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Initial burial and subsequent degradation of sedimented phytoplankton: relative impact of macro- and meiobenthos

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Abstract: The initial burial (transfer through the sediment–water interface) and subsequent degradation of sedimented phytoplankton was examined in the laboratory in sediments containing meiofauna, both with and without macrofauna, over a 10-day period. Burial and degradation were monitored by following changes in vertical profiles of Chl *a* and phaeopigments in sediment columns with and without an addition of senescent *Skeletonema costatum* Greville (Cleve) cells to the sediment surface. The macrofauna present in the cores consisted of a subsurface deposit-feeder assemblage typical of organically enriched habitats. Upon diatom addition, the visual redox potential discontinuity (RPD) rose to or near the sediment surface. Chl *a* and phaeopigment levels increased 6 and 3 days after diatom addition, respectively, with no difference in concentrations in the presence or absence of macrofauna. These increases appeared to be confined to the top 5 mm of sediment. Overall, phaeopigment concentrations were higher in cores containing macrofauna. A minimum of 83% of the added Chl *a* was transferred through the sediment–water interface in 10 days. In organically enriched habitats, the initial burial and subsequent degradation of sedimented phytoplankton appears to be a process dominated by the meiofaunal and microbial communities, and unaffected by subsurface deposit-feeding macrofauna.

Key words: Benthic–pelagic coupling; Macrofauna; Meiofauna; Phytoplankton

Introduction

Sedimentation onto the sea-floor is the fate of a significant proportion of phytoplankton biomass in the oceans (e.g., Townsend & Cammen, 1988; Hansell et al., 1989; Riebesell, 1989; Legendre, 1990; Wassmann et al., 1990). The ultimate fate of this sedimented phytoplankton C is either remineralization back to CO_2 via microbial decomposition, and metazoan grazing and respiration, or permanent burial in the sediments (see Santschi et al., 1990). An understanding of the factors and processes affecting the magnitude of phytoplankton C remineralization is necessary to determine the role of marine sediments as a buffer in sequestering large amounts of C away from the water-column and atmosphere.

Little is known of the influence of various benthic animal groups on the burial and

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subsequent degradation of sedimented phytoplankton (Gooday & Turley, 1990). While bacteria may ultimately remineralize most of this deposited organic matter (Rowe & Deming, 1985; Turley & Lochte, 1990), the macrofauna (organisms $\geq 500\ \mu m$; e.g., adult polychaetes and bivalve molluscs) are thought to be the dominant metazoans influencing initial burial (defined here as transfer through the sediment–water interface), by bioturbation, and subsequent degradation, through feeding, of phytodetritus in marine sediments (Aller, 1982; Andersen & Kristensen, 1991). The role of other faunal groups such as the meiofauna (organisms between 63 and 500 μm; e.g., nematodes, harpacticoid copepods, ciliates and juvenile polychaetes) is unclear. The meiofauna have been observed to bioturbate and mix sediments near the sediment–water interface (Cullen, 1973) and can build intricate networks of tubes within the sediment (Chandler & Fleeger, 1984; Nehring et al., 1990). The meiofauna are also known to feed on phytodetritus (Rudnick, 1989) and can have a significant positive impact on rates of detrital mineralization in general (Findlay & Tenore, 1982). While intuitively, because of their larger size, macrofauna should be expected to have a greater impact on initial burial and degradation of phytodetritus, the high abundance of the meiofauna ($10^6 \cdot m^{-2}$ sediment, on average; Coull & Bell, 1979) suggests that these animals may also have a significant, and at least ancillary, role in initial phytodetrital burial and degradation.

Here we present the results of an experiment designed to follow the initial burial and subsequent degradation of phytoplankton settled onto the sediment surface of cores containing meiofauna, both in the presence and absence of macrofauna, over a 10-day period. We used changes in vertical profiles of sediment Chl *a* concentration (an index of phytodetrital concentration) to follow initial burial. Also, changes in Chl *a* breakdown products (phaeopigments) were tracked as an index of degradation (e.g., Bianchi et al., 1988).

