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Microbial Response of a Freshwater Benthic Community to a Simulated Diatom Sedimentation Event: Interactive Effects of Benthic Fauna

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ABSTRACT

The response of a sediment microbial assemblage to a pulse of diatoms was studied over 36 days by measuring bacterial activity and biomass, ATP concentration, and overall community respiration in laboratory microcosms. Also, the contribution of macrofaunal chironomids to the decomposition of settling diatoms in benthic communities, and the relative importance of benthic meiofauna in community metabolism, were determined.

The addition of diatoms resulted in an immediate response by sediment bacteria, with higher bacterial production recorded after only 2 h, and a more than tenfold increase within one day. The rapid response by sediment bacteria was accompanied by relatively high initial concentrations of dissolved organic carbon. In treatments receiving diatoms, higher bacterial production was sustained throughout the experiment. Surprisingly, neither these elevated production estimates, nor the starvation of controls affected bacterial abundance. Mean bacterial cell volume, however, was markedly affected by the addition of diatoms. Combining community respiration measurements and bacterial production estimates showed that growth efficiencies for sediment bacteria ranged from 14.6 to 34.5%. The contribution of ambient meiozoobenthos to carbon metabolism was less than 1%. Carbon budgets showed that 1.3 mg C was cooxidized along with 4.3 mg added diatom C.

Sediment reworking by *Chironomus* larvae initially enhanced bacterial production, but the presence of *Chironomus* resulted in lower bacterial production estimates after 16 and 36 days. This was interpreted as a result of faster decomposition of diatoms in treatments with chironomids, which was validated by a faster decline of ATP and chlorophyll *a* in the sediment. Our results indicate that *Chironomus* larvae compete with sediment bacteria for available organic substrates.

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Introduction

Deposition of autochthonous C following seasonal (spring and autumn) blooms of diatoms represents a considerable share of the annual C input to the benthic communities of relatively deep, nonhumic, temperate lakes. This sedimenting algal detritus, due to its labile nature [25], can have profound effects on a number of benthic processes, including invertebrate growth patterns [32] and lipid contents [15], community metabolism [18, 22], bacterial activity [7, 51], bacterial cell size [52], and enzymatic activity [41]. The input of fresh detrital material may also generate a cooxidation of more refractory organic compounds in the sediment [19]. Although the concept of pelagic-benthic coupling is generally accepted, most of the evidence supporting this conjecture is qualitative (e.g., [20, 30]). Quantitative studies using radioactive labeling techniques have recently been performed by Fitzgerald and Gardner [12] and Gullberg et al. [26], who found that the major share of added diatoms is rapidly assimilated by the deposit-feeding macroinvertebrates *Pontoporeia hoyi* and *Chironomus riparius,* respectively. Furthermore, Gullberg et al. [26] found that 9.8% of the added diatom pulse was respired by sediment microheterotrophs within 8 days, whereas Fitzgerald and Gardner [12] attributed 2.3% to bacterial production and respiration in their carbon budget for pelagic-benthic coupling in Lake Michigan. Neither of these studies, however, specifically quantified the microbial response in its experimental units.

The response of sediment microbes (in terms of an increased activity and/or biomass) to the deposition of organic substrate (pelagic phytodetritus, diatoms) may be immediate [22, 19] or display a lag phase from days to months [8, 51]. The nature of the microbial response will generally be dependent on intrinsic factors such as temperature and the deposition rate and quality of organic matter (see [48] for review). A number of studies have examined the response of microbes to sedimentation events in comparatively nutrient-poor marine sediments (see [21] for review). Few studies, however, have focused on the microbial element of pelagic-benthic coupling in organic-rich lake sediments [16, 51]. In Lake Erken (Sweden), Goedkoop and Johnson [16] found that bacterial production was weakly, albeit significantly, correlated with both chlorophyll *a* concentrations in surficial sediment (a measure of pelagic phytodetrital deposition) and temperature, after corrections were made for serial autocorrelations. In field studies, however, it may be precarious to distinguish a benthic response from a simple translocation of microbial activity from pelagic to benthic environments during sedimentation events. Detritus-associated, pelagic bacteria may be largely responsible for the observed increase in bacterial activity in sediment samples during sedimentation events, i.e., cosedimentation [17]. Therefore, controlled external conditions are a necessary prerequisite to the study of benthic microbial processes involved in the decomposition of organic matter.

Deposit-feeding chironomid larvae stimulate the activity of sediment bacteria by their burrowing behavior [5] and feeding activity [31], and thereby enhance the regeneration of inorganic nutrients [23] and oxygen consumption [24] in the sediment. Also marine macroinvertebrates, generally larger than the freshwater macrofauna, can have profound effects on the activity of sediment bacteria [8, 37] and the decomposition rates of organic matter [36]. In both freshwater and marine environments, important mechanisms comprise physico-chemical modifications of the sediment [36, 40], but the gut tracts of macroinvertebrates may also be sites of elevated bacterial activity [45].

In this study, we followed the response of the microbial assemblage of a freshwater sediment (Lake Erken) to a pulse of diatoms by measuring bacterial activity and biomass, ATP concentration, and overall community respiration of the sediment, under laboratory conditions. The decomposition of added diatom C was studied over a period of 36 days. Additionally, we tested to what extent macrofaunal chironomids, directly through diatom digestion and/or indirectly through their stimulatory effects on sediment bacteria, can contribute to the decomposition of diatom POC in benthic communities.

Materials and Methods

The centric diatom *Stephanodiscus hantzschii* v. *pusillus* Grun. was cultured in initially sterile, 1-liter flasks containing a modified (50% reduction of $NaHCO_3$) KL 16 × 2 medium [39] at 10 ± 1°C under a 14 L:10 D (25–30 μE m^{-2} s^{-1}) regime. To quantify concentrations and fluxes of dissolved organic carbon (DOC) in the microcosms, ^{14}C-labeled diatoms were cultured under the same external conditions in a culture medium containing 1 mCi $H^{14}CO_3$ $liter^{-1}$ (Amersham, 55 Ci $mmol^{-1}$, 2 mCi ml^{-1}) (see Gullberg et al. [26]). Diatoms were harvested when growth reached a stationary phase, i.e., after approximately 10 days. Diatoms were concentrated by gentle centrifugation (550 *g,* 10 min), washed 3 times (550 *g,* 10 min), resuspended in a small volume of water, and stored at −20°C. After washing 3 times, the radioactivity in the supernatant no longer decreased.

