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Fate of phytodetritus in marine sediments: functional importance of macrofaunal community

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ABSTRACT: A 54 d incubation of intact sediment box-cores from 2 different macrofaunal sediment communities from the Swedish west coast was performed under controlled laboratory conditions in April to June 1999. One community was dominated by passive suspension feeders the other by subsurface deposit feeders. The box-cores were seeded with ^{14}C-labelled detritus of the diatom *Skeletonema costatum* in order to mimic a post-spring-bloom situation. In addition to the labelled diatom phytodetritus, the box-cosms initially contained chlorophyll *a* with concentrations between 1 and 1.5 µg ml^{-1} in the top cm of the sediment. The experiment thus provided an opportunity to estimate degradation rates of the naturally occurring chlorophyll with a natural benthic fauna present over a ca. 2 mo period. Using a diagenetic model to describe the vertical distribution of chlorophyll *a* (chl *a*), and using the same, previously published, degradation rate constant in both communities (0.03 d^{-1}), gave mixing coefficients (D_B, cm^2 d^{-1}) that were on average >2 times higher in the community (L18) dominated by deposit feeders than in the suspension-feeding community (S3): 2.5 ± SD 1.7 and 0.86 ± SD 0.50, respectively. This indicates a higher mixing rate at L18. This difference in mixing between the 2 communities was supported by changes in vertical distribution of ^{14}C-labelled phytodetritus over the 54 d period. The mixing coefficients (D_Bs) were positively correlated with biomass of subsurface deposit feeders but not with total biomass. Background chl *a* was higher at L18 than at S3. A quantitative comparison of the total chl *a* inventories at the start and end of the experiment suggested a low overall degradation rate (no significant overall change) in the chl *a*, far from the reaction rate constant of 0.03 d^{-1} often used in the literature. Similarly, the total ^{14}C activity in the cosms did not change significantly over the study period, suggesting a small loss of $^{14}CO_2$ from the cosms relative to the ^{14}C-pool size. The labelled algal matter distributions showed clear mixing over the 2 months in both communities with a higher mixing rate in the deposit-feeding community than the suspension-feeding community. Mixing also occurred deeper in the deposit-feeding community. Uptake of labelled matter by macrofauna was similar in the 2 communities, but differed markedly between species and trophic groups. At the end of the incubation, surface deposit feeders had an order of magnitude higher weight-specific ^{14}C activity than suspension feeders and subsurface deposit feeders. The proportion of macrofaunal uptake of total ^{14}C activity in the cosms was small, on the order of 5%. The results support the idea that community species composition is important for the fate of sedimented phytodetritus and that macrofaunal influence on degradation of sedimentary chlorophyll is small at this time of the year. The initial fate of the bloom material was burial in the sediment rather than consumption by heterotrophs. The findings are thus in accordance with the hypothesis that a part of the spring phytoplankton bloom may be buried for a while in the sediment before being remineralised.

KEY WORDS: Phytodetritus · Bioturbation · Benthic community function · Tracer · Chlorophyll · Deposit-feeding

INTRODUCTION

The common photosynthetic plant pigment chl *a* is often used as a tracer of phytoplankton flux between compartments in aquatic ecosystems. In principle, data on the concentration and loss rates of chl *a*, be these by biogenic/physical advection and/or decay, enables estimation of the flux under steady state conditions. This approach has been used with varying success both in pelagic systems (e.g. the gut fluorescence

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method) and to estimate flux of algal matter into sediments (Sun et al. 1991, 1994, Boon & Duineveld 1998). However, in sediment systems, loss rates of chl *a* have only been estimated in a few experiments, and the generality of the published loss rates is not clear. It is conceivable that chl *a* is often present in the sediment in several different pools, each of different lability (Sun et al. 1991, 1993a, 1993b). Even less is known about how animals influence decay rates in sediments, and available experiments using single species are conflicting. For example, Hawkins et al. (1986) showed that chl *a* decayed rapidly in the alimentary system of the blue mussel *Mytilus edulis*, while Webb (1993) reported no effect at all by another bivalve (*Macoma baltica*) on sedimentary chl *a*. Data on how whole macrofaunal communities affect degradation and mixing of chlorophyll are few, although Bianchi et al. (1988) showed that coexistence of more than one species differentially affected pigment dynamics in microcosms compared to a single species.

