



Effects of Experimental Sediment Resuspension on a Coastal Planktonic Microbial Food Web

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Effects of sediment resuspension on microbial food web dynamics in the water column of microcosms consisting of sediment cores with the overlying water have been studied. These microcosms were obtained from Rassower Strom, coastal Southern Baltic, and incubated for 108 h under *in situ* light and temperature conditions. They were resuspended with oscillating grids at intensities that reproduced the range of naturally occurring seston concentrations during resuspension events in these waters.

After 12 h of resuspension, the abundances of pico- and nanoautotrophs, rhizopods (naked and testate amoebae) and heterotrophic nanoplankton had increased and were significantly positively correlated to seston concentration, indicating that resuspension of benthic representatives directly affected their water column abundances. Similar trends were found for benthic diatoms and ciliates. In addition, resuspension enhanced population growth of pico- and nanoautotrophs and resuspended diatoms over the whole course of the experiment. This enhancement was independent of a direct transport of cells from the sediment and was most likely caused by reduced nitrogen limitation due to resuspension. The abundance of heterotrophic nanoplankton was tightly correlated to those of their main food organisms, pico- and nanoautotrophs and bacteria. It was also significantly increased by resuspension over the whole course of the experiment. This is consistent with decreased bottom-up control of heterotrophic nanoplankton due to resuspension.

These results indicate that sediment resuspension may strongly affect the planktonic microbial food web of coastal waters, both by a direct transport of cells from the sediment into the water column and by indirect effects mediated by dissolved nutrients and trophic interactions.

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Introduction

Understanding the microbial food web of shallow coastal waters requires knowledge about effects of the physical processes which act on these waters. Sediment resuspension by tides or winds is one of these processes. Field data from various coastal waters indicate that sediment resuspension may act as a means of passive dispersal of autotrophic and heterotrophic protists from the sediment, thereby increasing total abundances and changing the taxonomic composition of the protistan community in the water column (Shaffer & Sullivan, 1988; De Jonge & Van Beusekom, 1992, 1995; Rogerson & Laybourn-Parry, 1992b, Shimeta & Sisson, 1999; Garstecki *et al.*, 2000). It is also known that the susceptibility of benthic microphytobenthos and protozoa to resuspension may vary between species (De Jonge & Van den Bergs, 1987; Shimeta & Sisson, 1999).

Direct effects of resuspension on the abundance of benthic protozoa and algae in the water column are well-documented and inevitable, but much less is known about what happens to these organisms once they are resuspended. Resuspension may enhance remineralization and induce dissolved nutrient and particulate organic matter fluxes into the water column, which can be used by algae and bacteria (Wainright, 1990; Balls *et al.*, 1994; Arfi & Bouvy, 1995; Pedersen *et al.*, 1995). An increase in bacterial abundance and biovolume due to resuspension has been shown both in field and experimental studies (Ritzrau & Graf, 1992; Wainright, 1987). Nutrient-related resuspension effects were found in freshwater phytoplankton (Reynolds 1996; Ogilvie & Mitchell 1998). Although bacterivorous and herbivorous protists should benefit from increased abundances of their prey, the response of higher levels of the microbial food web to the processes described has only occasionally been addressed (Wainright, 1987).

Direct and indirect effects of experimental sediment resuspension were studied on the microbial food

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web of natural sediment cores including the overlying water. These cores were obtained from the Boddengewässer, shallow, non-tidal, mesotrophic to eutrophic, brackish lagoons on the north-eastern Baltic coast of Germany. The microbial food web of these waters has been studied extensively (e. g. Arndt *et al.*, 1990; Schiewer, 1998). Recent field data indicate that benthic and planktonic protistan communities are closely coupled in the Boddengewässer, and that sediment resuspension is one of the mechanisms responsible (Garstecki *et al.*, 2000).

Materials and methods

Study site

The experiment was carried out with natural sediment cores from Rassower Strom, Nordrügensch Boddengewässer, coastal Southern Baltic. Rassower Strom (54°34'N, 13°10'O) is mesotrophic with an average salinity of 9.0 and a mean water depth of 3.8 m. Muddy sediments (4% organic content) prevail. The frequency of resuspension events at Rassower Strom has been estimated from turbidity (S. Dahlke, pers. comm.) and wind speed measurements (J. Meyercordt, pers. comm.) in 1996. According to this estimate, 66 wind-induced resuspension events (situations with less than 10% light transmission 0.5 m above the sediment and more than 5 m s^{-1} wind speed) occurred during a total of 142 d between May and November 1996.

Experimental design

The experiment was run in June 1997. Twenty sediment cores with 2.6 l overlying water were obtained by a ship-operated multicorer from Rassower Strom. The cores were randomized before being assigned to treatments. Four cores were sacrificed and sampled at the start of the experiment. Sixteen cores were transferred into plastic tubes (length 400 mm, inner diameter 100 mm) and incubated in a water basin at 18 °C under 220 mE m^{-2} illumination with a light/dark-cycle of 16 h/8 h. Light and temperature conditions were chosen to correspond to field conditions. Different resuspension intensities were achieved by oscillating grids [Figure 1(a),(b); apparatus modified from Davis, 1993]. Experimental groups were treated with piston frequencies of 0.71 s^{-1} , 1.22 s^{-1} , and 1.60 s^{-1} , respectively, for one period of 12 h per day. These frequencies were chosen because they reproduced the range of naturally occurring seston concen-