Surficial sediment (0–1 cm layer) was collected with a gravity core sampler (i.d. 69 mm) in early spring (7 days after ice-out, 3

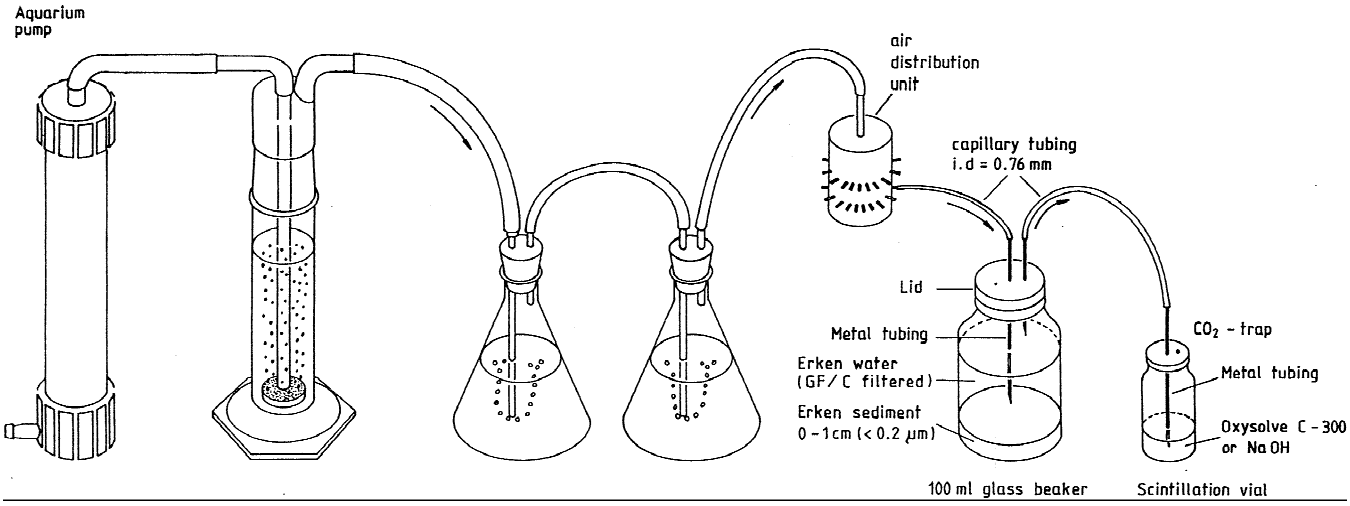

Fig. 1. Schematic illustration showing the experimental set-up. The CO_2 is stripped from ingoing air from an aquarium pump in a 160-ml plexiglass tube containing soda lime pellets and a 100-ml gas-washing bottle containing 100 ml 10 M NaOH. In two subsequent 100-ml E-flasks containing deionized water, the air is washed to avoid changes in pH in the microcosms. Microcosms (100 ml) are each equipped with a CO_2 trap containing 1 M NaOH (nonradioactive units) or the CO_2 absorbing scintillation cocktail Oxysolve C-300 (radioactive units).

weeks before the start of the experiment) from a 15-m station in the eastern basin of Lake Erken, and transported at 4°C to the laboratory. The sediment was wet-sieved (0.5 mm) to remove ambient macrofauna, and kept dark in an aquarium containing a water phase of approximately 40 cm of aerated Lake Erken water at 4°C.

Three days before the start of the experiment, the overlying water was removed, and the sediment was mixed to a homogeneous slurry. Aliquots of sediment were frozen for later analyses of chlorophyll *a.* Of the sediment slurry, 8 ml (8.3 ± 0.10 g wet wt., mean ± SD) was transferred to microcosms (100-ml glass vials with a bottom area of 16.5 cm^2) with a pipette, resulting in a sediment layer of approximately 1 cm. After addition of 80 ml of GF/C-filtered Lake Erken water, the microcosms were closed (polyethylene snap cap) and aerated 15 min h^{-1} with CO_2-free air (see below), using capillary tubing (i.d 0.76 mm) and an aquarium pump (Fig. 1). Intermittent aeration was used, since previous work has shown that it keeps oxygen concentrations close to 100% saturation and minimizes disturbance of the organisms. Aeration of the microcosms was switched off for 6 h at night to allow algal material to settle. CO_2 was stripped from the ingoing air in a 160-ml plexiglass tube containing soda lime pellets (size 2–5 mm), and a 100-ml gas-washing bottle containing 100 ml NaOH (10 M.) In two subsequent 100-ml E-flasks containing deionized water, the gas was washed to avoid changes in pH in the microcosms. The pH of this water was checked regularly with a pH indicator strip and changed when pH exceeded 8 (on day 16 and 32). By aerating with CO_2-free air, a gradient was established between the sediment and the overlying water in the microcosms, enhancing the efflux of CO_2 from the sediment and increasing the accuracy of community respiration measurements (see below). The air outlet from each microcosm was connected to a 20-ml glass scintillation vial with NaOH (10 ml, 1.0 M), for quantification of respired CO_2.

Chironomus riparius, harvested from laboratory cultures at 10°C, was added to the microcosms 2 days before the start of the experiment. The following day, frozen diatoms were carefully thawed at 4°C and rinsed 3 times in Lake Erken water (as described above). CO_2 traps were connected to the microcosms, and a pulse of diatoms representing 2–3 days of sedimentation under field conditions during spring in Lake Erken [16] was added to the experimental units (see below). The microcosms were then sealed and incubated in the dark at 10 ± 1.5°C. To quantify the experimental conditions in the microcosms, dissolved oxygen concentrations in the overlying water were measured with an oxygen meter (YSI, model 51B, equipped with a 5719 probe), and pH was determined.

Seven groups of microcosms were established, with each group corresponding to one of the sampling days (see below). Each group was driven by a separate aquarium pump connected to a CO_2 elimination unit (see above). The experimental design comprised the following treatments in four replicates each: (1) diatom addition (diatoms-only treatment), (2) addition of four (4th instar) *Chironomus riparius* Meigen larvae and diatoms (diatoms-plus-*Chironomus* treatment), (3) controls (no additions), and two additional treatments (4 and 5) that resembled treatments 1 and 2 except for the exchange of the diatom pulse for an equally large pulse (4.1 ± 0.02 mg C) of $H^{14}CO_3$-labeled diatoms. Treatments 1 and 2 received a diatom pulse of 4.3 ± 0.10 mg C, constituting 8.3% of overall sediment C in the microcosms. Microcosms of treatments 1, 2, and 3 were sacrificed after 0, 1, 2, 4, 8, 16, and 36 days. At each timepoint one group of nonradioactive microcosms was intensively aerated for 20 min to transport the accumulated CO_2 to the CO_2 traps. Following aeration, CO_2 traps were disconnected, closed, and stored in a hermetic container filled with CO_2-free air prior to analyses. The water phase from each microcosm was carefully removed with a syringe, and stored in the dark at 4°C.

In treatments 4 and 5, concentrations of $DO^{14}C$ in the interstitial water and overlying water of the microcosms were determined. Radioactive experimental units were sacrificed after 0, 2, 4, 8, and 16 days by injecting 5 ml of an acid-formaldehyde solution (1.1 mol H_2SO_4 and 0.9 mol HCHO $liter^{-1}$), with a syringe, through the cap of the microcosms. Subsequently, these units were intensively aerated for 20 min to remove accumulated CO_2. The overlying water from each microcosm was then removed with a syringe and filtered through 0.2-μm Millipore filters. Interstitial water was separated from the sediment by centrifugation (550 g, 20 min) and filtered (0.2 μm). To determine $DO^{14}C$ concentrations, 10-ml aliquots of overlying water, and freeze-dried interstitial water were transferred to scintillation vials and measured using a LKB-Wallac 1217 scintillation counter and a OptiPhase Hisafe 2 scintillation cocktail. Activities were corrected for quenching, using external standard ratios. Total DOC concentrations originating from added diatoms were calculated from $DO^{14}C$ levels using the ratio between ^{14}C and total C content in the added diatom pulse. The remaining sediment pellet in the microcosms was preserved and stained with borax-buffered (200 g $Na_2B_4O_7 \times 10\ H_2O$ $liter^{-1}$) formaldehyde solution containing Rose-Bengal (0.2 g $liter^{-1}$) to a final concentration of 4% [44], for later extraction of ambient meiofauna (see below).