Materials and Methods

Sediment cores were collected from the drainage channel of a fish-holding facility (temperature = 27 °C, salinity = 29 PSU) near Port Aransas, Texas, USA (27° 50′ N, 97° 00′ W) on 28 May 1990. The channel sediment was medium sand (median grain size 300 μm) and was known to contain high densities of both macrofauna and meiofauna ($10^4 \cdot m^{-2}$ and $10^6 \cdot m^{-2}$, respectively). 72 1.8-cm^2 cores (5 cm deep) were collected randomly within a 0.25-m^2 quadrat and returned to the laboratory.

In the laboratory, cores were assigned randomly to two treatments: (1) macrofauna and meiofauna (M&M); and (2) meiofauna only (M). The M& M treatment consisted of the sediment sequentially sieved on 500- and 63-μm meshes, with the animals and sediment trapped on the 500-μm mesh added back to the core. The M treatment was treated the same except that the animals trapped on the 500-μm mesh were removed and counted, and only the sediment was added back. Seawater (0.22-μm-filtered) was

gently added to the surface of each core to a depth of 2 cm. The cores were allowed to equilibrate for 2 days to allow the animals to redistribute themselves.

66 sediment cores were assigned randomly to spaces in two joined test-tube racks and incubated at ambient temperature and salinity in the dark. Aliquots (6.0×10^7 cells, 2.6 μg Chl *a*, 0.14 μg phaeopigments; representing 33% of total core Chl *a*) of a stationary-phase culture of the planktonic diatom *Skeletonema costatum* Greville (Cleve) were added to half the cores of each treatment and allowed to settle. Before diatom addition, three cores of each treatment (M&M and M) were sacrificed and sectioned into 0–5 mm, 5–10 mm, 1–2, 2–3 and 3–4 cm depth strata for determination of initial faunal densities. Sediment below 4 cm depth ($\approx$0.5 cm) was not sampled. Chl *a* and phaeopigment levels in three replicate cores of the four treatments (M&M and M both with (+) or without (–) diatom addition) were monitored at 1, 3, 6 and 10 days after diatom addition, with cores vertically sectioned as described above. The diatom fluff layer formed after diatom addition on the sediment surface ($\approx$2 mm deep) is not considered part of the sediment in this study and was not sampled. Before sectioning, the depth of the transition from brown, Fe-stained sediment to grey, S-stained sediment (visual RPD) in each core was noted as an index of chemical stratification. A further three cores were sacrificed and vertically sectioned after 10 days for determination of final faunal densities. All sediment samples for faunal determinations were immediately fixed in 4% formaldehyde.

Sediment samples for Chl *a* and phaeopigment determinations were extracted in 100% acetone [to prevent artifactual production of chlorophyllide (Jeffrey & Hallegraeff, 1987) for 24 h in the dark at 4 °C. Pigment levels were measured by fluorescence before and after acidification (Parsons et al., 1984) on a Turner Designs model 10 fluorometer. Pigment levels were then expressed as $\mu g \cdot cm^{-3}$ sediment. Changes in vertical profiles of Chl *a* and phaeopigments measured fluorometrically in the sediment of the diatom addition treatments will indicate the extent of initial burial and degradation, respectively, of the sedimented phytoplankton in the presence and absence of macrofauna. While estimation of pigment concentrations by HPLC would likely be more accurate than fluorometric analysis, fluorometry provides an adequate and rapid way of comparing pigment concentrations between treatments. Any errors associated with the fluorometric technique should be similar between treatments. Sediment samples for faunal determinations were stained with Rose Bengal for 24 h. Animals were counted and densities expressed as number of $ind \cdot cm^{-3}$ sediment.

Variations in Chl *a* and phaeopigment concentrations were analysed by four-way fixed-factor ANOVA, with TIME (four levels; 1, 3, 6 and 10 days after diatom addition), FAUNA (two levels; M&M and M), DIATOM (two levels; + and – diatom addition) and sediment DEPTH (five levels; 0–5 mm, 5–10 mm, 1–2 cm, 2–3 cm and 3–4 cm depth) being the main factors. The factor DEPTH was of little interest unless it interacted with FAUNA or DIATOM. When the interaction terms were significant, the ANOVA was broken down as necessary. Changes in depth of the visual RPD were analysed by three-way fixed-factor ANOVA, with TIME, FAUNA and DIATOM

(levels as described above) as the main factors. For comparisons of faunal densities, only depth-integrated totals were used. Differences between treatments in faunal densities were analysed by Student's t test (time 0 sampling) or two-way fixed-factor ANOVA (10 day sampling) with the factors being FAUNA and DIATOM (levels as described above). Factors in all the ANOVAs were considered significant at $\alpha = 0.05$. Homogeneity of variances was examined using Cochran's test at $\alpha = 0.05$ and data were natural-log-transformed when appropriate. Transformation was not always successful in stabilizing the variances but no significant differences were ever found between treatments when data were heteroscedastic, so the results are robust (Underwood, 1981). All statistical analyses were performed using SYSTAT (Wilkinson, 1990).