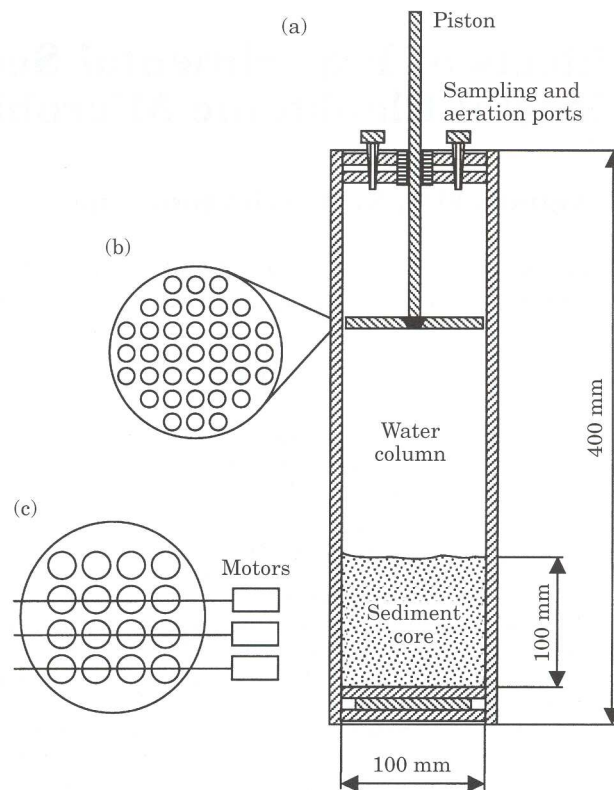


FIGURE 1. Experimental setup: (a) section from top to bottom of an experimental microcosm, (b) schematic view of the oscillating grid, (c) arrangement of experimental microcosms in the water bath.

trations during resuspension events in preliminary short-term experiments. Another group of four cores was left as control [Figure 1(c)].

At the beginning of the experiment, water samples were obtained from four reference cores that had been taken together with the 16 experimental cores. Three water samples were taken from each experimental microcosm at 12 h, 60 h and 108 h into the experiment. All water samples were analysed for seston parameters, mineral nutrients, chlorophyll *a* concentration (last sampling only), and microbial community structure.

Abiotic parameters and chlorophyll *a*

Seston dry weight and the concentrations of particulate organic carbon (hereafter POC), dissolved phosphate and dissolved ammonium in the water column were measured according to standard protocols of Grasshoff (1983). Nitrate and Nitrite concentration was measured with a Sykam 4110 ion chromatographer (S. Dahlke, pers. comm.). Measurements of chlorophyll *a* concentration followed the guidelines of

the BMERC (1988). Oxygen saturation was measured with an electronic oxygen sensor (WTW, Germany).

Microbial community structure

Water column bacteria, heterotrophic nanoplankton (hereafter HNAN), picocautotrophs (autotrophs <2 µm maximum dimension) and nanoautotrophs (autotrophs between 2 and 20 µm maximum dimension), and benthic bacteria, picocautotrophs, and nanoautotrophs, were fixed with 1.5% (final concentration) glutaraldehyde, stained with DAPI (4',6'-diamidino-2-phenylindole) and counted using epifluorescence microscopy (Sherr *et al.*, 1993). Briefly, 0.5–2.0 ml subsamples were stained and concentrated on black polycarbonate filters (Millipore) of 0.2 µm pore size. At least 50 pico- and nanoautotrophs, 50 HNAN, and 300 bacteria on a minimum of 50 grids were counted. Prior to filtration, sediment samples for the enumeration of benthic organisms were diluted with 0.2 µm filtered, autoclaved seawater. The resulting slurry and all water samples were sonicated for 5 min (1 s pulse mode) with a Branson Sonic Power S-125 ultrasonic probe (protocol modified from Epstein *et al.*, 1997). After this treatment, there were no aggregates visible under the epifluorescence microscope, and an increase of the strength and duration of sonication beyond the reported values did not lead to increased cell counts in preliminary trials. It was not possible to identify and count fixed rhizopods, and as a result, the abundance of both benthic and planktonic rhizopods was determined with a modified version of the liquid aliquot method (Butler & Rogerson, 1995). Briefly, 48 subsamples of the overlying water (planktonic rhizopod enumeration, aliquot volume 100–500 µl) or of sediment slurries (benthic rhizopod enumeration, aliquot volume 10 µl) were inoculated into wells of two tissue culture plates containing 2 ml Føyns-Erdschreiber medium (Page & Siemensma, 1991). The sediment slurries were extensively shaken prior to inoculation. After 14 d incubation at 18 °C in the dark, the wells were screened for the presence of rhizopod species and initial abundance was calculated from aliquot volumes, sediment dilution factors and from the frequency of wells positive for each species assuming a Poisson distribution (Garstecki & Arndt, 2000). Sediment and water samples for the enumeration of ciliates, diatoms and other large algae were fixed in Bouin's fixative (Lee *et al.*, 1985). Water samples were counted after sedimentation of subsamples of 10–50 ml (Utermöhl, 1958), while sediment samples for the enumeration of diatoms were diluted in 0.2 µm filtered, autoclaved

seawater and homogenized by shaking. The resulting slurries were sedimented and diatoms were counted as above. Only samples containing no aggregates larger than the minimal diatom size, and only diatoms with a clearly visible cytoplasm were counted. No benthic ciliates were counted. An overview of the taxonomic composition of algae, HNAN and ciliates at the end of the experiment was obtained by live observation.

Statistical analysis

The significance of direct transport effects of resuspension was tested using one-way-ANOVAs based on log-transformed data from the first two sampling occasions ($t=0$ h, $t=12$ h). The data were log-transformed for the tests to equalise variance between treatments, but untransformed data are given in the figures. Dunnett's post-hoc test was used to test the significance of individual treatment levels, as compared with the control group. Since it was assumed that the susceptibility of individual microcosms to resuspension might differ within experimental treatments, correlations between microbial food web components and seston concentration at the first sampling occasion were analysed in addition to the ANOVAs. Untransformed data and Pearson's correlation coefficients were used for this analysis because it was assumed that direct transport effects would result in linear correlations to seston concentration.

The significance of long-term resuspension effects on microbial food web components, and of possible interactions with time, were tested using repeated-measures-ANOVAs based on log-transformed data, followed by Dunnett's post-hoc test for individual treatment levels. Spearman's rank correlation coefficients were used to analyse the relationship between seston concentration and microbial food web components over the whole course of the experiment because it was assumed that this relationship would not be mediated by direct transport mechanisms alone, and thus not necessarily be linear. In addition to seston correlations, correlations between microbial abundances were analysed (Spearman's rank correlation coefficient) in order to gauge the degree of coupling within the microbial food web. All statistical procedures were carried out using SPSS.