For bacterial activity measurements, 0.5-ml aliquots of well-mixed sediment slurry were incubated with 0.44 nmol [^{3}H]thymidine (45–55 Ci $mmol^{-1}$, Amersham) in 10-ml Oak Ridge centrifuge tubes at 11.7 ± 0.5°C in a water bath [3]. The degree of [^{3}H]thymidine incorporated during bacterial DNA synthesis was determined by performing an isotope dilution experiment, according to Pollard and Moriarty [46], and was found to be 61.8%, on average (44.5–84.3%, 95% c.l.). Counts were corrected for the degree of participation. Bacterial production was calculated using a conversion factor of 0.44×10^{18} cells mol^{-1} [14] and converted to carbon units, assuming a carbon content of 2.2×10^{-13} g C μm^{-3} cell volume [4]. Chironomids were removed from the remaining sediment on a watch glass prior to [^{3}H]thymidine incubations. For quantifying bacteria, 0.5 ml sediment was diluted to 50 ml with filter-sterilized (0.2 μm) 4% formaldehyde, and stored in the dark at 4°C. Formaldehyde-preserved samples were diluted 50 times with filter-sterilized (0.2 μm) water, and sonicated (100 W, 1 min) in an ice-bath. A subsample was then stained with acridine orange (final concentration 0.005%) and filted onto 0.2-μm filters (Nuclepore) prestained with Sudan Black [2]. Bacterial abundance and mean cell volume were determined by epifluorescence microscopy (NIKON filters combination B-2A: dichroic mirror 510, excitation filter 450–490, and barrier filter 520). At least 400 cells, or 20 random fields, were counted, and at least 100 cells were measured using an eyepiece graticule to determine mean cell volume.

ATP extractions were performed on 0.5 g wet wt. of sediment by the addition of 3 ml chloroform and 10 ml of a Na_3PO_4 buffer, and subsequent homogenization in a Polytron homogenizer at maximum speed for 1 min, according to Tobin et al. [49]. Samples were then centrifuged for 10 min at 1650 *g*, and the supernatant was filtered through cellulose-acetate filters (Lida, 0.2 μm). Subsamples of 0.5 ml were transferred to scintillation vials and stored in the dark after the addition of 5.0 ml Tris-EDTA buffer (12.12 g Tris-(hydroxymethyl)-aminomethane and 0.744 g EDTA $liter^{-1}$, pH 7.75). ATP concentrations were measured on a luminometer (LKB-Wallace 1250), using a monitoring agent (LKB 1243-200) and an internal ATP standard (LKB 1243-201). Carbon and nitrogen content of the sediment and the diatom addition were determined on freeze-dried (24 h) samples using a Carlo-Erba elemental analyzer. For the diatoms-only treatment, all samples were analyzed. Sediment from the diatoms-plus-*Chironomus* treatment and controls was analyzed only after 0 and 36 days of incubation.

Accumulated CO_2 was measured by gas chromatography (Shimadzu GC-14A), with helium as a carrier gas. Briefly, a subsample of NaOH (from CO_2 traps) was transferred with a syringe to a 13.5-ml CO_2-free gas bottle and sealed with a Fermpress. The subsample was acidified by injecting 10 M H_2SO_4, and vigorously shaken for half a minute. One milliliter of the gas phase was then injected into the gas chromatograph, and CO_2 concentrations in samples were calculated using Na_2CO_3 standards. Values for the different treatments were corrected for the average initial CO_2 concentration in the NaOH solution used in CO_2 traps (134.6 ± 10.16 μg CO_2 $liter^{-1}$, $n = 5$).

Meiofauna was extracted from the sediment using density centrifugation with the colloidal silica Ludox-TM (slightly modified from Pfannkuche and Thiel [44]). In this procedure, sediment samples were transferred to 100-ml centrifuge tubes, and, in the first step, the formalin fraction was decanted after centrifugation at 550 *g* for 10 min. Approximately 1 g of kaolin was then added, and the sediment and kaolin were resuspended in 40 ml Ludox-TM (specific density 1.2 g cm^{-3}). During consecutive centrifugation, the rotor speed was increased stepwise over 5 min to 1500 rpm (550 *g*). This speed was then maintained for another 5 min. During centrifugation, the fine-grained kaolin formed a rigid lid on top of the sediment pellet, which facilitated decantation of the supernatant onto paper filters (Ø = 5.5 cm). Each sample was processed three times. Rose Bengal–stained meiofauna were hand-picked from the filters at 10–40× magnification using a dissecting microscope, sorted to major taxa, and counted.

Meiofauna respiration was calculated from abundance using a series of empirical relationships. First, abundances were converted to biomass using the dry weight estimations by Nauwerck (Doctoral thesis, Uppsala University, 1963) for copepods, chydorids, and cladocerans, and the standardized dry weight values reported by Faubel [10] for remaining taxa. Second, biomass was converted to carbon units by assuming that ash-free dry weight is 40% of dry weight [11]. Respiration was then calculated using the relationships between body size (as dry weight) and respiration rates described by Ivleva [29] for microcrustaceans, and Banse [1] for other taxa. In the final step, respiration rates were corrected for the experimental temperature according to Winberg [54], and converted to carbon using a respiratory quotient of 0.90 (i.e., 0.34 μg C released 1 μg^{-1} O_2 consumed).

The data were analyzed using ANOVA and Scheffé's contrast tests. Time trends within treatments were analyzed using linear regression.

Results

The addition of diatoms to the microcosms resulted in a rapid response by the bacterial assemblage of the sediment, as indicated by higher production estimates throughout the experiment ($P \leq 0.023$), compared with controls. Bacterial production increased to 106 ± 12.5 ng C g^{-1} wet wt h^{-1} (mean ± standard deviation, used unless else is indicated), and 125 ± 27.6 ng C g^{-1} wet wt h^{-1} in the diatoms-only and the diatoms-plus-*Chironomus* treatments, respectively, within two hours after the addition of diatoms, compared with 66.5 ± 8.32 ng C g^{-1} wet wt h^{-1} for the controls (Fig. 2A). On day 1, bacterial production in the diatoms-only treatment was 13 times higher than controls and peaked at 815 ± 85.2 ng C g^{-1} wet wt h^{-1}. In the diatoms *Chironomus* treatment, bacterial production on day 1 was 1087 ± 169 ng C g^{-1} wet wt h^{-1}, i.e., 17 times higher than controls (62.9 ± 9.29 ng C g^{-1} wet wt h^{-1}). On day 4, bacterial production in both treatments with diatom additions had declined to values of 459 ± 58.6 and 396 ± 80.9 ng C g^{-1} wet wt h^{-1}. After 36 days, bacterial production in the diatoms-only and the diatoms-plus-*Chironomus* treatments was still 3.4 and 2.1-fold higher ($P \leq 0.023$), respectively, than in the controls (35.5 ± 2.68 ng C g^{-1} wet wt h^{-1}).