If the macrofaunal influence on mixing is greater than physical mixing (or sedimentation), it may be assumed that mixing rates of organic matter are higher in deposit-feeding communities (Sandnes et al. 2000) (and in particular those dominated by subsurface deposit feeders) than in communities dominated by suspension feeders. This is because the former category redistributes sediment over a wider depth horizon than others through their feeding activities. In this study we report on an experiment designed to evaluate the effects of macrofaunal community differences in terms of feeding mode on the fate of chlorophyll in the sediment and a spring bloom pulse of microalgal detritus applied to the sediment surface. We have taken undisturbed box-cosms from 2 communities with different quantitative relationships between subsurface deposit feeders and the other faunal categories. The cosms were incubated for 54 d with a fresh detritus pulse of the spring-bloom diatom *Skeletonema costatum* uniformly radiolabelled with ^{14}C. Replicated inventories of both ^{14}C activity and chl *a* concentrations in the top 20 cm of the sediment were taken at the start and at the end of the experiment in the cosms. In addition, all macrofauna (> 1mm) visible to the naked eye was identified to species, counted and weighed on termination of the experiment. The ^{14}C activity was measured in each species at the end of the experiment.

The aim of the experiment was to test the overall null hypothesis of no effect attributable to faunal community differences on the fate of the added phytodetritus, be it mixing or degradation rates. Alternative hypotheses were that mixing was higher/deeper in the community dominated by subsurface deposit feeders compared to the suspension-feeding community. Additional aims were to assess the effects of macrofauna on degradation of chl *a* in the sediment, and to trace the labelled pulse into functional feeding groups.

MATERIALS AND METHODS

Studied communities. Two different types of macrofaunal communites in the innermost part of the Gullmarfjord were chosen for this study; one at ca. 24 m water depth (S3) on a sandy mud bottom (58° 25.16′ N, 11° 35.58′ E), and the other at ca. 40 m depth (L18) on a mud bottom (58° 24.96′ N, 11° 38.63′ E). The selection of communities was based on extensive knowledge of the species composition obtained in Swedish monitoring programs. The S3 community was strongly dominated by the passive filter-feeding, burrowing ophiuroid *Amphiura filiformis*. The L18 community was dominated by deposit feeders; notably surface-feeding ampharetid polychaetes and head-down subsurface-feeding polychaetes and particularly maldanids (*Rhodine loveni*). To illustrate differences in redox conditions and depth distribution of infaunal activity in the sediment, sediment profile images (SPIs) were taken *in situ* at Stns L18 and S3. The camera, a digital Canon Power Shot Pro 70, took vertical pictures in the sediment through a prism (30 × 15 cm) as described in Nilsson & Rosenberg (1997). Image contrast was enhanced in Adobe Photoshop 5.0.

Experimental set-up. In mid-April 1999, USNEL box-cores with Plexiglas linings were taken at the 2 stations. Three cores each covering 0.25 m^2 and 20 to 30 cm deep were taken at random from each of the 2 communities and set up in the meso-cosm system in the Kristineberg Marine Research Station the same day as sampling was performed. Each box-cosm was supplied with its own inlet for running seawater (ca. 34 PSU) and its own outlet, and the water depth above the sediment was ca. 5 cm. The water was taken at 35 m depth and had passed sedimentation basins, and therefore contained negligible amounts of particulate matter. The water flow through each cosm was adjusted to ca. 2 l min^{-1}, which under complete mixing equals a water renewal every 10 to 15 min. However, the flow was made close to laminar along the sediment surface, and therefore the residence time just above the bottom was probably shorter than 10 min. The flow over the sediment surface was never strong enough to cause resuspension of sediment. The cosms were kept dark in a room at constant temperature, 7 to 10°C. Following set-up, the cosms were allowed to stand with experimental water flow for 2 d before addition of label.

On Day 3 after sampling, the water flow was shut off and the radiolabelled microalgal slurry was added. Care was taken to apply the algae as evenly as possible over the sediment surface. The algae were allowed to

settle in still water for 9 h before initial sampling of the box-cosms. After sampling the water flow was turned on and kept at 2 l min^{-1} for the rest of the experiment.

Nine hours after addition of the algal pulse, 3 sleeved Plexi-cores (i.d. 5 cm) were taken randomly in each of the cosms to a sediment depth of > 21 cm. The sleeves (i.d. ca. 8 cm) were left in the cosms in order to minimise physical disturbance. The cores were immediately sliced into 1 cm sections down to 10 cm, thereafter into 2 cm sections to 20 cm, and the remaining (>20 cm) was treated as 1 sample. From each slice, 2 subsamples were taken in the centre of the slice, one of exactly 1 ml for fluorometric determination of chlorophyll, and one of 1 to 2 g WW (wet weight) for determination of ^{14}C activity in the sediment. Samples were deep-frozen for at least 1 d at –20°C before analysis.