Results

Abiotic parameters

Seston concentration increased from an initial value of 17 mg l⁻¹ to a maximum of 425 mg l⁻¹ at the highest resuspension level after 12 h [Figure 2(a)]. It

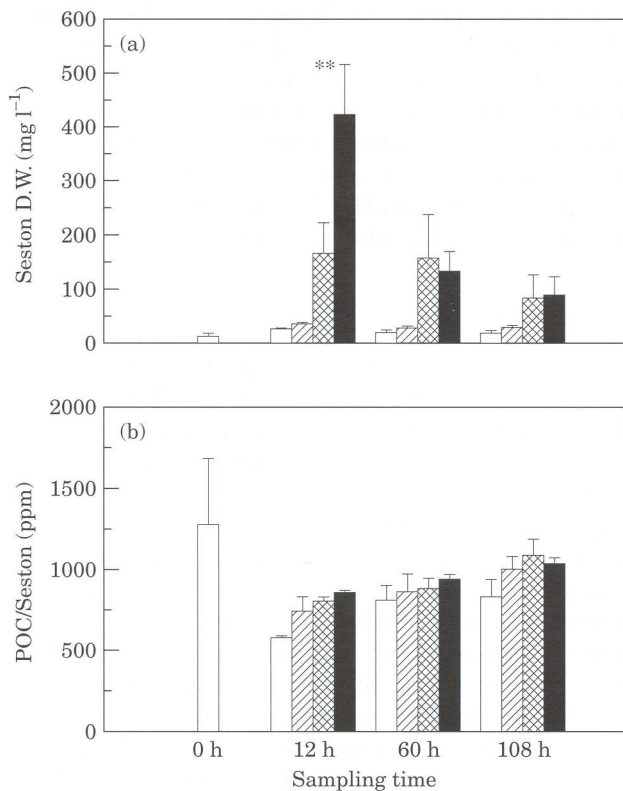


FIGURE 2. Seston concentration (a) and relative contribution of particulate organic carbon to seston (b) (error bars: standard error, $n=4$; $**P<0.01$, one-way-ANOVA). Resuspension level: $\square=0$; $\text{diagonal lines}=1$; $\text{cross-hatch}=2$; $\blacksquare=3$.

subsequently decreased to final values of 32–91 mg l⁻¹ in the resuspended groups, while it remained below 30 mg l⁻¹ in the controls. Seston concentration significantly varied with resuspension intensity after 12 h (one-way-ANOVA, data not shown) and also over the whole course of the experiment (RM-ANOVA, Table 3), but due to an interaction between resuspension intensity and sampling occasion, the latter effect was time-dependent. The relative contribution of POC to seston concentration decreased from an initial value of 0.13% to less than 0.1% after 12 h [Figure 2(b)]. Thereafter, it tended to increase with time and with resuspension intensity, but this trend was not significant [Figure 2b].

Oxygen saturation increased from values of 68–78% at the 12 h sampling occasion to final values of 101–130% (data not shown). Saturation values were significantly negatively correlated to seston concentration (Table 2).

Prior to the experiment, the water column concentrations of dissolved ammonium, nitrate and phosphate were 2.1 μM , 0.22 μM , and 0.94 μM , respectively. No significant effects of resuspension on nutrient concentration, but some trends were found:

TABLE 1. Pearson's correlation coefficients for correlations of microbial and protistan abundances to seston concentrations, first sampling occasion

Group	Pearson's c.c., $t=12$ h
Picoautotrophs	0.779**
Nanoautotrophs	0.613**
Benthic diatoms	0.397
Dinoflagellates	0.044
Bacteria	0.035
HNAN	0.543*
Rhizopods	0.938**
Benthic ciliates	0.379

c.c. correlation coefficient; * $P<0.05$; ** $P<0.01$; $n=16$.

TABLE 2. Spearman's correlation coefficients for correlations of oxygen and nutrient concentrations, and microbial abundances to seston concentrations. Data are from all sampling occasions

Parameter	Spearman's c.c., all data
O ₂	-0.440**
Ammonium	0.318*
Picoautotrophs	0.649**
Nanoautotrophs	0.371**
Benthic diatoms	0.641**
Dinoflagellates	-0.263
Bacteria	0.231
HNAN	0.514**
Rhizopods	0.840**
Planktonic ciliates	-0.142
Scuticociliates	0.379**
Benthic ciliates	0.231

c.c. correlation coefficient; * $P<0.05$; ** $P<0.01$; $n=52$.

ammonium concentration increased until 12 h, and this increase tended to be stronger in the resuspended microcosms [Figure 3(a)]. Ammonium concentration subsequently decreased to less than 1.50 μM . It was significantly positively correlated to seston concentration (Table 2). Nitrate concentration tended to be higher in the resuspended microcosms at the first sampling occasion, but not after 60 h and 108 h [Figure 3(b)]. Phosphate concentration reached maximum values of 1.21–1.48 at the lowest resuspension intensity throughout the experiment [Figure 3(c)].

Autotrophs

The planktonic autotrophic community subjected to the experiment initially consisted of picoautotrophs

TABLE 3. *P*-values of ANOVAs of main effects of resuspension and interactions with time for seston concentrations, microbial and protistan abundances during the experiment

Variable	<i>P</i> -values	
	Main effect	Interaction
Seston	0.003	0.015
Picoautotrophs	0.132	0.323
Nanoautotrophs	0.030	<0.001
Benthic diatoms	0.010	0.627
Dinoflagellates	0.010	0.117
Bacteria	0.947	0.534
HNAN	0.036	0.220
Rhizopods	<0.001	0.595
Benthic ciliates	0.556	0.190
Planktonic ciliates	0.281	0.452

n=16, repeated measures ANOVA with three sampling occasions, log-transformed data.

($260 \times 10^3 \text{ ml}^{-1}$), nanoautotrophs ($92 \times 10^3 \text{ ml}^{-1}$, mainly *Cryptomonas* spp., other autotrophic flagellates and coccal chlorophytes), and a relatively low abundance of pigmented dinoflagellates (13 ml^{-1} , *Gymnodinium* spp., *Peridinium* spp. and *Dinophysis* sp.) and diatoms (28 ml^{-1} , mainly benthic *Gyrosigma* spp., *Amphora* spp. and *Amphiprora* spp.). Initial benthic abundances of pico- and nanoautotrophs were $31 \times 10^6 \text{ cm}^{-3}$ and $33 \times 10^6 \text{ cm}^{-3}$, respectively. The initial abundance of benthic diatoms was $220 \times 10^3 \text{ cm}^{-3}$.