Neither the elevated production estimates recorded for the diatoms-only treatment, nor the starvation of controls (no diatom addition) affect bacterial abundance in the sediment ($r^2 = 0.13$ and 0.16, $P \geq 0.06$). Only in microcosms with *Chironomus* was a decreasing time trend in bacterial abundance observed ($r^2 = 0.41$, $P \leq 0.0003$). Bacterial population ranged between $2.4 \pm 0.021 \times 10^9$ and $4.3 \pm 0.46 \times 10^9$ cells g^{-1} wet wt for all treatments (Fig. 2B). Conversely, mean bacterial cell volume (MCV) displayed a clear treatment effect (Fig. 3). In both treatments receiving diatoms, MCV was higher than in controls on day 2, 4, and 8 ($P \leq 0.03$). On day 1, bacterial cells in the diatoms-only treatment were already larger than in controls ($P = 0.018$). MCV in controls decreased from 0.143 ± 0.019 to 0.093 ± 0.010 μm^3 during the first two days of the experiment and were then relatively stable during the remainder of the experiment. After 16 and 36 days, as on the initial day of the experiment (day 0), no differences between treatments were noted ($P \geq 0.47$). Bacterial abundance in the added diatom suspension was $8.5 \pm 2.4 \times 10^7$ cells g^{-1} wet wt, i.e., 2.6% of the bacterial abundance in the sediment at day 0. Small rod-shaped bacteria dominated these samples. MCV for these bacteria was determined 0.220 μm^3, but this value is ambiguous since cells appeared as diffuse images in the microscope, probably due to freezing. Unfortunately, three of four replicate bacterial counts for controls on day 16 showed unreasonably high numbers ($7.0 \pm 1.3 \times 10^9$ cells g^{-1} wet wt) of large cells (MCV = 0.179 ± 0.0076 μm^3) and were eliminated from the data set.

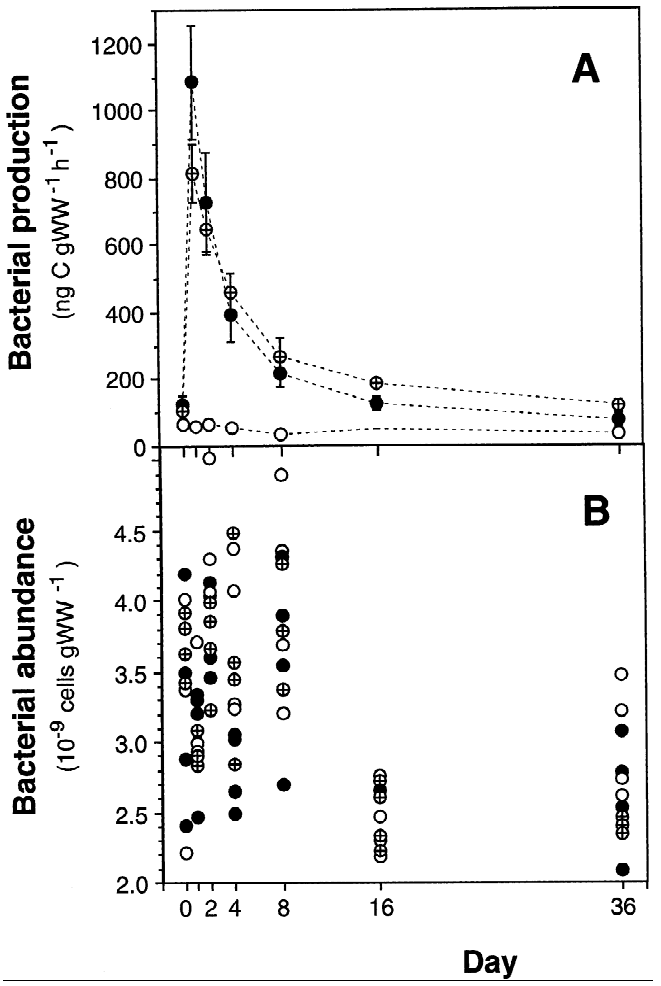

Fig. 2. Bacterial production (**A**) and abundance (**B**) in the experimental sediment (Lake Erken, 0–0.5 cm, <0.3 mm) for controls (○), the diatoms-only treatment (⊕), and the diatoms-plus-*Chironomus* treatment (●). *Error bars* denote ±1 SD.

The high bacterial activity noted on days 1 and 2 in both treatments receiving diatoms probably resulted in the rapid decline of the initially high concentrations of DOC in interstitial water. The total concentrations of DOC (sum of DOC in interstitial and overlying water) decreased from 322 to 141 µg C in the diatoms-only treatment and from 360 to 113 µg C in the diatoms-plus-*Chironomus* treatment between day 0 and day 2 (Fig. 4). Changes in DOC concentrations with time could also be related to the presence of *Chironomus*. After 2 h of incubation (day 0), interstitial DOC levels were 22 ± 9.3 µg C for the diatoms-only treatment, but signifi-

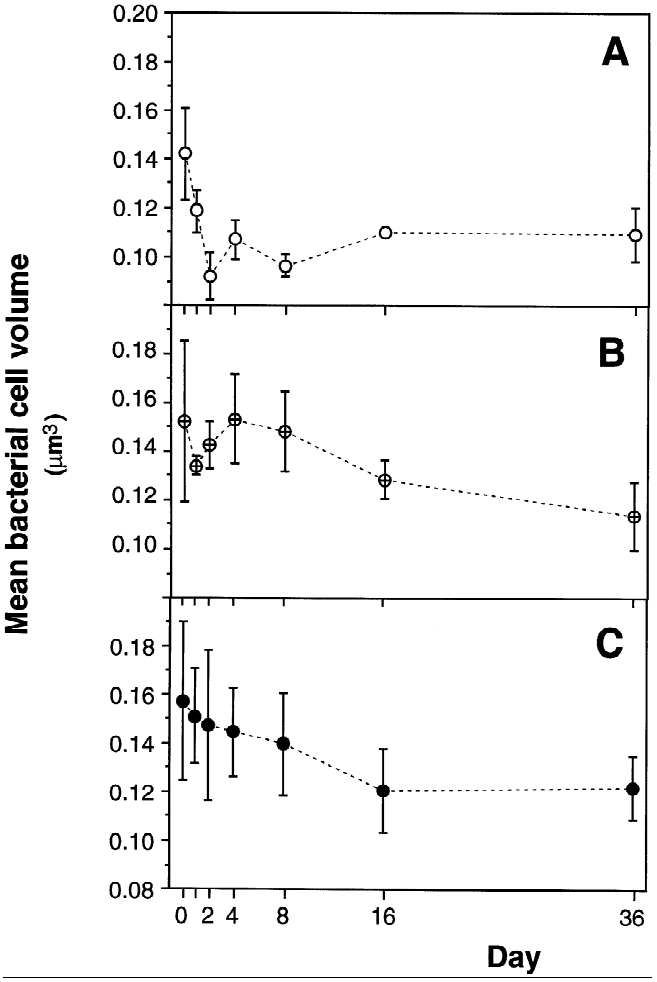

Fig. 3. Mean bacterial cell volume in experimental sediment (Lake Erken, 0–0.5 cm, <0.3 mm). ○, controls (**A**); ⊕, diatoms-only treatment (**B**); ●, diatoms-plus-*Chironomus* treatment (**C**). *Error bars* denote ±SD.