The cosms were left under experimental conditions for 54 d until termination of the experiment. Final sampling of the sediment was performed with unsleeved cores in the same way as initial sampling, except that 5 replicate cores were taken from each cosm. The remaining sediment from each cosm was sieved though a 1 mm mesh and the macrofaunal organisms were collected and further processed alive.

^{14}C-labelling of diatoms. In order to follow a fresh diatom pulse into the communities, a batch of the spring-bloom diatom *Skeletonema costatum* was cultured (15°C, salinity of 28 to 30, B1-growth medium; Hansen 1989) over a 4 wk period prior to setting up the box-cosms. After ca. 2 wk, when the algae were rapidly dividing, 2.5 mCi of $NaH^{14}CO_3$ was added to the culture. At the end of the 4 wk, the algae aggregated and fell to the bottom of the 2 culture flasks (10 l medium and algae in each). The supernatant was decanted off and the bottom slurry of radiolabelled algal detritus was divided into 6 equal portions by volume (for later addition to each of the experimental box-cosms) and kept cool in the dark.

Sample treatment. Identification of the macrofauna and sediment preparation were as follows.

Macrofauna: The macrofauna was identified alive to the lowest possible taxon using a magnifying lamp. For each taxon the number of individuals were counted and the wet weight (WW) was determined. For each species from each cosm, a sample with a maximum weight of ca. 1 g WW, consisting of 1 or several whole individuals, was put into a pre-weighed glass vial; the WW was determined, the sample was dissolved with Soluene (1 ml) overnight, and 10 ml of Ultima Gold scintillation fluid were added. The samples were counted on a liquid scintillation counter, quench-corrected, and ^{14}C activity (dpm) was determined for each species. Wet weights were transformed to ash-free dry weights (AFDW) using published conversion factor for each of the major taxonomic groups (Rumohr et al. 1987).

Sediment: Samples for ^{14}C activity were weighed after drying at 80°C to constant weight to get the dry weight, and subsequently treated identically to the samples for faunal ^{14}C activity. Samples for chlorophyll determinations were thawed and extracted in 96% ethanol (Jespersen & Christoffersen 1987) for at least 6 h in the dark. The volume of extraction fluid (10 ml) was ca. 10 times the volume of the sediment sample to ensure complete extraction. Extracts were filtered through a GFC filter before analysis on a Turner 10 model fluorometer for chl *a* using the acid method (Strickland & Parsons 1972). Phaeopigments were not analysed because we believe that background fluorescence (which is high relative to loss on acid addition: ca. 80% of fluorescence before acid addition) is to a great extent due to acid non-labile components other than phaeopigments; consequently, estimates of phaeopigments would be grossly overestimated (Falkowski & Sucher 1981). Chlorophyll *a* is also likely to be overestimated by this method, and a more appropriate term would be the acid-labile fluorescent fraction at the actual wavelength. However, for the sake of simplicity, we use the term chl *a* throughout the paper, knowing that it may include other fluorescent substances.

Numerical methods. A diagenetic model was used to describe the vertical distribution of chl *a* concentrations and the ^{14}C activity in the sediment (Sun et al. 1991, their Eq. 7).

$$C_x = (C_o - C_\infty) \cdot \exp\left(-x \cdot \sqrt{(\lambda / D_B)}\right) + C_\infty \qquad (1)$$

where C_x is the concentration (mass/volume) at sediment depth x (cm), C_o the concentration in the surface of the sediment, C_∞ the background concentration in the sediment, λ the degradation constant (first order reaction rate constant, d^{-1}) and D_B the mixing coefficient (biodiffusion rate constant, $cm^2\ d^{-1}$). The model was fitted by the method of least squares using the Newton-Gauss algorithm (SYSTAT 8.0) to estimate C_o and D_B, assuming a constant λ of 0.03 d^{-1} (Sun et al. 1991) and assuming C_∞ equals the value in the deepest section(s) for chl *a*, and 100 dpm g^{-1} for ^{14}C-activity in the sediment.

Effects of the experiment were analysed with a mixed 3-factor ANOVA using the General Linear Model (GLM) option in SAS v8. Log-transformation was used throughout to remove dependence between mean and variance. Community and date/trophic group assignment were treated as fixed factors and box-cosm nested within communities was treated as a random factor. The mean square (MS) of the community was tested against the MS of the random factor separately for each date.

Non-metric multi-dimensional scaling (MDS) of Bray-Curtis similarity was used to analyse for differences in species composition between the 6 box-cosms (Clarke & Gorley 2001).

