of meiofauna. When the biomass of individual meiofaunal groups was considered, no significant differences were observed between the D-layer and the upper layer of control cores (Fig. 4). Neither was there a significant difference in the relative proportions of meiofaunal groups. This suggests that also the initial composition was re-established. Comparing the U-layers of the treated and control cores, showed that the proportion of harpacticoid copepods decreased significantly under the deposition layer, indicating that harpacticoids move upward.

Discussion

Experimental Set-up and Methods

Most colonization studies have allowed immigration by organisms from the surrounding sediment, and from the water column above. Undoubtably, both these processes are important for recolonization in nature (e.g., Palmer 1988; Smith and Brumsickle 1989). We excluded these sources of recolonization intentionally, because we wanted to specifically focus on the inherent capacity of the "covered" sediment to re-establish the microbial community and its function at the sediment-water interface (bacterial import from the incoming water could not, however, be avoided). Also, settling sediment particles themselves are likely to contain microorganisms in situ. We used natural, but autoclaved, sediment to exclude this import for the same reasons as mentioned above, and for making it easier to discern colonization (e.g., by upward movement).

As the added sediment layer was only 2.5 mm deep, our treatment can be considered as a simulation of a moderate disturbance. The added layer of organically rich, fine-particle sediment could well simulate an increased natural sedimentation caused by changed current velocity as a consequence of building constructions. For comparison, 2.5 mm of deposition equals ≈8 d of sedimentation on a locality in the Dutch Wadden Sea after the enclosure of the Zuidersee (Cadée 1984). An input of 15 g C m^{-2} is equivalent to roughly 1–3 wk of carbon sedimentation in eutrophic lakes or nearshore waters (Bloesch et al. 1977). Our treatment may also simulate a situation following dredging some distance away, rather than direct effect of dredging on site. However, sediment load after dredging is likely to be less carbon-rich, and often toxic (heavy metals), as compared with the surface sediment we used. Thus our treament may have resembled a favourable case of dredging.

When sampling the upper 2.5 mm of the soft sediment with cut-off plastic syringes, it was impossible to avoid taking a few micrometres of the lower layer because the soft sediment was compacted. However, as the same sampling method was used throughout the experiment, the error should not be of major importance.

Keeping in mind the above mentioned methodological limitations, it should also be emphasized that the "new" aspects in our study are that