The autotrophs clearly responded to resuspension. Compared to the concentration of chlorophyll *a* prior to the experiment ($10.2 \mu\text{g l}^{-1}$), final concentration was generally higher, and increased with resuspension [$23.5\text{--}82.0 \mu\text{g l}^{-1}$, Figure 3(d)]. This finding was reflected in the abundances of picoautotrophs, nanoautotrophs and resuspended benthic diatoms [Figure 4(a),(b),(d)], which were significantly positively correlated to seston concentration throughout the experiment (Table 2). The picoautotrophs responded very quickly to resuspension and showed a highly significant, positive linear correlation to seston concentration after 12 h [Figure 4(a), Table 1]. However, the effect of resuspension on picoautotrophs was not significant over the whole experiment (Table 3), which was partly due to their decline at the highest resuspension level after 108 h [Figure 4(a)].

Nanoautotrophs also showed a significant linear correlation to seston concentration at the first sampling occasion (Table 1). In addition to a moderate increase to up to $120 \times 10^3 \text{ ml}^{-1}$ during the

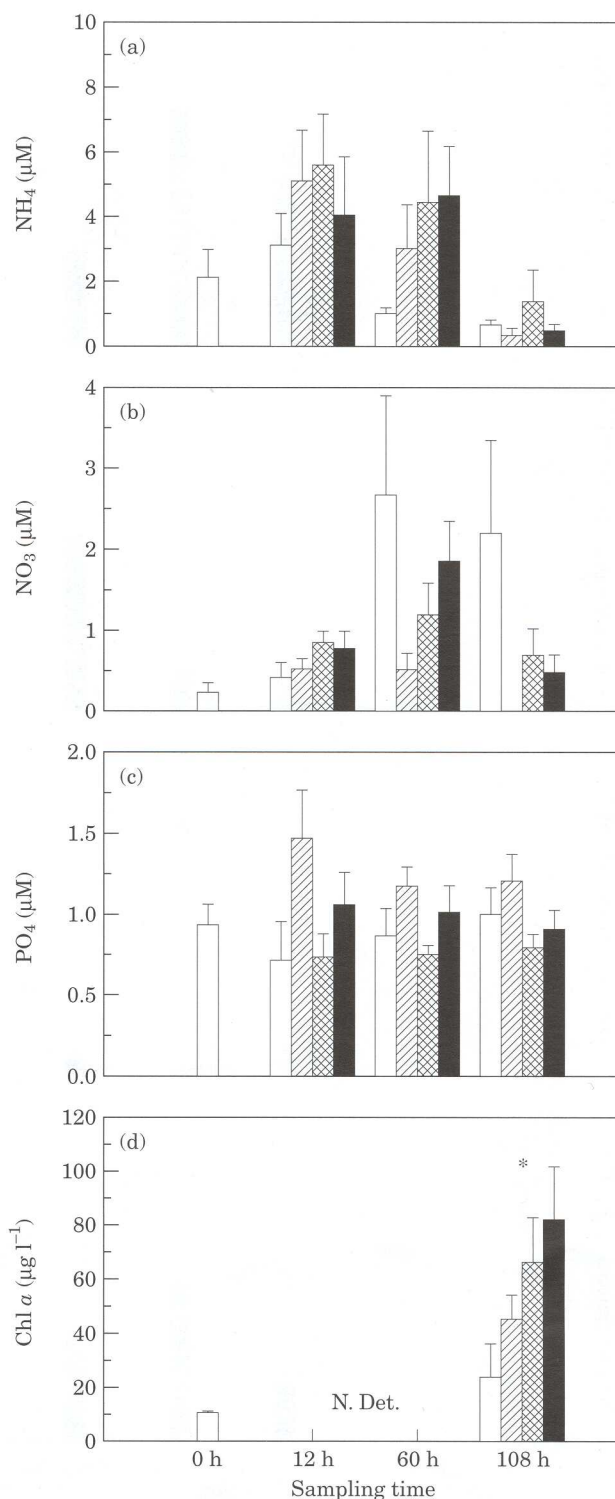


FIGURE 3. Concentrations of dissolved ammonium (a), nitrate (b), phosphate (c) and chlorophyll *a* [(d); error bars: standard error, *n*=4; **P*<0.05, one-way-ANOVA]. Resuspension level: □=0; ▨=1; ▩=2; ■=3.