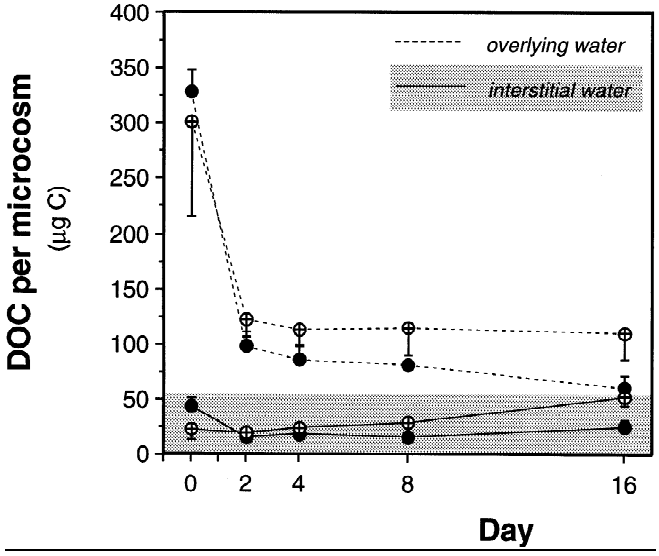

Fig. 4. Concentrations of DOC in overlying water (*dotted lines*) and interstitial water (*solid lines*) for the diatoms-only treatment (⊕), and the diatoms-plus-*Chironomus* treatment (●). *Error bars* denote ±1 SD.

cantly higher ($P = 0.027$) for the diatoms-plus-*Chironomus* treatment, 43 ± 8.8 µg C. At day 2, interstitial DOC levels had dropped to mean values under 20 µg C in both treatments. An increasing time trend ($r^2 = 0.71$, $P = 0.001$) was found for interstitial DOC levels in the diatoms-only treatment and was accompanied by a decreasing trend ($r^2 = 0.26$, $P = 0.022$) for DOC in the overlying water. The latter significant regression was, however, entirely dependent on the high values recorded on day 0 (300 ± 85.5 µg C or 3.8 ± 1.1 µg C ml^{-1}). The total concentrations of DOC in the diatoms-only microcosms did not change over time ($r^2 = 0.15$, $P \geq 0.09$). Conversely, in the diatoms-plus-*Chironomus* treatment, both DOC in overlying water and total DOC showed a significant decline ($r^2 = 0.39$, $P \leq 0.004$, and $r^2 = 0.32$, $P \leq 0.01$, respectively) between day 0 and day 16. Between day 2 and day 16, total DOC concentrations were consistently higher in the diatoms-only treatment compared with the diatoms-plus-*Chironomus* treatment ($P \leq 0.03$).

The elevated activity of bacteria following the diatom pulse was also detected by measurements of community respiration (CO_2 production), peaking between day 1 and day 2 at 35 ± 0.96 µg C h^{-1} for the diatoms-only treatment, and 44 ± 4.4 µg C h^{-1} for the diatoms-plus-*Chironomus* treatment (Fig. 5). This also implies higher community respiration ($P = 0.0099$) for the diatoms-plus-*Chironomus* treatment than for the diatoms-only treatment over this time interval. Surprisingly, also in the controls, CO_2 production was higher between day 1 and day 2 than during the previous and following time interval. Carbon dioxide production in the microcosms was significantly higher in the treatments receiving diatoms than in controls ($P \leq 0.021$), except for day 36, when only the diatoms-plus-*Chironomus* treatment still displayed higher CO_2 production rates than controls ($P = 0.020$).

Combining measurements of bacterial production, community respiration, and calculated meiofauna respiration (from abundances, see below) showed that the growth efficiency of sediment bacteria ranged between 14.6 and 34.5% (Table 1). These estimates assumed that microheterotroph activity in the sediment was strongly dominated by bacteria, that respiration by autotrophs was negligible, and that the majority of bacteria had the capability to incorporate exter-

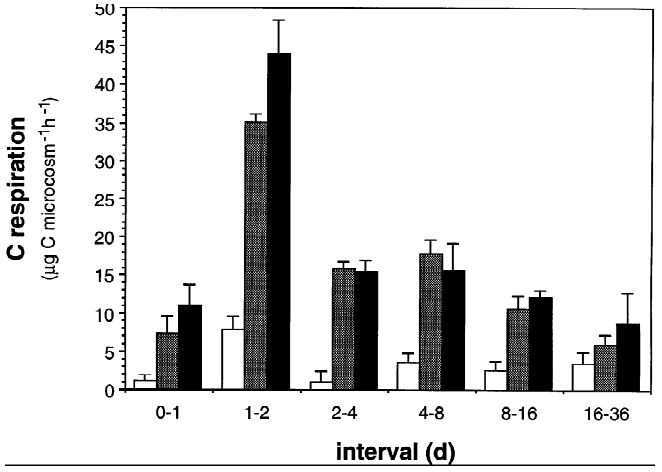

Fig. 5. Community respiration over the various experimental intervals in controls (*white bars*) and microcosms belonging to the diatoms-only treatment (*gray bars*) and diatoms-plus-*Chironomus* treatment (*black bars.*) *Error bars* denote ±1 SD.

nally added [^{3}H]thymidine. Overall growth efficiency of sediment bacteria, determined as the slope of a linear regression (forced through the origin) of bacterial production on meiofauna-corrected community respiration, was 0.168 (or 16.8%) (r^2 = 0.93). Meiofauna respiration contributed only marginally to overall community metabolism, never exceeding 1.3% of the overall community respiration (Table 1). Ambient meiofauna abundance in the experimental sediment was 12 ± 4.5 individuals per microcosm, ranging between 9.8 ± 3.8 and 16 ± 4.6 individuals per microcosm. Copepoda was the dominant taxa with densities averaging 6.3 ± 2.3 individuals per microcosm. Nematodes, juvenile chironomids, ostracods, chydorids, cladocerans, and oligochaetes were present at low densities.

Chironomus larvae initially had a stimulating effect on the activity of sediment bacteria, with higher bacterial production recorded on day 1 compared with the diatoms-only treatment ($P \leq 0.020$). After 16 and 36 days, the presence of *Chironomus* larvae resulted in lower bacterial production estimates ($P \leq 0.012$), compared with the diatoms-only treatment. *Chironomus* larvae also markedly stimulated the degradation of the added diatoms, as indicated by a more rapid decline in concentrations of both chlorophyll *a* in the sediment (Fig. 6A). After 4 days, and continuing for the duration of the experiment, the sediment chlorophyll *a* concentrations in microcosms containing *Chironomus* were lower than in the diatoms-only treatment ($P \leq 0.024$). In the controls, chlorophyll *a* concentrations did not change over the time course of the experiment (Fig. 6A), indicating that ambient chlorophyll *a* in the sediment was associated with organic matter resistent to decomposition. Survival of *Chironomus* larvae was 100%, except on day 36 when three live and one dead larvae were recaptured from one of the microcosms. On day 36, many pupae and even a few adult chironomids were encountered in the microcosms. By the end of the experiment, chlorophyll *a* concentrations were almost back at the level prior to diatom addition in the treatment with *Chironomus* (Fig. 6A). Maximum chlorophyll *a* concentrations in the sediment were recorded on day 4, indicating that part of the diatom addition was in suspension during the initial 4 days of the experiment.