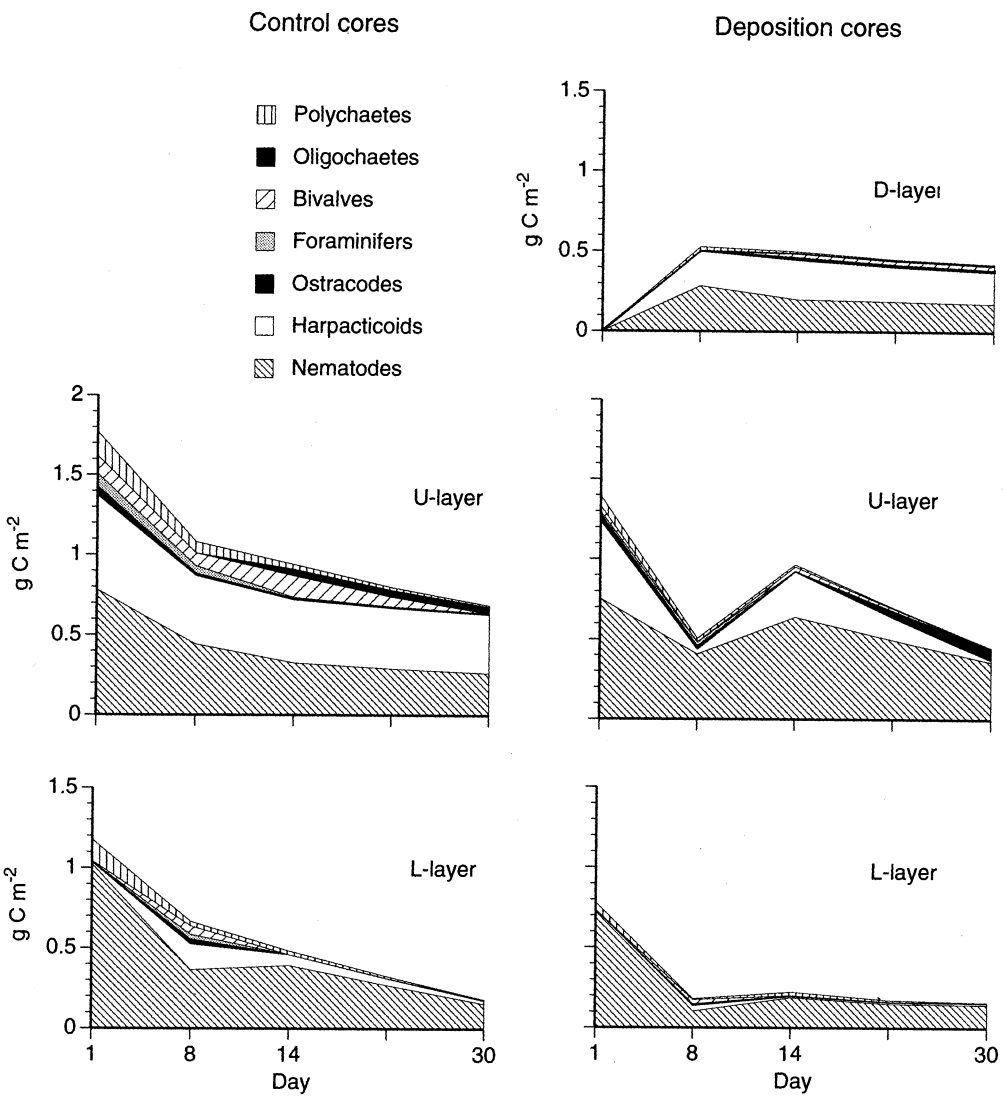

Fig. 4. Biomass and composition of meiofauna in the different layers of control and deposition cores. Curves are based on means of three replicate cores. Cores were untreated (control cores) or treated (deposition cores) with deposition of 2.5 mm of silty sediment. D-layer represents the deposition layer of 2.5 mm sediment on the top, U-layer the original upper 2.5 mm, and L-layer the original lower 2.5 mm.

we considered sediment deposition on a sandy shallow-water sediment with a typical epipsammic algal community and that we studied simultaneously the response of three living components: algae, meiofauna, and bacteria. Moreover, we studied a nontidal site, where the hydrodynamics are clearly different from that of tidal flats.

Degree of Colonization

The level of both algal and meiofaunal, as well as bacterial, biomass was restored in the deposited autoclaved sediment during the experiment. In this recovery process, the benthic microalgae appear to have played a key role. Microalgal biomass and chlorophyll *a* content, as well as the development of oxygen profiles, suggested that benthic diatoms can rapidly colonize new-deposited sediment in shallow waters through upward migration. This process restores the oxygen producion at the sediment surface. The fact that naviculoid diatoms (>16 μm) appeared in greater amount in the D-layer within a week, supports this conclusion, since these species are motile and known to migrate vertically.

The importance of benthic diatoms in the recovery process of disturbed sediment communities has been shown also by others. These studies have considered effects of, for example, biodeposits and oil (Plante-Cuny et al. 1993), as well as biocides (Underwood and Paterson 1993). In a previous ex-

periment on the response of a sediment community to decomposing macroalgal mats, benthic diatom biomass was not negatively affected by temporary anoxia and recovery was rapid (Sundbäck et al. 1990). This capacity of benthic diatoms to aid recovery, appears to be related to their capability to survive in darkness, tolerate anoxia, and even sulphurous conditions (Kennet and Hargraves 1985). The production of extracellular polymeric substances (EPS) in microbial mats may play a role as a buffer against chemical changes (Decho 1990; Freeman and Lock 1995) and in stabilizing deposits (Underwood and Paterson 1993).

The rapid fall in algal biomass (based on counts of fluorescing cells) in all layers except the deposition layer, during the first week, was mainly due to a decreased number of cyanobacteria. The low, but fairly stable, biomass of diatom cells in the L-layer of both the control and treated cores could be due to the ability of the diatoms to survive at low irradiance and even in darkness. Since they already live deep down, a few more millimetres of sediment apparently do not affect them. Some algal groups constantly live below the surface as described for some *Amphora* species (Round 1979) and they are not likely to migrate. Benthic diatoms can compensate for low light levels by heterotrophy (Admiraal 1984). They can also survive for long periods in the dark without damage to their photosynthetic capacity (Gargas and Gargas 1982; Admiraal 1984; Kennet and Hargraves 1985; Sundbäck and Granéli 1988).

The deposited layer offered a new habitat that differed from the original sandy sediment in several aspects. A primary effect of the deposition of fine sediments was that the photic layer became thinner. Measurements using light microsensors have shown that, while light may penetrate down to ≈4 mm in sandy sediment, and even be enhanced through scattering (Kühl et al. 1994), in silty sediments the photic zone is often much thinner, <1 mm (Revsbech 1988; Lassen et al. 1992). Secondly, the nature of the substratum for microalgae was altered, implying that the species composition of assemblages can be expected to change. In exposed or moderately wave-exposed sandy sediments, attached (epipsammic) algae dominate (Miller 1989; Sabbe and Vyverman 1991; Sundbäck and Snoeijs 1991). These are small, slowly moving species that can survive on moving sand grains (Jonge 1985; Delgado et al. 1991b). In silty and muddy sediments, implying more sedimentation, motility is an advantage and large motile diatoms dominate (cf. Paterson 1986; Jönsson et al. 1994). Therefore, it was not surprising that the proportion of larger and motile species increased in the deposited layer. However, in our study, the species pool was limited to the species that inhabited the original sandy sediment. As larger species of diatoms were initially scarse, they were not likely to become very abundant in the course of the experiment.