RESULTS

Faunal composition

Faunal data from the box-cosms at the end of the experiment are shown in Table 1. Species from the experimental boxes were categorised with respect to trophic group using information from the literature (e.g. Fauchald & Jumars 1979, Josefson 1987) into suspension feeders (here mainly the ophiuroid *Amphiura filiformis*), surface deposit feeders (polychaetes and bivalves), subsurface deposit feeders (mainly polychaetes and echinoids) and predators (polychaetes and ophiuroids). Subsurface deposit feed-

Table 1. Macrofaunal taxa. Data from the box-cosms on termination of the experiment (after 54 d): categorisation of the species into feeding groups (int: surface deposit feeders; sus: suspension feeders; sub: subsurface deposit feeders; pre: predators) means ±SE for each community of number of individuals per cosm (Ind.) ash-free DW (AFDW) in g per cosm (ca. 0.25 m^2), and the weight-specific ^{14}C activity (dpm μg^{-1} AFDW) of each species

Species	Feed	Deposit feeding community (L18)			Suspension-feeding community (S3)		
		Ind.	AFDW	dpm μg^{-1}	Ind.	AFDW	dpm μg^{-1}
Amphiura filiformis	sus	99.0 ± 10.7	0.469 ± 0.076	1.09 ± 0.103	273 ± 14.6	1.00 ± 0.099	0.447 ± 0.160
Corbula gibba	sus				2.0 ± 1.0	0.043 ± 0.034	1.37 ± 1.28
Ascidia	sus				2.0	1.00	1.34
Amphiura chiajei	sub	84.7 ± 3.0	0.695 ± .084	0.794 ± 0.242	73.7 ± 4.3	0.401 ± 0.033	0.968 ± 0.586
Brissopsis lyrifera	sub	1.7 ± 0.3	1.20 ± 0.219	1.19 ± 0.721			
Echinocardium cordatum	sub				5.7 ± 1.8	0.655 ± 0.363	3.08 ± 2.72
Rhodine loveni	sub	17.7 ± 3.0	0.439 ± 0.016	1.06 ± 0.643	1.0	0.121	0.393
Polyphysia crassa	sub	1.3 ± 0.3	0.177 ± 0.066	0.672 ± 0.252	1.5 ± 0.5	0.278 ± 0.106	1.06 ± 0.356
Maldane sarsi	sub	8.3 ± 2.9	0.060 ± 0.032	8.13 ± 2.15			
Pectinaria auricoma	sub	2.0	0.022	3.01			
Pectinaria koreni	sub	1.0 ± 0.0	0.014 ± 0.004	2.47 ± 0.413			
Brada villosa	sub	10.7 ± 2.3	0.052 ± 0.012	5.82 ± 1.71	1.5 ± 0.5	0.014 ± 0.012	8.12 ± 3.61
Heteromastus filiformis	sub	2.0	0.002	1.17			
Scalibregma inflatum	sub				8.5 ± 0.5	0.186 ± 0.006	0.991 ± 0.431
Onoba vitrea	sub	2.0	0.000	0.418	6.0 ± 4.0	0.002 ± 0.001	0.912 ± 0.255
Mysella bidentata	sub	3.0 ± 0.0	0.001 ± 0.001	10.5 ± 6.52	31.0 ± 6.1	0.017 ± 0.005	4.70 ± 1.24
Nucula sp.	sub	10.5 ± 1.5	0.035 ± 0.006	2.30 ± 0.983	11.0 ± 2.5	0.062 ± 0.015	1.25 ± 0.462
Nucula sulcata	sub	1.0	0.157	0.105			
Nuculoma tenuis	sub	4.0	0.005	2.98			
Nuculana pernula	sub	1.0	0.001	0.188			
Thyasira equalis	sub	18.0 ± 3.8	0.045 ± 0.009	0.923 ± 0.219			
Amphicteis gunneri	int	1.0 ± 0.0	0.006 ± 0.002	62.3 ± 59.3	1.0	0.003	5.05
Melinna cristata	int	12.7 ± 1.8	0.122 ± 0.026	19.4 ± 6.80			
Anobothrus gracilis	int	1.0	0.001	139.6	1.0 ± 0.0	0.003 ± 0.001	21.1 ± 0.356
Pista cristata	int				1.0	0.017	3.36
Terebellides stroemi	int	3.0 ± 2.0	0.009 ± 0.006	3.54 ± 0.657			
Laonice cirrata	int	2.5 ± 0.5	0.020 ± 0.006	14.3 ± 0.042			
Spiophanes kroeyeri	int	1.0	0.001	0.923			
Abra nitida	int	2.0	0.013	80.5	25.0 ± 5.3	0.097 ± 0.017	35.3 ± 3.24
Amphipoda	int	1.0	0.001	13.0			
Golfingia sp.	int	2.0	0.001	78.7	1.0	0.004	8.05
Ophiura sarsi	pre				4.0 ± 0.6	0.139 ± 0.033	0.275 ± 0.239
Pholoe minuta	pre	13.5 ± 0.5	0.018 ± 0.002	2.95 ± 1.79	17.0 ± 8.0	0.007 ± 0.003	17.4 ± 0.916
Nephtys sp.	pre	1.0	0.006	4.10	3.5 ± 2.5	0.070 ± 0.054	3.95 ± 2.30
Goniada maculata	pre	1.5 ± 0.5	0.006 ± 0.001	4.81 ± 3.08			
Glycera sp.	pre	3.0 ± 1.0	0.235 ± 0.107	0.345 ± 0.134	1.7 ± 0.3	0.018 ± 0.002	8.28 ± 3.34
Lumbrineris sp.	pre	1.0 ± 0.0	0.011 ± 0.005	35.4 ± 9.81			
Chaetoderma nitidulum	pre	1.0	0.000	276.2	1.0	0.040	5.99
Cylichna cylindracea	pre	2.7 ± 1.7	0.004 ± 0.002	9.85 ± 1.51	7.0 ± 2.7	0.016 ± 0.007	4.87 ± 0.620
Calocaris macandreae	pre	1.0	0.178	0.404			
Priapulus caudatus	pre				1.0	0.002	15.4
Turbellaria	pre				1.0	0.007	195.5
Polychaeta		10.0	0.023	13.5			