The time trends for sediment ATP concentrations were similar to the patterns observed for chlorophyll *a* (Fig. 6B). On day 16, conspicuously high ATP concentrations were found in sediment of diatoms-only microcosms and controls. Also the carbon content of the sediment in the diatoms-only treatment increased during the first 4 days of the experiment from 75.7 ± 0.727 mg C g^{-1} dry wt sediment to 79.0 ± 1.20 mg C g^{-1} dry wt. on day 4. After this maximum, the sediment carbon content gradually declined to 75.9 ± 0.663 mg C g^{-1} dry wt. on day 36. This was in agreement with the diatoms-plus-*Chironomus* treatment, where sediment carbon was 76.1 ± 2.91 mg C g^{-1} dry wt after 36 d of incubation. The carbon content of control sediments was 73.3 ± 1.58 mg C g^{-1} dry wt on day 36. Nitrogen concentrations in the sediment of the diatoms-only treatment ranged from 9.2 to 11.3 mg N g^{-1} dry wt. No significant trends for sediment carbon and nitrogen concentrations were found. Oxygen concentrations in the microcosms were between 7.8 and 10.5 mg O_2 $liter^{-1}$, and pH ranged between 7.1 and 7.8.

Discussion

The added pulse of diatoms markedly affected benthic community metabolism. Carbon budgets calculated for this 36-day microcosm study showed a threefold increase in community respiration after diatom addition (Fig. 7). Respired carbon in microcosms exceeded the added diatom pulse by a factor 1.9 and 2.3 for the diatoms-only and diatoms-plus-*Chironomus* treatments, respectively. Interestingly, the difference in community respiration between the diatoms-only treatment and controls (5.6 mg C) exceeded the quantity of carbon added as diatoms (4.3 mg C), implying that 1.3 mg C was cooxidized along with the oxidation of added diatoms. This may, however, be an overestimation of cooxidation in

Table 1. Bacterial and meiofaunal contribution to benthic community metabolism over experimental time intervals in microcosms receiving a pulse of diatoms at day 0 (diatoms-only treatment), including bacterial production (from [^{3}H]thymidine incorporation rates), overall community respiration (from CO_2 production), meiofauna abundance and respiration, and the growth efficiency (GE) for sediment bacteria (corrected for meiofauna respiration)[a]

Day	Time interval (h)	Bacterial production (μg C/microcosm)	Community respiration (μg C/microcosm)	Meiofauna abundance (ind/microcosm)	Meiofauna respiration (μg C/microcosm)	Bacterial GE[b] (%)
0–1	24	91.93 (21.22–162.7)	175.2 ± 53.79	10.3 ± 4.57	1.05 ± 0.283	34.5
1–2	20	121.7 (107.8–135.3)	703.2 ± 19.16	9.80 ± 3.77	1.99 ± 0.409	14.8
2–4	48	221.1 (183.3–258.8)	765.8 ± 39.91	12.8 ± 4.57	2.75 ± 1.68	22.5
4–8	92	291.3 (215.8–366.7)	1714 ± 182.2	10.8 ± 5.12	4.84 ± 2.10	14.6
8–16	196	364.8 (431.6–298.1)	2025 ± 340.6	16.3 ± 4.57	14.7 ± 2.95	15.4
16–36	480	611.5 (477.9–745.1)	2871 ± 569.4	ND[c]	36.8 ± 7.37[d]	17.7

[a] Mean ± 1 SD are given, except for bacterial production where the range is shown in parentheses.
[b] Corrected for meiofauna respiration
[c] ND, Not determined
[d] From abundances at day 16

the sediment, as respiration in the water phase probably was also stimulated by the diatom addition. Carbon budgets further showed that community respiration was 1.7 mg C higher in the presence of *Chironomus* larvae (Fig. 7), reflecting the sum of chironomid respiration and stimulatory effects on sediment microbes by *Chironomus* activity (see below). *Chironomus* larvae contributed significantly to overall community respiration during the first 2 days of the experiment (Fig. 5), indicating a high activity after 2 days of acclimation in nutrient-poor sediment. After 4 days, *Chironomus* activity no longer affected overall community metabolism. Incorporation of diatom carbon into *Chironomus* biomass was estimated to be 0.63 ± 0.02 mg C using individual lengths of *Chironomus* larvae and a length-wet weight relationship (wet wt {as mg} = 0.919 × length {as mm} − 3.633; $r^2 = 0.68$, $P = 0.0001$, $n = 77$), and assuming (1) that ash-free dry weight was 15% of the wet weight [53], and (2) that carbon content equaled 50% of ash-free dry weight [34]. This number should, however, be regarded as an underestimate, since calculations are based on body length measurements for remaining larvae after 36 d, i.e., individuals that had not pupated or emerged. For comparison, Gullberg et al. [26] determined incorporation of diatom C by *C. riparius* under the same experimental conditions as 0.81 mg C after 8 days of incubation. The negligible role of benthic meiofauna in carbon turnover found in this study (Table 1) corroborates earlier findings for the same sediment under laboratory conditions (Gullberg et al., [26]). In a field study in Lake Erken, however, Goedkoop and Johnson [16] calculated that the role of meizoobenthos in C turnover after spring bloom deposition equaled the C metabolism of sediment bacteria and deposit-feeding chironomids.

The fast, short-term response (in terms of production and respiration) observed in this study may be attributed to relatively high concentrations of DOC (DOM) in the diatom addition (high leaking rates of diatoms), despite extensive washing of the diatom suspension. The rapid assimilation of DOC is in agreement with previous studies focused on the decomposition of different fractions of organic matter in marine sediments, showing that the labile, soluble fraction of diatom cells is decomposed at a much higher rate than the particulate fraction [28, 43]. Also Henrichs and Doyle [28], measuring decomposition rates of ^{14}C-labeled diatoms in marine sediment, noted a rapid decrease in DOC during the initial phase of their incubations. The rapid decline in bacterial production noted between day 1 and day 2 in this study may seem surprising, since DOC levels in the sediment were still relatively high (Figs. 2A and 4). Presumably, the optimum conditions for bacterial growth during the initial phase of the experiment were altered when easily assimilable, i.e., low-molecular DOM, was depleted. During the remainder of the experiment, bacterial production was probably constrained by the rates at which these specific compounds became available through diffusion from the overlying wa-