RESULTS

FAUNAL PATTERNS

Mean macrofaunal density removed in creating the macrofauna-free (M) treatment exceeded 3×10^4 ind·m^{-2} (Table I). The removed macrofauna was dominated by oligochaetes and polychaetes, with a smaller number of ostracods and large nematodes. The macrofaunal polychaete community was composed mainly of subsurface deposit-feeders (*Haploscoloplos*, *Capitella*, unidentified Capitellidae) with a smaller proportion of surface deposit-feeders (*Streblospio*, *Nereis*) (Fauchauld & Jumars, 1979) (Table II).

Mean faunal densities in the cores at the start of the experiment exceeded 1.3×10^6 ind·m^{-2} (Table III). Nematodes, oligochaetes, ostracods and polychaetes comprised 99% by number of the organisms in both the M&M and M treatments (Table III). Total abundance and abundance of each group except ostracods did not differ between treatments (Student's t test, $t_{0.05(4)} < 2.78$, $P > 0.05$). We were unable to detect a difference between treatments in the abundance of oligochaetes and polychaetes caused by removal of macrofaunal individuals because of the relatively large error in abundance estimates for these two groups, with resulting low power of the statistical test (Table III).

TABLE I

Identity and abundance of macrobenthos removed from cores during treatment preparation. Abundance ($\bar{x} \pm 1$ SE, $n = 36$) is expressed as 10^4 ind·m^{-2}.

Taxa	Abundance (10^4·m^{-2})
Oligochaetes	1.78 ± 0.27
Polychaetes	1.31 ± 0.14
Ostracods	0.24 ± 0.07
Nematodes	0.02 ± 0.02
Total	3.33 ± 0.31

TABLE II

Identity and percent composition of macrofaunal polychaetes from Table I that were removed during treatment preparation. Number of individuals identified = 64.

Species	Percentage (%)
Haploscoloplos foliosus Hartman	68.8
Capitella capitata (Fabricius)	17.2
Streblospio benedicti Webster	10.9
Nereis (Neanthes) succinea (Frey et Leuckart)	1.6
Unidentified Capitellidae	1.6

TABLE III

Identity, abundance ($\bar{x} \pm 1$ SE, $n = 3$, expressed as 10^4 ind·m^{-2}) and percent composition (%) of dominant fauna in cores both with (M&M) and without (M) macrofauna at start of experiment (Day 0).

Taxa	Treatment			
	M&M		M	
	Abundance	%	Abundance	%
Total	136.7 ± 36.9	100	151.9 ± 13.4	100
Nematodes	128.9 ± 34.4	94.3	144.8 ± 11.9	95.3
Oligochaetes	3.33 ± 3.06	2.44	3.70 ± 1.21	2.44
Ostracods	1.67 ± 0.32	1.22	0 ± 0	0
Polychaetes	1.48 ± 0.37	1.08	1.85 ± 0.37	1.22

Mean total faunal densities after 10 days were slightly lower than those at the start of the experiment (Table IV), but there was no effect of FAUNA or DIATOM (two-way ANOVA, $F_{1,8} < 5.32$, $P > 0.05$). No interaction was found. Nematodes, oligocha-

TABLE IV

Identity, abundance ($\bar{x} \pm 1$ SE, $n = 3$, expressed as 10^4 ind·m^{-2}) and percent composition (%) of dominant fauna in cores with (M&M) and without (M) macrofauna and with (+) and without (−) diatom addition at end of experiment (Day 10).