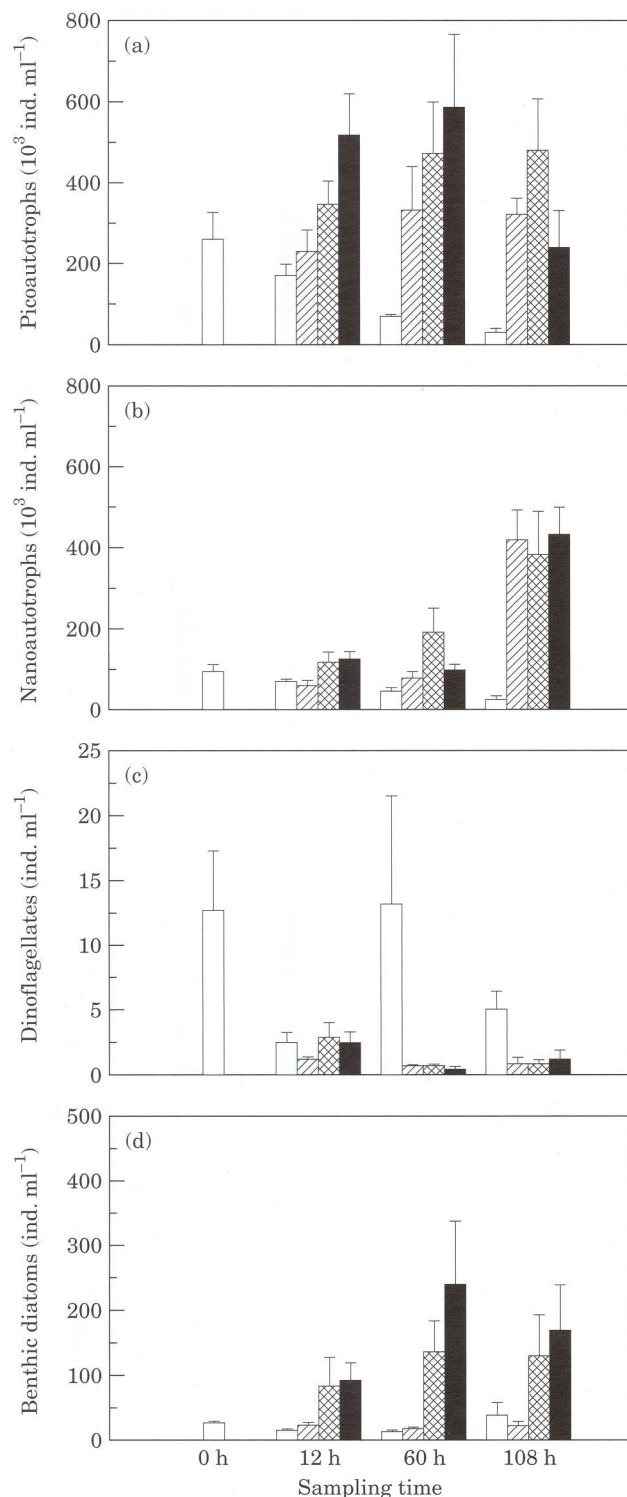


FIGURE 4. Abundances of picoautotrophs (a), nanoautotrophs (b), dinoflagellates (c) and benthic diatoms (d) in the water column of the microcosms (error bars: standard error, $n=4$). Resuspension level: $\square=0$; $\text{diagonal lines}=1$; $\text{cross-hatch}=2$; $\blacksquare=3$.

first 12 h, their abundance multiplied in all resuspended groups and reached $380\text{--}430 \times 10^3 \text{ ml}^{-1}$ towards the end of the experiment [Figure 4(b)], which was not accompanied by increasing seston concentration. This resulted in a significant positive effect of resuspension intensity throughout the experiment (Table 3).

Compared to initial values, dinoflagellate abundance at $t=12$ h declined irrespective of resuspension [Figure 4(c)]. They continued to fall to below 2 ml^{-1} in the resuspended cores, while growth of a *Peridinium* sp. in two control microcosms lead to higher average values of up to 13 ml^{-1} in the control group.

Resuspension of benthic diatoms resulted in a moderate increase of their abundance in the water column to a maximum of 92 ml^{-1} after 12 h. In spite of decreasing seston concentration in the resuspended microcosms, diatom abundance continued to rise until it reached up to 240 ml^{-1} at the second sampling occasion [Figure 4(d)]. According to the RM-ANOVA, benthic diatom abundance in the water column were significantly increased by resuspension during the whole experiment (Table 3).

Bacteria and heterotrophic protists

Prior to the experiment, the heterotrophic part of the microbial food web consisted of bacteria ($6.22 \times 10^6 \text{ ml}^{-1}$), HNAN ($21 \times 10^3 \text{ ml}^{-1}$, among flagellates heterotrophic chryomonads and katablepharids dominated), ciliates (7.3 ml^{-1} , mainly naked oligotrichs such as *Strobilidium* spp., and prostomatids such as *Urotricha* spp.) and a very low abundance ($<1 \text{ ml}^{-1}$) of naked rhizopods. Initial benthic abundances of bacteria and rhizopods were $1.4 \times 10^9 \text{ cm}^{-3}$ and 5.1×10^3 , respectively.

Bacterial abundance responded little to resuspension [Figure 5(a)]. They were positively correlated to seston concentration after 12 h (Table 1), but not over all sampling occasions (Table 2). In contrast, the abundance of HNAN in the water column was increased by resuspension [Figure 5(b)]. For the first sampling occasion ($t=12$ h), this was shown by a significant resuspension effect (one-way-ANOVA, data not shown), and by a significant linear correlation to seston concentration (Table 1). The same relationships were found for HNAN abundance of all sampling occasions combined (Tables 2, 3). According to live observations, approximately 20% of HNAN were heterotrophic nanoflagellates (hereafter HNF), with the remaining 80% consisting of other heterotrophs in the same size range (see Arndt *et al.*, 2000). While HNF in the controls and in the cores with the lowest resuspension intensity were comprized of typical