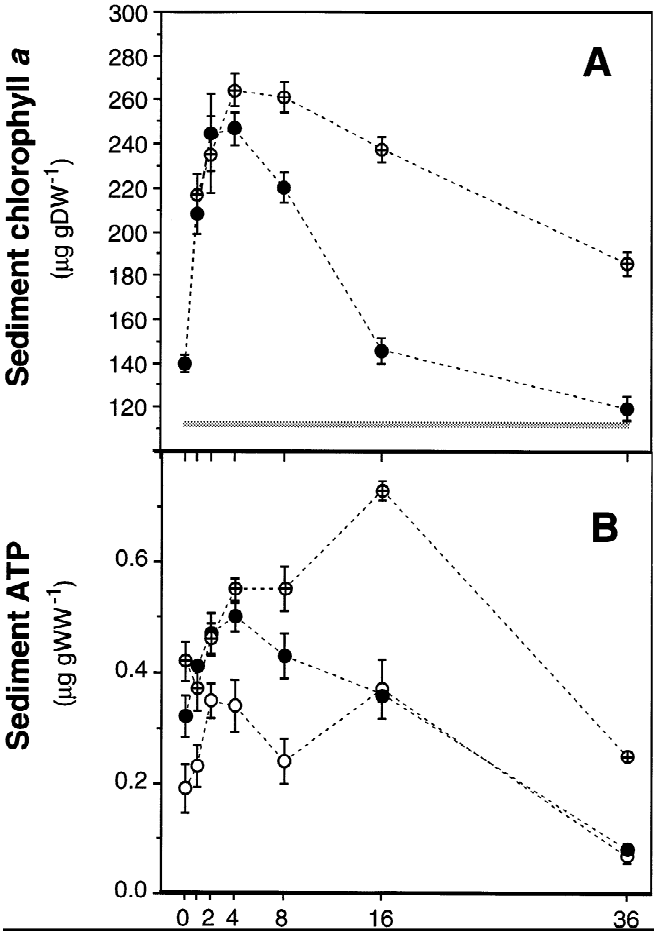

Fig. 6. Concentrations of sediment chlorophyll *a* (**A**) and ATP (**B**) in experimental sediment (Lake Erken 0–0.5 cm, < 0.3 mm) for controls (○), the diatoms-only treatment (⊕), and the diatoms plus *Chironomus* treatment (●). The gray line in **A** represents the level of chlorophyll *a* in the controls at the start and at the termination of the experiment. *Error bars* denote ± 1 SD.

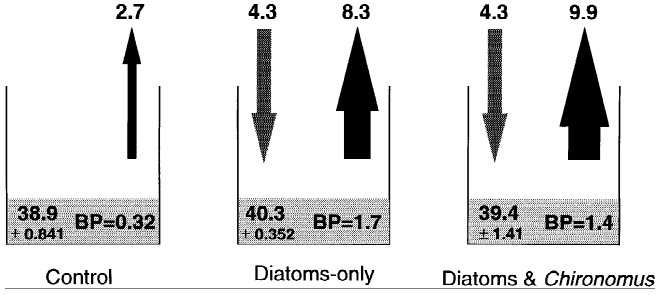

Fig. 7. Carbon budgets after 36 days of incubation for controls (**A**), diatoms-only treatment (**B**), and diatoms-plus-*Chironomus* treatment (**C**), showing diatom addditions (*gray arrows*), community respiration (*black arrows*), bacterial production (BP), and sediment carbon, all expressed as mg C. The carbon content of start sediment was 40.2 ± 0.04 mg C. g^{-1} dry wt.

ter, leakage from diatom cells, extracellular enzymatic hydrolysis, and/or excretion by abundant fauna, especially *Chironomus* larvae.

The time-scale of the microbial response may be largely dependent on the quality of the added organic substrate and the temperature regime (Table 2). Concentrations and generation rates of DOM in the sediment, caused by interrelated factors such as leaking rates from algae and/or bacterial exoenzyme activity, and the presence of bacteria associated with the added organic substrate, are important factors influencing the microbial response. For example, it may be difficult to distinguish the response of sediment microbiota from an increase in activity due to seston-associated microbial cells. Törnblom (Doctoral thesis, Uppsala University, 1995) found that bacterial production of seston (>20 µm) samples was more than twice as high as that of surficial sediment (both as mg C m^{-2} day^{-1}). In addition, cosedimentation of detritus-associated bacteria has been postulated as an important coupling between pelagic and benthic communities [17]. The immediate response detected by heat production measurements and determinations of ETS, under in situ conditions at low temperature by Graf et al. [22] (Table 2), may possibly reflect the input of metabolically active cells to the sediment rather than a response of ambient sediment microbiota. Conversely, if diatoms are frozen, centrifuged or heat-shocked, cells will exhibit increased leaking rates of fluids (DOM).

The growth efficiencies for the bacterial assemblage calculated in this study agree with those reported by Bell and Ahlgren [2] (based on Cartesian Diver techniques and [^{3}H]thymidine incorporation rates) and Törnblom [50] (combining microcalorimetry and [^{3}H]thymidine incorporation rates). Both studies measured bacterial growth efficiencies in the range of 10–30%; these values are consistent with those reported for bacterioplankton in Lake Erken [3]. The estimates of growth efficiencies presented herein are influenced by the various factors that affect the parameters and conversion factors used in calculations. For example, microbes in both the sediment (e.g., microfauna, cyanobacteria) and in the overlying water (e.g., bacterioplankton) contribute to the carbon respiration in the microcosms, thereby causing a potential underestimation of growth efficiency for sediment bacteria. Conversely, the inability of some types of bacteria, for example anaerobes, to incorporate [^{3}H]thymidine (see [47] for review) may result in relatively low estimates of bacterial production. However, this should have had a limited impact on the outcome of growth

efficiency calculations, since aerobic metabolism should have predominated in the aerobic, well-mixed, high water content sediments used in this study. Virtually all heterotrophic bacteria in plankton samples, where oxic conditions prevail, take up externally added thymidine [14].

Anaerobic bacteria were probably not of quantitative importance under the experimental conditions. Although redox potential measurements were not made, indirect evidence for this conclusion is provided by a relationship between hypolimnetic oxygen saturation (O_2%) and the redox potential (Eh) of surficial sediment (at 1 cm depth) under field conditions in Lake Erken during 1990–1991 (Eh = 4.76 × O_2% − 113.9; $r^2 = 0.57$, $P = 0.0001$, $n = 25$, range −215 to 430 mV and 10.3–114% O_2). Using this relationship and the observed oxygen saturation levels in the microcosms (71–91%), the redox potential (at 1 cm depth) in experimental sediment should have ranged from 224 to 317 mV, indicating clearly oxidized conditions. It is, therefore, also unlikely that CO_2-reducing methanogens significantly affected overall community respiration. Since bacterial production tends to be underestimated, whereas community metabolism is overestimated to some unknown degree, the growth efficiencies presented in this study should be regarded as minimum values.