Taxa	Treatment							
	M&M +		M&M −		M +		M −	
	Abundance	%	Abundance	%	Abundance	%	Abundance	%
Total	72.6 ± 14.1	100	67.2 ± 7.25	100	92.4 ± 29.1	100	74.4 ± 13.0	100
Nematodes	64.1 ± 12.6	88.3	54.4 ± 10.0	81.0	85.0 ± 27.5	92.0	65.2 ± 13.5	87.6
Oligochaetes	3.89 ± 0.56	5.36	1.85 ± 0.98	2.75	2.78 ± 1.95	3.01	1.48 ± 0.49	1.99
Ostracods	2.96 ± 0.98	4.08	3.52 ± 0.74	5.24	1.85 ± 0.81	2.00	2.78 ± 0.56	3.74
Polychaetes	0.93 ± 0.37	1.28	5.74 ± 2.67	8.54	1.11 ± 0.85	1.20	2.96 ± 0.98	3.98

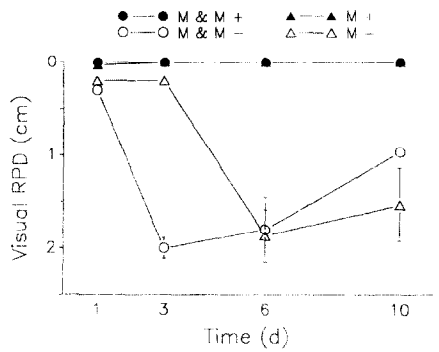

Fig. 1. Depth of visual RPD (cm) in sediment cores with (M&M) and without (M) macrofauna and with (+) and without (−) diatom addition during 10-day experimental period. Values are $\bar{x} \pm 1$ SE, $n = 3$.

etes, ostracods and polychaetes again dominated the communities (> 97% by number) (Table IV). Abundances of these animal groups also showed no effect of FAUNA or DIATOM (two-way ANOVA, $F_{1,8} < 5.32$, $P > 0.05$).

VISUAL RPD

On each sampling date, the depth of the visual RPD had no variance in at least one of the treatments, making statistical comparisons impossible. However, obvious patterns were apparent over the course of the experiment (Fig. 1). After diatom addition, the visual RPD moved closer to, or was at the sediment surface in both the M&M + and M + treatments. After 3 days, the visual RPD in the M&M − treatment had descended to ≈2 cm depth and stayed between 1 and 2 cm for the remainder of the experiment. The visual RPD in the M − treatment, however, stayed at ≈2 mm until Day 6 when it descended to a similar depth as in the M&M − treatment.

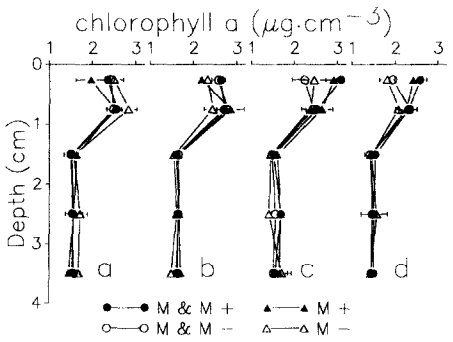

Fig. 2. Vertical profiles of Chl *a* (μg·cm^{-3}) with depth (cm) in sediment cores with (M&M) and without (M) macrofauna and with (+) and without (−) diatom addition during 10-day experimental period. Values are $\bar{x} \pm 1$ SE, $n = 3$. (a) Day 1, (b) Day 3, (c) Day 6, (d) Day 10.

CHL *A* PATTERNS

Changes in Chl *a* concentrations during the experiment are graphically summarized in Fig. 2. Results of the four-way ANOVA for Chl *a* exhibited significant main effects for TIME, DIATOM and DEPTH, with a significant TIME × DIATOM interaction (Table V). The lack of a significant FAUNA effect indicated that the presence or absence of macrofauna had no effect on Chl *a* concentrations. To tease apart the TIME × DIATOM interaction, three-way ANOVAs, with factors of FAUNA, DIATOM and DEPTH, were performed for each sampling time (1, 3, 6 and 10 days after diatom addition). A significant DEPTH effect ($F_{4,40} > 2.61$, $P < 0.05$), but no effect of FAUNA ($F_{1,40} < 4.08$, $P > 0.05$), was observed on each date. Chl *a* concentrations were higher near the sediment surface (Fig. 2). A significant DIATOM effect was observed 6 days after diatom addition ($F_{1,40} = 7.61$, $P = 0.009$; 2.09 vs. 1.87 $\mu g \cdot cm^{-3}$ in the + and − treatments, respectively; $n = 30$) and also 10 days after diatom addition ($F_{1,40} = 5.73$, $P = 0.022$). However, at 10 days, there was a significant DIATOM × DEPTH interaction ($F_{4,40} = 3.49$, $P = 0.016$). To decompose this interaction, two-way ANOVAs with factors of FAUNA and DIATOM, were performed for each depth. FAUNA had no effect at any depth and DIATOM was only significant in the 0–5 mm depth horizon ($F_{1,8} = 20.0$, $P = 0.002$; 2.50 vs. 1.88 $\mu g \cdot cm^{-3}$ in the + and − treatments, respectively; $n = 6$).