ers dominated biomass in the L18 community, while suspension feeders were more dominant in the S3 community (Fig. 1a). It is also clear that species composition was different in the 2 communities, which is illustrated by the MDS-plot in Fig. 1b. The suspected key organisms in terms of sediment mixing and irrigation were the head-down feeding maldanid polychaete *Rhodine loveni* in the deposit-feeding community, and the ophiuroid *A. filiformis* in the suspension-feeding community. The burrows of the former species can reach ca. 20 cm and the burrows of the latter species reaches 5 to 6 cm into the sediment.

Several oxic voids appeared in the sediment profile images from both stations (Fig. 2). The penetration of the prism was greater at Stn L18 than Stn S3. Oxidised burrows are visible down to the bottom of the profiles, i.e. they were at least 16 and 11 cm long at Stns L18 and S3, respectively. The mean apparent redox potential discontinuity (RPD) at the 2 stations were approximately 9 and 5 cm, respectively.

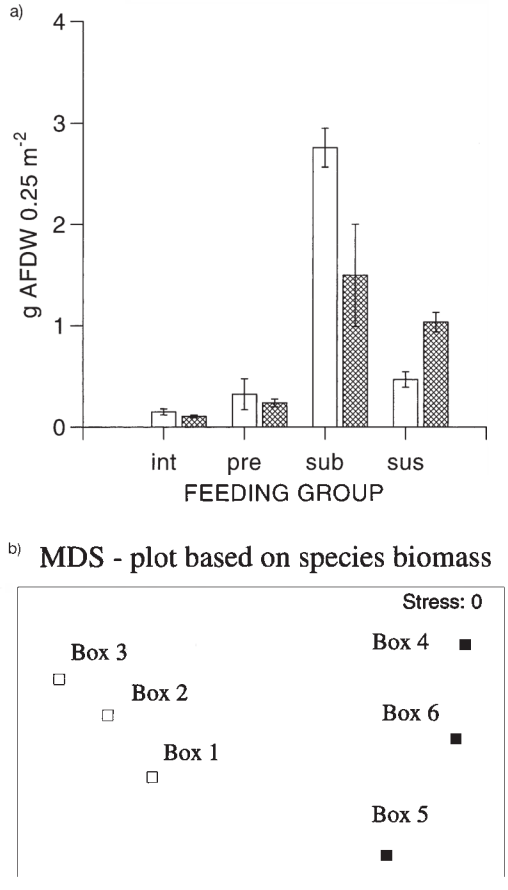

Fig. 1. (a) Bar-plot of mean biomass (ash-free DW; means ± SE) of 4 feeding groups in the 2 communities measured on termination of the experiment. Open bars: deposit-feeding community (L18); cross-hatched bars: suspension-feeding community (S3). Note the higher dominance of subsurface deposit feeders in the deposit-feeding community at Stn L18. int: surface deposit feeders; pre: predators and omnivores; Sub: subsurface deposit feeders; sus: suspension feeders. For categorisation of taxa into trophic groups, see Table. (b) Non-metric multi-dimensional scaling (MDS) plot based on Bray-Curtis similarities between box-cosms calculated from biomass (AFDW) of each species. Boxes 1–3 are from the L18 community and Boxes 4–6 are from the S3 community