Bacterial abundance did not change during the experiment, despite high production estimates. Between day 1 and day 2, when the highest production estimates were recorded, $5.0 \pm 0.43 \times 10^8$ cells g^{-1} dry wt and $5.4 \pm 0.39 \times 10^8$ cells g^{-1} dry wt were produced in the microcosms receiving diatoms. Thus, an 11 to 15% increase in bacterial abundance

Table 2. Summary of results of marine and freshwater studies focusing on the sediment microbial response to organic enrichment with different organic substrates and temperature regimes

Study	System	Lab/field	Organic input (treatment)	Microbial parameters	T regime (°C)	Time scale of response
Graf et al. (1982) [22]	Kiel Bight	Field	Deposited spring seston	Heat production, ETS, ATP	1–4.9	Immediate
Kelly & Nixon (1984) [35]	Narragansett Bay	Laboratory	Collected seston (>63 μm) (dried at 70°C and dehydrated)	O_2 consumption, CO_2 release	15	Within 3 days
Graf (1987) [19]	Kiel Bight	Laboratory	Cultured diatoms (temperature treated 40–0°C)	Heat production, ATP, O_2 consumption	8	Within hours
Turley & Lochte (1990) [52]	NE Atlantic	Laboratory	Collected detritus (>53 μm) (frozen and gamma irradiated)	Bact. biomass, POC, DOC	2	Within 5 days
van Duyl et al (1992) [8]	North Sea	Laboratory	Collected spring seston (>50 μm) (frozen)	Bact. biomass and productivity, O_2 consumption	0.5	Within 5 days
Flindt & Nielsen (1992) [13]	Roskilde Fjord	Field	Deposited autumn seston	Bact. biomass, O_2 consumption	14	5 days
Enoksson (1993) [9]	Laholm Bay	Laboratory	Axenically cultured diatoms (fresh)	O_2 consumption	10	Within 1 day
Törnblom & Boström (1995) [51]	Lake Vallentunasjön	Laboratory	Collected spring seston (>20 μm) (washed with sterile lake water)	Heat production, ATP, BP	4	4–6 days
Törnblom (Doctoral Thesis, Uppsala University)	Lake Erken	Laboratory	Collected autumn seston (>20 μm) (washed with lake water)	Bact. biomass and productivity, heat production	9.0–6.5	1 day
Goedkoop & Johnson (1996) [16]	Lake Erken	Field	Deposited spring seston	Bact. biomass and productivity	4.3–8.7	10 days
Goedkoop et al. (this study)	Lake Erken	Laboratory	Cultured diatoms (frozen)	Bact. biomass and productivity, CO_2 release	10	Within hours

was expected over this period. These moderate increases may have been obscured by the error in bacterial counts. Conversely, marked differences in MCV were noted between treatments and controls (Fig. 3). Apparently, actively growing bacteria are larger than slowly or nongrowing cells. An increase in bacterial cell size following sedimentation events was also found in marine field studies by Flindt and Nielsen [13] and Turley and Lochte [52], and probably reflects cell enlargement prior to division. The declining MCV trends in treatments and controls show that cell size decreases during starvation. The initial decline in MCV in controls (day 0–2) may reflect a stimulation of bacteria due to sediment manipulation 3 days before the start of the experiment.

Macrobenthic deposit-feeders, such as *Chironomus,* may stimulate the generation of suitable organic substrates for bacteria through their feeding behavior. Ingestion, partial digestion of sedimenting organic particles (e.g., diatoms), and subsequent excretion of dissolved compounds will enhance the conversion of particulate matter into dissolved compounds. Also, the handling and intake of food items by *Chironomus* may cause a loss of DOC from cell contents, in accordance with sloppy feeding described for grazing zooplankton [38]. In the present study, the faster decline in levels of sediment chlorophyll *a* and ATP in the presence of *Chironomus* lends support to the conjecture of an increased conversion of diatom POM to DOM through *Chironomus* activity. *Chironomus* gut tracts may be sites of high decomposition rates of POM. Furthermore, the faster decline in overall DOC (sum of interstitial and overlying water) in the diatoms-plus-*Chironomus* microcosms (from 360 ± 11.8 μg C on day 0 to 85 ± 9.0 μg C on day 16) compared with the diatoms-only treatment (322 ± 79.3 to 160 ± 22.2 μg C over the same time interval) may indicate higher POC-DOC conversion rates.

The lower bacterial production estimates on days 16 and day 36 for the microcosms containing *Chironomus,* however, show that sediment bacteria are not favored by the increased levels of DOM/DOC generated by *Chironomus* activity. Therefore, we conclude that this DOC may be efficiently taken up inside the digestive tract of *Chironomus* larvae, either by the gut flora or by the larvae themselves. If this is the case, *Chironomus* larvae competed with sediment bacteria for available organic substrate under the experimental conditions. High bacterial activity inside invertebrate guts has been found for both marine [45] and freshwater invertebrates (R. K. Johnson, unpublished data). Johnson (unpublished data) found larger bacterial cells in the hindgut of *Chironomus plumosus* than in the foregut, indicating active growth. Furthermore, a large proportion of dormant/inactive cells results in long doubling times and low specific activities for sediment bacteria (e.g., [17]). If only a small proportion of sediment bacteria are metabolically active (e.g., [42]), and bacteria inside invertebrate gut tracts are highly active, then gut-living bacteria may contribute significantly to the overall decomposition of organic material in the sediment, especially at high invertebrate densities.

Macroinvertebrate burrowing activity in the sediment (bioturbation) may stimulate bacterial activity [5, 36]. Bioturbation by chironomids will result in increased water content of the sediment [5] and, consequently, increased diffusion rates of DOC into the sediment. Even under in situ conditions, the fauna-mediated processes described above may be important for the decomposition and mineralization of organic matter at the sediment-water interface [8, 37]. In the present study, *Chironomus* bioturbation caused an increased flux of DOC from the overlying water into the sediment. On day 0, only 2 h after the diatom pulse, 43 ± 8.8 μg C was recovered as DOC in the interstitial water of sediment from the diatoms-plus-*Chironomus* treatment, compared with 22 ± 9.3 μg C in the diatoms-only treatment. This DOC was, however, rapidly utilized within the sediment, since the elevated interstitial DOC concentrations leveled out rapidly; on days 2, 4, and 8, interstitial DOC levels did not differ between the two treatments. Assimilation of diatom C by *Chironomus* larvae (see [26]) is a probable explanation for the lower DOC values recorded in both overlying and interstitial water for the diatoms-plus-*Chironomus* treatment after 2, 4, 8, and 16 days. The assimilation of dissolved compounds by freshwater invertebrates contradicts classical feeding theory [33]. Perhaps indirect uptake pathways, mediated by extracellular polymeric compounds secreted by bacteria or diatoms [6] constitute an alternative mechanism.

The findings from this study show that bacterial assemblages in freshwater sediments can respond extremely rapidly to an input of organic matter, and suggest that easily assimilable DOM is the main causal factor for this response. *Chironomus* (deposit-feeding macroinvertebrates) may interact with sediment bacteria in a multidimensional way. They can stimulate bacterial production by increasing fluxes of nutrients and electron acceptors into the sediment as a consequence of bioturbation. Our data also indicate that *Chironomus* may compete with sediment bacteria for available DOM. Although assimilation of DOM by *Chironomus* was not measured directly, this conclusion can be explicitly drawn from the differences in DOC concentrations between treatments with and without *Chironomus.* The digestive

tracts of *Chironomus* larvae may be sites of high decomposition rates, whose overall quantitative importance may be considerable in systems with high macroinvertebrate densities.

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