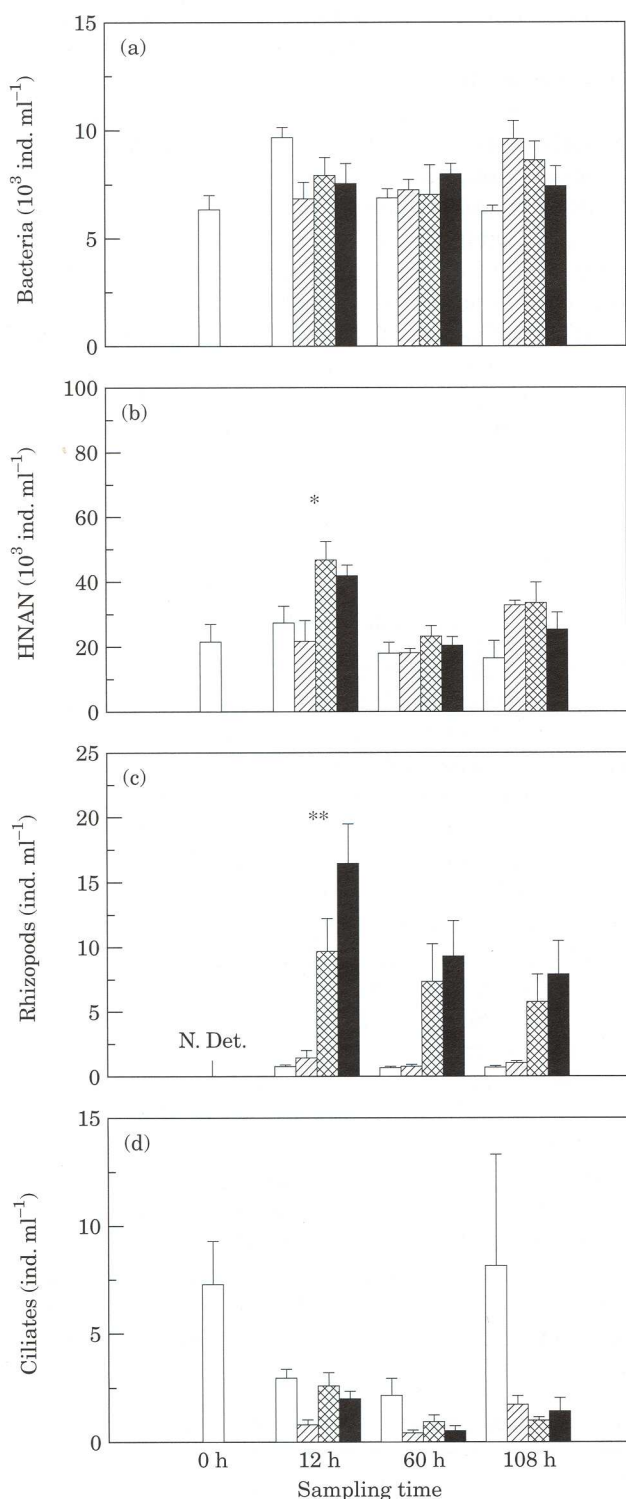


FIGURE 5. Abundances of bacteria (a), HNAN (b), rhizopods (c) and ciliates (d) in the water column of the microcosms (error bars: standard error, $n=4$; * $P<0.05$, ** $P<0.01$, one-way-ANOVA). Resuspension level: $\square=0$; $\square=1$; $\square=2$; $\blacksquare=3$.

planktonic forms (e.g. katablepharids and chrysomonads), some typical benthic forms (e.g. bodonids and euglenids) with a surface-associated mode of living were found in cores of the highest resuspension level.

The positive resuspension effect on water column abundance was even more pronounced in the rhizopods, which increased to up to 16.4 ml^{-1} in the resuspended microcosms while they remained below 1 ml^{-1} in the controls [Figure 5(c)]. The rapid increase of rhizopod abundance at the beginning of the experiment, as well as their subsequent decrease and their highly significant linear correlation to seston concentration after 12 h (Table 1), indicate that this increase was mainly due to an import of rhizopods from the sediment. The positive resuspension effect was highly significant both for the first sampling occasion (one-way-ANOVA, data not shown) and for the whole experiment (Table 3). Based on biovolume estimates, however, the contribution of rhizopods to the protistan community of the water column was still relatively low even in the most intensely resuspended microcosms (data not shown). The species composition of water column rhizopods resembled that of the benthic community of the study area, and did not change during the course of the experiment. Small species (biovolume less than $200 \mu\text{m}^3$) of the genera *Vannella* and *Vexillifera* attained a higher relative abundance in the controls than in resuspended groups.

The ciliate community showed an initial decline to below 3.0 ml^{-1} in all microcosms. Subsequently, ciliate abundance in some of the control microcosms recovered, and growth of *Urotricha* spp. and *Strobilidium* spp. resulted in a relatively high average ciliate abundance of 8.1 ml^{-1} in the control group at the end of the experiment. Although there was a trend towards increased abundance of benthic ciliates (stichotrichs, hypotrichs, and benthic pleurostomatids) and scuticociliates (a group that comprises both benthic and planktonic species, in this case mainly *Cyclidium* spp. and *Pleuronema* sp.) in the water column of the resuspended microcosms [Figure 6(b),(c)], this trend was not significant (Table 3). The increase of benthic ciliate abundance due to resuspension was low (maximum 1.1 ml^{-1}) compared to the decrease of planktonic ciliate abundance in the resuspended microcosms [Figure 6(a)].

Microbial food web interactions

The correlations between microbial abundances in the experimental microcosms indicate that the lower levels of the microbial food web were closely coupled to each other (Table 4). Bacterial abundance was

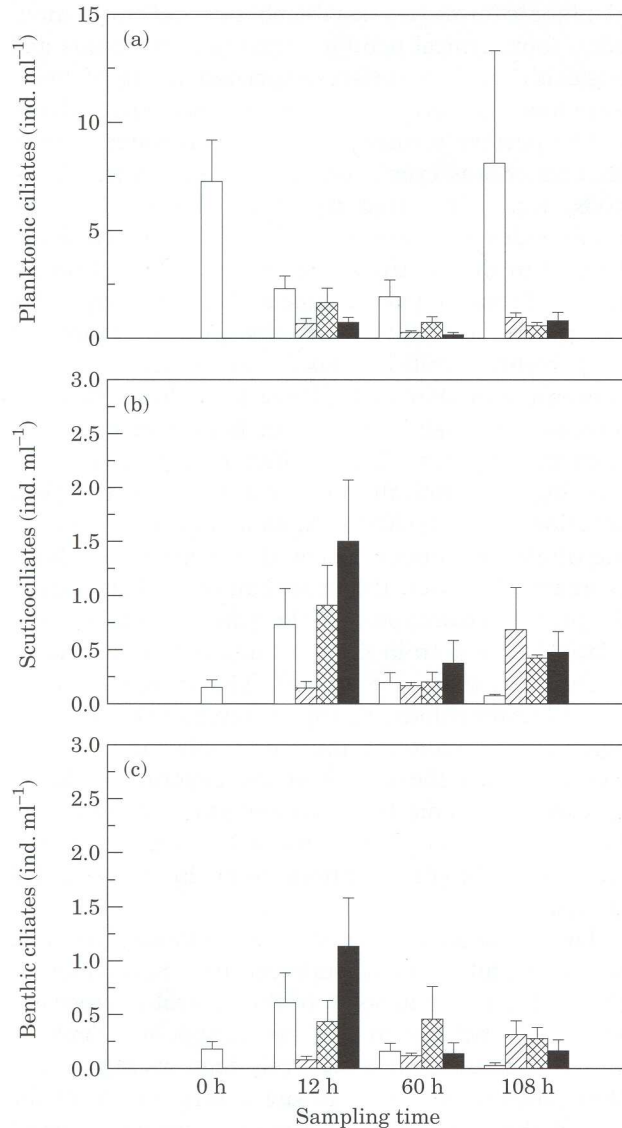


FIGURE 6. Abundances of planktonic ciliates (a), scuticociliates (b) and benthic ciliates (c) in the water column of the microcosms. Note the different scales in (a) and (b)–(c) (error bars: standard error, $n=4$). Resuspension level: $\square=0$; \square (diagonal lines)=1; \square (cross-hatch)=2; $\blacksquare=3$.

positively correlated to those of pico- and nanoautotrophs, and the abundance of HNAN was

positively correlated to those of bacteria, pico- and nanoautotrophs, their main food organisms. This pattern was reflected by HNAN abundance dynamics: in addition to the initial increase in the resuspended microcosms that could be attributed to an import of HNAN from the sediment, HNAN abundance increased again, and independently of seston concentration, towards the end of the experiment [Figure 5(b)]. In contrast to the HNAN, weak correlations were found between ciliate abundance and those of the other components of the microbial food web (Table 4). Diatoms and dinoflagellates were excluded from this analysis because there were no herbivores within the experimental microbial food web, and rhizopods were excluded because their contribution to the community in the water column was negligible.