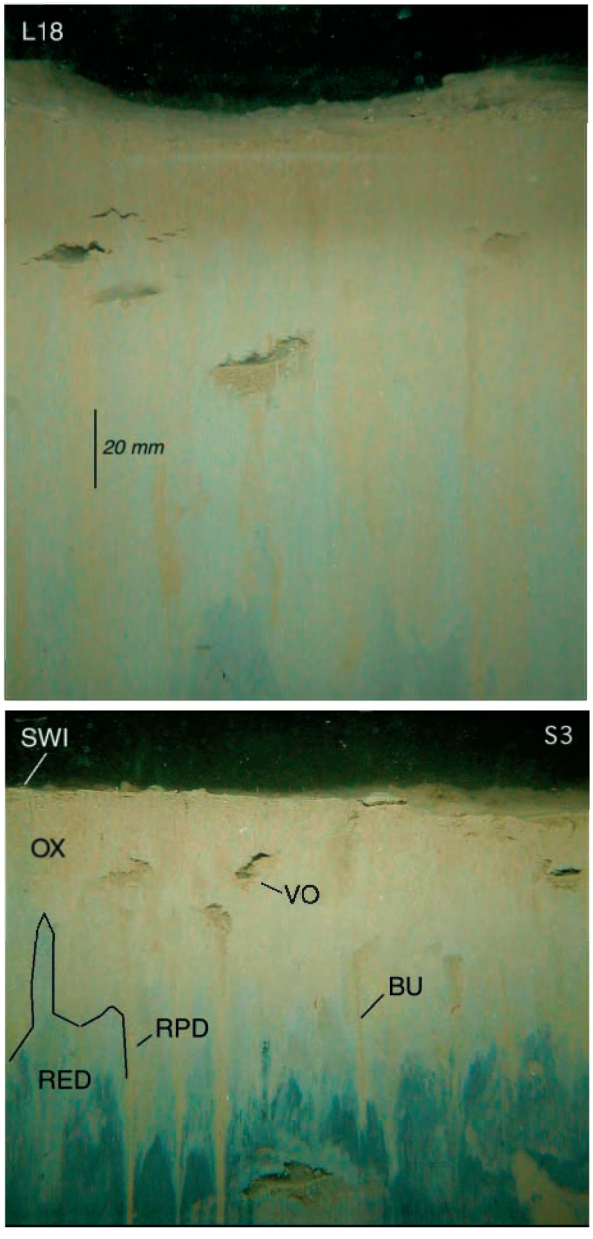

Fig. 2. Sediment profile images taken in the field at the 2 stations, L18 and S3 (contrasts digitally enhanced). SWI: sediment water interface; OX: oxidised sediment; RED: reduced sediment; RPD: redox potential discontinuity; VO: void; BU: burrow. Note the narrower extension of the bioturbated zone in the suspension-feeding community (S3) compared to the deposit-feeding community (L18)

Table 2. Results of a 3-factor ANOVA with trophic group assignment and community type as fixed factors and and box-cosm nested in communities [Cosm(Community)] as random factor and the log dpm g^{-1} AFDW of each species as response factor

Source	df	MS	*F*-ratio	p
Trophic group	3	5.951	12.60	0.000
Community	1	0.372	0.79	0.377
Troph × Community	3	0.105	0.22	0.881
Cosm(Community)	4	0.180	0.38	0.822
Troph × Cosm(Comm.)	12	0.299	0.63	0.808
Error	91	0.472		
Community MS vs Cosm(Community) MS			0.58	0.487

^{14}C uptake by macrofauna

A 3-factor ANOVA with trophic group assignment and community type as fixed factors and with box-cosms nested within communities as random factor was used with the log dpm g^{-1} AFDW of each species in each cosm as response factor (Table 2). There was a highly significant difference between trophic groups but no difference between communities or for the interaction terms (Table 2). Testing community MS against the nested factor MS did not indicate a significant difference ($p > 0.05$).

The ^{14}C activity in the total biomass, expressed as AFDW of each trophic group showed a consistent pattern in the 2 communities, with the highest activity in the biomass of surface deposit feeders, for both total (Fig. 3a) and weight-specific unit (Fig. 3b) activity. The weight-specific activity of surface deposit feeders was 1 order of magnitude higher than of subsurface deposit feeders and suspension feeders; predators also showed high activity (Fig.3b). Among surface deposit feeders the highest weight-specific activity was found in the bivalve *Abra nitida*, the ampharetid polychaetes *Melinna cristata*, *Amphicteis gunneri* and *Anobothrus gracilis* and the sipunculid *Golfingia* sp. (Table 1). Some of the predators showed also a very high activity (*Chaetoderma nitidulum*, *Lumbrineris* sp. and Turbellaria). The commensal of *Amphiura filiformis*, the bivalve *Mysella bidentata*, showed high activity relative to its host (Table 1). The highest activity in the subsurface deposit feeder *Rhodine loveni* was found in Box-cosm 2. This box-cosm showed the deepest penetration of labelled material of all the cosms (Fig. 4).