To summarize, the presence of macrofauna had no effect on sediment Chl *a* concentrations throughout the experiment. A significant increase in Chl *a* concentration in the diatom addition treatments was observed 6 days after addition, with the increase confined to the top 5 mm of sediment at 10 days after addition.

TABLE V

Four-way ANOVA table (fixed-factor) for effect of time (TIME), presence or absence of macrofauna (FAUNA), diatom addition (DIATOM) and sediment depth (DEPTH) on Chl *a* concentration. df, degrees of freedom; SS, sums of squares; MS, mean square.

Source of variation	df	SS	MS	*F*	*P*
TIME	3	1.94	0.646	9.02	0.00001
FAUNA	1	0.036	0.036	0.501	0.480
DIATOM	1	0.366	0.366	5.10	0.025
DEPTH	4	46.4	11.6	161.8	<0.00001
TIME × FAUNA	3	0.216	0.072	1.00	0.393
TIME × DIATOM	3	0.965	0.322	4.49	0.00463
TIME × DEPTH	12	1.48	0.123	1.72	0.066
FAUNA × DIATOM	1	0.014	0.014	0.197	0.658
FAUNA × DEPTH	4	0.271	0.068	0.946	0.439
DIATOM × DEPTH	4	0.387	0.097	1.35	0.253
TIME × FAUNA × DIATOM	3	0.275	0.092	1.28	0.284
TIME × FAUNA × DEPTH	12	0.303	0.025	0.352	0.977
FAUNA × DIATOM × DEPTH	4	0.257	0.064	0.896	0.468
TIME × FAUNA × DIATOM × DEPTH	12	0.286	0.024	0.333	0.982
ERROR	172	12.3	0.072		

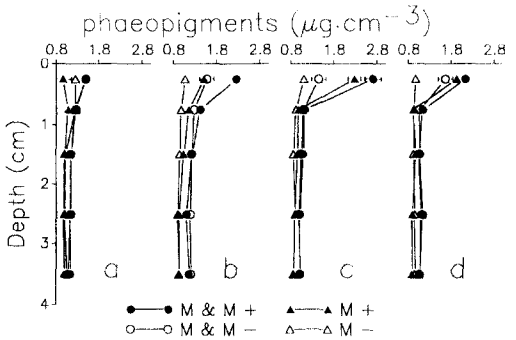

Fig. 3. Vertical profiles of phaeopigments ($\mu g \cdot cm^{-3}$) with depth (cm) in sediment cores with (M&M) and without (M) macrofauna and with (+) and without (−) diatom addition during 10-day experimental period. Values are $\bar{x} \pm 1$ SE, $n = 3$. (a) Day 1, (b) Day 3, (c) Day 6, (d) Day 10.

PHAEOPIGMENT PATTERNS

Changes in phaeopigment concentrations during the experiment are graphically summarized in Fig. 3. Results of the four-way ANOVA for phaeopigments exhibited significant main effects for FAUNA, DIATOM and DEPTH, but many significant interactions were observed, especially with DEPTH (Table VI). To tease apart these interactions, three-way ANOVAs, with TIME, FAUNA and DIATOM as the main factors, were performed at each depth. In the 0–5 mm depth horizon, TIME, FAUNA

TABLE VI

Four-way ANOVA table (fixed-factor) for effect of time (TIME), presence or absence of macrofauna (FAUNA), diatom addition (DIATOM) and sediment depth (DEPTH) on phaeopigment concentration. df, degrees of freedom; SS, sums of squares; MS, mean square.