Discussion

Effectiveness of experimental design

In order to discuss resuspension effects on the microbial food web, it needs to be established to what extent the experimental design used resulted in realistic physical resuspension effects. An exact simulation of the water movements involved in wave-induced sediment resuspension was not possible as part of this study (see Gabrielson & Lukatelich, 1985 and Booth *et al.*, 2000 for detailed discussions of this subject). However, the range of seston concentrations ($32\text{--}425\text{ mg l}^{-1}$) produced with the experimental apparatus [Figure 4(a)] compares well with data from the coastal Southern Baltic and comparable coastal waters: Georgi *et al.* (1980) found average seston concentrations of 39 mg l^{-1} and maximum values of 138 mg l^{-1} during storms in the Darss-Zingster Boddenkette, close to the source of the material used in the experiment. Higher values of up to 895 mg l^{-1} were recorded by autosamplers in Ringkøbing Fjord, Denmark, a system similar to the Boddengewässer (Pedersen *et al.*, 1995). The decrease of seston concentration in the resuspended microcosms towards the end of the experiment was probably caused by

TABLE 4. Spearman's rank correlation coefficients for correlations between microbial abundances

	Picoautotrophs	Nanoautotrophs	Bacteria	HNAN
Nanoautotrophs	0.563**			
Bacteria	0.535**	0.500**		
HNAN	0.603**	0.493**	0.574**	
Ciliates	0.151	0.018	0.234	0.250

* $P<0.05$; ** $P<0.01$, $n=52$.

resedimentation of heavier mineral components. This mechanism is consistent with the observed increase in organic carbon content of seston material. A differential resedimentation of organic material and heavier mineral particles has also occurred after natural resuspension events (Arfi & Bouvy, 1995). It is concluded that the experimental setup realistically reproduced seston dynamics during resuspension events in our study area.

Direct transport effects of resuspension

According to the increase in abundances during the first 12 h of the experiment, significant direct transport effects of resuspension were found for the HNAN and rhizopods, and non-significant positive trends for all autotrophic groups except dinoflagellates. The close coupling of water column abundance of rhizopods to suspended sediment concentrations supports the idea that rhizopods in coastal waters are essentially benthic and only passively enter the water column during resuspension events (Rogerson & Laybourn-Parry, 1992b; Garstecki *et al.*, 2000). The same appears to be true for some benthic heterotrophic flagellates which contributed significantly to the HNAN community in the most intensely resuspended microcosms. Similar contributions were found during field studies in various shallow coastal waters (Rogerson & Laybourn-Parry, 1992a; Zimmermann-Timm *et al.*, 1998; Garstecki *et al.*, 2000). Data on short-term effects of wind-induced resuspension on HNAN abundance have not been presented to our knowledge, but an increase in water column abundance of HNAN has also been found following tidal resuspension (Shimeta & Sisson, 1999).

Pico- and nanoautotroph abundances did not show significant resuspension effects, but they were tightly correlated to seston concentration, which is consistent with a transport of cells from the sediment into the water column. The initial benthic abundance of nanoautotrophs ($33 \times 10^6 \text{ cm}^{-3}$) was sufficiently high to account for their observed increase in the water column, but the initial benthic number of picoautotrophs per cm^3 of sediment was only 60 times higher than their subsequent peak per cm^3 of water at the highest resuspension intensity. Based on an average sediment density of 2 g cm^{-3} (Stodian, pers. comm.) and an increase in seston concentration of 400 mg l^{-1} , the superficial sediment was diluted by an average factor of 5000 at this resuspension intensity. Even if picoautotrophs were part of an organic layer that was resuspended preferentially and thus diluted by a lower factor, resuspension of benthic picoautotrophs alone cannot account for the

observed increase in picoautotrophs during the first 12 h of the experiment. In addition to a direct import from the sediment, enhanced growth in the water column needs to be considered as a cause of the short-term increase in picoautotroph abundance (see below). Although the response of benthic diatoms to resuspension was relatively variable, a trend towards increased diatom abundance with increased resuspension intensity was obvious. This is in agreement with numerous field studies (Shaffer & Sullivan, 1988; De Jonge & van Beusekom 1992, 1995).

The lack of data on initial benthic ciliate abundance and the negative bottle effects on planktonic ciliate abundance in all microcosms render conclusions about resuspension effects on the ciliates problematic. However, it appears from our data that high seston concentrations and high turbulence do not foster growth of such planktonic ciliates as *Urotricha* spp. and *Strobilidium* spp. This is in agreement with field data from other high-turbidity environments, such as the River Rhine, Germany (Scherwass, pers. comm.), and consistent with experimental results about clay effects on the population dynamics of small freshwater oligotrichs (Jack *et al.*, 1993).