^{14}C activity in the sediment

The profiles of ^{14}C activity (Fig. 4) in general showed an exponential decrease with increasing sediment depth, and there was a tendency, particularly in the deposit-feeding community, towards higher values at depth at the end of the experiment. The change in total ^{14}C activity in the sediment over time and between communities was tested with 3-factor mixed ANOVA with communities and date as fixed factors and cosms nested within communities as random factor (Table 3). The response variable was the log of the sum of dpm g^{-1} for each profile.

There was no effect of date, community or cosm, and there were no significant interaction terms. Consequently there was no detectable losses of labelled material (such as $^{14}CO_2$) from the cosms in the experimental period (i.e. the losses must have been relatively small). This is further illustrated by Fig. 5, where means for inventories in each cosm are shown at the start and at the end of the experiment. Inventories were calculated as the sum of dpm g^{-1} for each to 21 cm and corrected for interval width. In particular, at

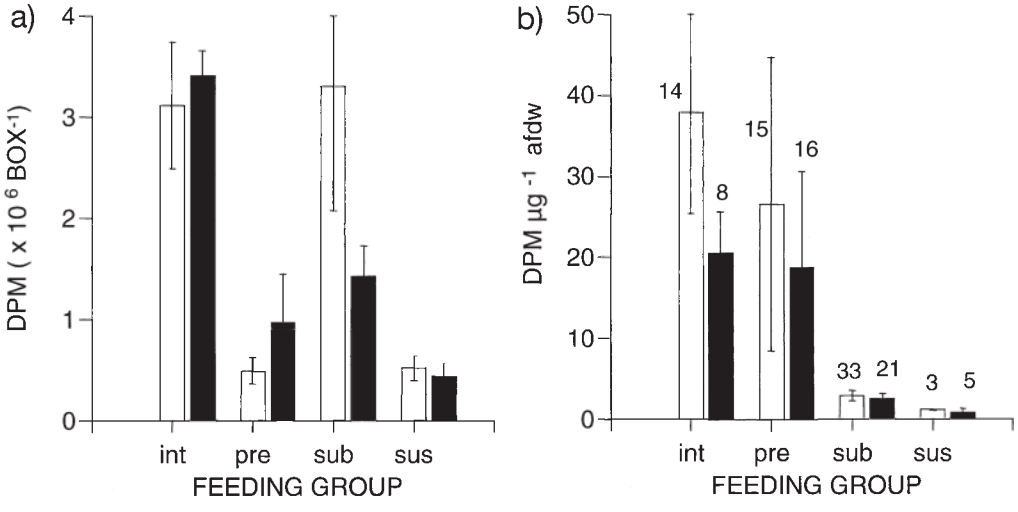

Fig. 3. Bar plots of ^{14}C activity (dpm; means ± SE) in biomass of the 4 feeding categories in each of the 2 communites (open bars: L18; filled bars: S3) on termination of the experiment. (a) Total activity; (b) weight-specific activity. Numbers above bars in (b) denote number of observations in each community. Other abbreviations as in Fig. 1