Source of variation	df	SS	MS	F	P
TIME	3	0.173	0.058	2.03	0.112
FAUNA	1	3.06	3.06	107.6	<0.00001
DIATOM	1	0.904	0.904	31.7	<0.00001
DEPTH	4	12.8	3.20	112.3	<0.00001
TIME × FAUNA	3	0.215	0.072	2.52	0.060
TIME × DIATOM	3	0.776	0.259	9.08	0.00001
TIME × DEPTH	12	2.75	0.230	8.06	<0.00001
FAUNA × DIATOM	1	0.0010	0.0010	0.036	0.849
FAUNA × DEPTH	4	0.858	0.214	7.53	0.00001
DIATOM × DEPTH	4	3.28	0.820	28.8	<0.00001
TIME × FAUNA × DIATOM	3	0.072	0.024	0.846	0.471
TIME × FAUNA × DEPTH	12	0.058	0.0048	0.169	0.999
FAUNA × DIATOM × DEPTH	4	0.019	0.0046	0.163	0.957
TIME × FAUNA × DIATOM × DEPTH	12	0.266	0.022	0.777	0.673
ERROR	172	4.90	0.028		

and DIATOM were significant, but a TIME × DIATOM interaction was found. The effect of FAUNA was an increase in phaeopigment concentration in the presence of macrofauna ($F_{1,32} = 49.1$, $P < 0.00001$; 1.85 vs. 1.38 $\mu g \cdot cm^{-3}$ in the M&M and M treatments, respectively; $n = 24$). To decompose the TIME × DIATOM interaction in the 0–5 mm depth horizon, two-way ANOVAs with factors of FAUNA and DIATOM were performed for each sampling time. As expected, there was a significant FAUNA effect at each time. A significant DIATOM effect ($F_{1,8} > 5.32$, $P < 0.05$) was observed at 3, 6 and 10 days after diatom addition, with enhanced phaeopigment concentrations in the diatom addition treatments (see Fig. 3). The lack of FAUNA × DIATOM interactions in these analyses indicates that phaeopigment concentrations were similar in the diatom addition treatment with and without macrofauna. The results of the three-way ANOVAs at all depths > 5 mm indicated significant TIME ($F_{3,32} > 2.90$, $P < 0.05$) and FAUNA ($F_{1,32} > 4.15$, $P < 0.05$) effects only, with no significant interaction and DIATOM effect. The effect of TIME was a general decrease in phaeopigment concentrations during the course of the experiment while the effect of FAUNA was an increase in phaeopigments in the treatments containing macrofauna, as observed in the 0–5 mm depth horizon (see Fig. 3).

To summarize, phaeopigment concentrations were higher in treatments containing macrofauna throughout the sediment column. Phaeopigment concentrations were elevated in the top 5 mm only of the diatom addition treatments 3 days after addition, with no difference in the amount of increase detected in the presence and absence of macrofauna.

Discussion

The macrobenthos found in the cores of this study were dominated by subsurface deposit-feeders (oligochaetes and the dominant polychaetes *Haploscoloplos* and *Capitella*) (Fauchauld & Jumars, 1979; Fisher et al., 1980). This macrofauna is typical of organically enriched sediments (Pearson & Rosenberg, 1978). Visual observation of the sediment cores showed obvious burrow structures throughout the sediment column when macrofauna were present. Little evidence of burrow construction was seen in the treatments containing only meiofauna. Considering the large numbers of macrofauna removed in treatment preparation ($> 10^4 \cdot m^{-2}$), this experiment should provide a valid test of the relative effects of meio- and macrofauna on the initial burial and subsequent degradation of sedimented phytoplankton. While obviously the macrofauna used in this study are not typical of all environments, the results of this study are most relevant to effects in nearshore, organically enriched habitats, or other areas receiving substantial organic input.

Chemical stratification in the sediment, as evidenced by the depth of the visual RPD, was affected by both diatom addition and the presence of macrofauna. Upon diatom addition, the visual RPD ascended to or near the sediment–water interface in both

treatments, indicating an inhibition of diffusive flux from the overlying water and/or a rapid utilization of oxygen by bacteria, whose productivity was likely increased by the addition (see Santschi et al., 1990, for review). In the cores without diatom addition, the temporal pattern of visual RPD depth varied depending on the presence or absence of macrofauna. In the presence of macrofauna, the visual RPD descended to a depth of ≈ 2 cm after 3 days. This descent of the visual RPD, indicating enhanced oxygen penetration through the sediment–water interface, was probably caused by sediment bioturbation and mixing by the fauna. The visual RPD descended to a similar level in the absence of macrofauna after 6 days, indicating that the meiofauna are also capable of significant bioturbation, as shown by Cullen (1973), albeit at a slower rate than the macrofauna. The specific organisms responsible for this mixing, such as the juvenile macrofauna ("temporary meiofauna") or groups such as the nematodes ("permanent meiofauna"), are unknown.