The deposition also implied a considerable increase of organic carbon and nitrogen (four and three times, respectively). Particulate matter is not directly available for benthic microalgae, but as a positive correlation between organic enrichment and microbial mineralization can be expected (e.g. Gillespie and MacKenzie 1990); dissolved inorganic nutrient levels should also increase. A stimulation of algal growth after nutrient addition has been observed in previous studies with sandy sediment (for references see Nilsson et al. 1991). This could explain the significantly higher diatom biomass in the D-layer as compared with the control after 1 wk. Addition of detritus has been shown to increase the biomass of diatoms (Levinton 1985; Schwinghamer et al. 1991).

Meiofauna recolonized the deposited layer in the course of the experiment. When interpreting meiofaunal colonization, it must be kept in mind that no horizontal immigration nor colonization from the water column was possible. During the experiment, no significant change in the biomass of the two dominating meiofaunal groups (nematodes and harpacticoids) in the new sediment layer was observed. The initial biomass of meiofauna was high for sandy sediments (cf. Sundbäck et al.1990; Nilsson et al. 1991). Meiofaunal bioturbation may have been one mechanism explaining the amount of epipsammic diatoms in the deposition layer. As meiofaunal biomass exceeded that of the microalgae, meiofaunal grazing could also have affected algal biomass (cf. Sundbäck et al. 1996).

In contrast to algae and meiofauna, bacteria could have been introduced from the incoming water. Bacterial biomass increased toward control levels within the added sediments of the deposition cores but did not increase above control levels, as might have been expected because of the additional carbon and nutrient usually associated with fine sediment. This lack of response is supported by our previous work (Sundbäck et al. 1990) and it has been suggested that the presence of EPS may be a controlling factor mediating bacterial response to increased organic loading (Freeman and Lock 1995). We did not analyze the particle composition of our inorganic <63 μm fraction further, but large proportion of clay particles has also been found to decrease bacterial abundance (DeFlaun and Mayer 1983).

Recovery of Function

The deposition of 2.5 mm of fine sediment caused only a temporary limitation to the photo-

autotrophic activity at the sediment surface. On the other hand, after activity was restored, the oxygenated layer was found to be thinner. This was probably a result of the changed light climate in combination with slower diffusion of oxygen in finer sediments. The shallowness of the oxygenated layer may imply that oxygen deficiency occurs more rapidly in fine sediments than in sandy sediments, where both upward and downward diffusion is faster (e.g. Revsbech et al. 1988).

Although we have no data on primary productivity, the oxygen profiles suggest a higher net production in the sandy, untreated sediment. However, the cell number and biomass of diatoms in the D-layer indicated that, at least during the experiment, the fine-grained sediment did not have a negative effect on the diatoms. On the other hand, the cyanobacteria seemed to be negatively affected, although this was not statistically proven. There are some disagreements about the role of sediment composition on microalgal production. Some have found the highest production in fine sediments (Cadée and Hegeman 1977; Revsbech, et al. 1988; Pinckney and Zingmark 1993), while others have found the highest production associated with more sandy sediments (Hickman and Round 1970; Riznyk and Phinney 1972). If biomass of benthic microagae is considered, higher values are often found in silty (more sheltered) than pure sandy (wave exposed) sediments (e.g., Pinckney and Zingmark 1993 and references therein).

A higher bacterial productivity might have been expected because of the high POC and PON content in the deposited sediment as compared with the sandy sediment. In this case, an increased heterotrophic activity and respiration may counteract the oxygen production. However, the data on bacterial production is limited to two occasions in the middle of the experiment, and no certain conclusions can be made.

The Rate of Recovery

Biofilms have been found to develop over a period of days to weeks (Findlay et al. 1992). In our experiment, the biomass became concentrated in the new D-layer by day 8. As horizontal immigration and settlement from the overlying water were prevented in our set up, the rate and degree of change depended on vertical migration rates and generation time of organisms. The inherent capacity of the microalgal community to restore the oxygen production depends on the type of the community (e.g., the motility of the algae). Thus, we can expect a different rate of recovery in sandy and muddy sediments. In this case, we studied a slowly-moving epipsammic community. Under our experimental conditions it took ≈2 d before the oxygen profile started to resemble that in the control cores. However, in finer sediments, often larger and faster-moving epipelic species dominate (Paterson 1986). Studies of vertical migration on tidal flats suggest that epipelic diatoms migrate vertically over distances of ≈3 mm or less on a time scale of hours (Hay et al. 1993). This was also shown in a preliminary experiment from a nontidal area where the large-size diatom *Gyrosigma balticum* (Ehrenberg) reappered at the sediment surface only 2 h after deposition of 5 mm sediment (Sundbäck et al. unpublished). Thus a stochastic moderate sediment deposition would give minor effects on an already silty sediment where organisms are adapted to sediment accumulation. The recovery of sandy sediment is slower. This was also shown in a later laboratory experiment, where oxygen profiles in sandy sediment were restored after ca 2 d (unpublished).

Conclusions

The results suggest that the microbial community of sandy sediments have an inherent capacity to recover after a moderate deposition of fine-particle sediment. Active upward migration of benthic diatoms is a key mechanism for restoring the oxygenation of the sediment surface by photosynthesis. However, the oxygen-producing layer is likely to become thinner in the fine-grained sediment when compared with sandy sediment. The community composition will change when the original sandy sediment is altered to a more fine-grained sediment.

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