Indirect effects of resuspension on autotrophic organisms

The direct transport of autotrophs and heterotrophic protists into the water column is a major effect of resuspension on the coastal planktonic microbial food web, but the present experiment reveals indirect resuspension effects of equal importance. Picoautotrophs and resuspended benthic diatoms continued to increase in abundance until the second sampling point, and the abundance of nanoautotrophs rapidly increased in all resuspended groups towards the end of the experiment. Maximum seston concentrations during the experiment were measured after 12 h, and preliminary short-term experiments with our experimental apparatus indicate that the peak of seston concentration was reached at this sampling occasion or earlier. Therefore, the increase in autotroph abundance beyond the 12 h sampling occasion, and part of the initial increase in picoautotroph abundance, must be due to growth in the water column. According to the present data, this was, at least partly, mediated by reduced nitrogen limitation: dissolved ammonium and nitrate concentrations ($2.1 \mu\text{M}$ and $0.2 \mu\text{M}$, respectively) and the molar N:P ratio of 2.5 at the onset of the experiment were sufficiently low to infer nitrogen limitation of autotrophic growth. They tended to increase in the resuspended microcosms until the first sampling at 12 h. This trend was not proportional to resuspension intensity, which is not surprising since

nutrient concentrations measured at this time represent net results of release processes from the sediment, enhanced remineralization, desorption from and adsorption to seston, and assimilation by organisms which were either resuspended or already present in the water column. However, dissolved ammonium concentrations were positively correlated to seston concentrations throughout the experiment. An increase of dissolved ammonium concentrations after resuspension was also found in various coastal systems (Ullman & Sandstrom, 1987; Balls *et al.*, 1994; Mortimer *et al.*, 1998). A rapid growth response of autotrophic picoplankton to dissolved nitrogen import by water column mixing has also been found in the southern Baltic Sea (Stal *et al.*, 1999), and resuspended algae have been reported to rapidly reduce water column ammonium concentrations (Arfi & Bouvy, 1995).

Increased light availability for resuspended benthic algae is an alternative explanation for the observed increase in autotrophs. However, an additional experiment in October 1997 tends to refute this explanation (T. Garstecki & S. A. Wickham, unpublished data). In this experiment, the water column of the microcosms was replete with nitrogen, reflecting the seasonality of dissolved nitrogen concentrations in the study area. With the higher nitrogen concentration, there was no resuspension effects on autotrophs.

According to several studies from lakes and coastal waters, the increased turbidity during resuspension events prevents resuspended autotrophic organisms from supporting a high primary productivity in the water column (Hellström, 1991; MacIntyre *et al.*, 1996; MacIntyre & Cullen, 1996). Although primary production was not measured, the present results do not support those findings: picoautotrophs did grow in the most intensely resuspended microcosms, even at the high turbidity during the first 12 h of the experiment. The relatively quick resedimentation of mineral particles after the 12 h sampling occasion decreased turbidity when picoautotrophs, nanoautotrophs, and diatoms were still present in the water column in sufficiently high numbers to benefit from the then improved light and nutrient conditions. Since differential resedimentation also occurs following natural resuspension (Arfi & Bouvy, 1995), our data point to a period of improved growth conditions for autotrophs at the end of, and immediately after, resuspension events.

Indirect effects of resuspension on heterotrophic organisms

The abundance of heterotrophic bacteria did not respond to resuspension, and was only weakly corre-

lated to seston concentration. Given the only 270-fold difference between benthic and planktonic bacterial density (cells per volume unit) at the onset of the experiment and the dilution of the sediment as it was resuspended, a direct transport effect was not to be expected. Effects triggered by fluxes of dissolved organic matter from the sediment (see Hopkinson *et al.*, 1998) may have been rendered insignificant by the relatively high DOC concentrations ($2\text{--}8\text{ mg l}^{-1}$, T. Rieling, pers. comm.) in the study area. Another possible explanation for the failure of bacterial abundance to show a positive net resuspension effect is bacterivory by HNF. After 12 h, the abundance ratio of bacteria and HNAN in the resuspended microcosms of the experiment averaged approximately 200, which is less than the ratio of 1000 typical of most freshwater systems (Sanders *et al.*, 1992). HNAN are generally not exclusively comprised of HNF (see Arndt *et al.* 2000), but even if only 20% of HNAN consisted of HNF, abundances were certainly high enough to exert a strong grazing impact on bacterial abundance in these microcosms.

A nutritive role of resuspended bacteria, algae and other particulate organic matter for protozoan and metazoan zooplankton has been postulated (Wainright 1987; 1990; Arfi & Bouvy, 1995), but empirical evidence for such a role is scarce. During the present experiment, HNAN abundance in the water column was strongly positively correlated to bacterial, pico-, and nanoautotroph abundance, which suggests bottom-up control of phagotrophic HNAN by food supply. HNAN abundance was also significantly increased by resuspension. Since this relationship held over the whole course of the experiment, it cannot be explained by transport of cells from the sediment alone. Rather, there may have been an indirect positive resuspension effect on phagotrophic HNAN mediated by feeding on bacteria and small autotrophs. Although a propagation of resuspension effects through the microbial food web cannot be proven based on correlation data alone, it appears to be the most likely explanation of HNAN abundance dynamics during the experiment.

Ciliates did not benefit from resuspension in a manner similar to HNAN. Although negative shear effects on ciliate population dynamics as an explanation of the lack of a positive response to resuspension cannot be excluded, it is also possible that the increased contribution of inedible mineral particles to the seston during resuspension interferes with the feeding mechanism of planktonic oligotrichs and scuticociliates, which are largely filter-feeders. Such a mechanism might lead to a temporal decoupling of the planktonic food web during resuspension events.

Generalizing the present experimental data, the resuspension effect on microbial food webs appears to be a combination of direct resuspension and indirect nutritive effects. Resuspension of benthic diatoms and other autotrophs increases water column chlorophyll *a* up to several-fold and alters phytoplankton community structure. After resuspension events, their relatively slow sinking rate enables resuspended algae to stay in the water column when mineral seston concentrations and turbidity have already decreased again. Increases in dissolved nitrogen, and possibly phosphorus concentration due to resuspension may enhance growth of these algae, or of phytoplankton already present in the water column. A persistent positive effect of resuspension on phytoplankton chlorophyll *a* and shifts in phytoplankton community structure towards smaller cell sizes were also found in shallow lakes (Padišak *et al.* 1988; Ogilvie & Mitchell, 1998). The pulse in nutrients and phytoplankton from a resuspension event has the potential to contribute a substantial proportion to the total water-column productivity of the Boddengewässer. Although primary production was not measured during this study, Shaffer and Sullivan (1988) showed that resuspended benthic diatoms increased water column primary productivity in coastal waters by up to several orders of magnitude.

Apart from transient effects on protozooplankton community structure, this experiment points to the possibility that positive resuspension effects on pico- and nanoautotrophs are propagated through the microbial food web and give rise to enhanced growth of HNAN. In contrast, ciliates showed negative effects from resuspension, due either to increased shear or impaired filtering.

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