The presence of macrofauna did not enhance the initial burial of Chl *a* (presumably intact diatom cells) through the sediment–water interface. A significant increase in Chl *a* was observed after 6 days in the top 5 mm of both addition treatments, with little variation in amount buried in the presence or absence of macrofauna. The amount of added Chl *a* buried (and not yet degraded) at 10 days after addition corresponds to 22.3 and 21.2% of the total added to the treatments when macrofauna were present or absent, respectively (mean increase of 0.64 vs. 0.61 $\mu g \cdot cm^{-3}$ in the presence and absence of macrofauna, respectively; absolute increase of 0.58 and 0.55 μg, respectively). The lack of difference in Chl *a* burial in the presence or absence of macrofauna suggests that these subsurface deposit-feeding macrofauna are unimportant in transferring phytodetritus through the sediment–water interface. In these sediments, the meiofauna were responsible for the initial burial of intact Chl *a*.

The patterns of phaeopigment production observed in the sediment columns in this study suggest an unimportant role of the presence of these macrofauna either through direct grazing (Welschmeyer & Lorenzen, 1985) or stimulation of microbial degradation of Chl *a*. Phaeopigment levels in the top 5 mm of both diatom addition treatments were enhanced similarly in the presence or absence of macrofauna, 3 days after diatom addition. Overall, macrofauna did not significantly enhance the degradation of the sedimented diatoms.

We can construct a rough budget of how much of the sedimented chloropigments were buried in the 10-day period, using the maximum increase in phaeopigment levels observed in the diatom addition treatments compared to non-addition treatments at 6 days (mean increase of 1.26 and 1.18 $\mu g \cdot cm^{-3}$ in the presence and absence of macrofauna, respectively; absolute increase of 1.13 and 1.06 μg, respectively). We estimated that these phaeopigment levels correspond to Chl *a* concentrations of 1.71 and 1.61 μg in the presence and absence of macrofauna, respectively, using a rough conversion of 66% by weight transfer from Chl *a* to phaeopigments during grazing (Shuman & Lorenzen, 1975). We obtained total transfers of Chl *a* through the sediment–water interface of 2.29 and 2.16 μg in the presence and absence of macro-

fauna, respectively, by adding these values to the previously estimated amounts of intact Chl *a* buried. These values correspond to a minimum of 83% of the Chl *a* added to the sediment surface, suggesting that initial burial of sedimented phytoplankton is quite rapid in soft-sediment systems. However, the shallow depth of penetration in the 10-day period (≤ 5 mm) leaves the possibility that much of this material could be easily resuspended under high flow conditions in faunal communities of this type.

An interesting pattern was that phaeopigment levels were significantly enhanced throughout the sediment core in the presence of macrofauna. These data suggest that the macrofauna found in this experiment are more significant in degrading Chl *a* deeper in the sediment column than transferring it through the sediment–water interface. In this type of sediment, perhaps the meiofauna are more important in intercepting phytodetritus at the sediment–water interface and are responsible for its initial burial, whereafter macrofauna are more influential in phytodetrital degradation. A scenario of this type has also been proposed by Bauer et al. (1990) in explaining differentiation of stable C isotope values in macrofauna and meiofauna from a California hydrocarbon seep.

Although the meiofauna have been observed to alter surficial sediment structure (Cullen, 1973) and to build intricate networks of tubes in sediments (Chandler & Fleeger, 1984; Nehring et al., 1990), they are generally ignored in studies of organic matter diagenesis and burial. In assessing the capability of sediments to absorb potential increases in phytodetrital C flux, a knowledge of the faunal groups involved in processing this organic matter is necessary. The results of this study suggest that the macrofauna common to organically enriched systems, such as used in this experiment, are unimportant in the initial burial and subsequent degradation of sedimented phytoplankton, at least during the first 10 days after deposition. In these types of systems, the microbial and meiobenthic community, rather than the macrobenthos, dominates the initial burial and subsequent degradation of sedimented phytoplankton.

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