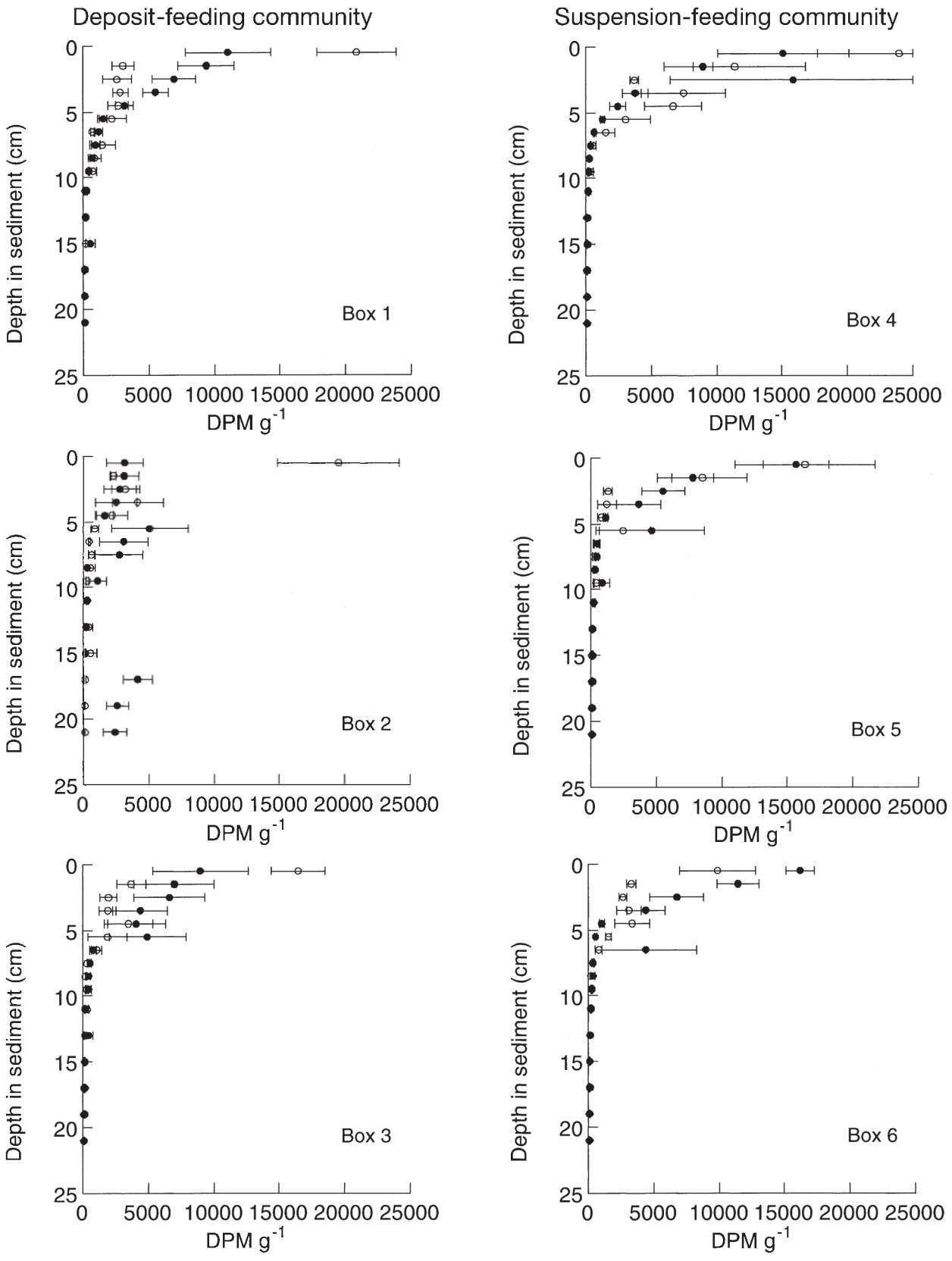

Fig. 4. Sediment profiles of ^{14}C activity (dpm g^{-1} dry sediment): means (±SE) for cosms 9 h after addition of label (○) and after 54 d (●)

Table 3. Results of a 3-factor ANOVA with date and community as fixed factors and box-cosm nested in communities as random factor; the response variable was the log of of the sum of dpm g^{-1} for each profile

Source	df	MS	*F*-ratio	p
Date	1	0.010	0.28	0.602
Community	1	0.034	0.94	0.339
Date × Community	1	0.028	0.78	0.384
Cosm(Community)	4	0.056	1.53	0.213
Date × Cosm(Community)	4	0.031	0.84	0.507
Error	36	0.036		
Community MS vs Cosm(Community) MS April			0.00	0.967
Community MS vs Cosm(Community) MS June			3.87	0.121

Table 4. Results of a 3-factor ANOVA with date and community as fixed factors and box-cosm nested in communities as random factor; the response variable was the log of the mixing coefficient, D_B from the activity profiles assuming a constant degradation rate of 0.03 d^{-1}

Source	df	MS	*F*-ratio	p
Date	1	10.583	44.49	0.000
Community	1	0.087	0.37	0.549
Date × Community	1	5.584	23.48	0.000
Cosm(Community)	4	0.836	3.51	0.016
Date × Cosm(Community)	4	0.276	1.16	0.344
Error	36	0.238		
Community MS vs Cosm(Community) MS April			7.89	0.048
Community MS vs Cosm(Community) MS June			4.20	0.110

the end of the experiment the differences between cosms were very small.

Least-square fitting of Eq. (1) to the individual profiles, and assuming a constant λ, (here set to 0.03 d^{-1}; Sun et al. 1991), the mixing coefficient D_B was estimated, being an estimate of the slope of the profiles. Background activity was set at 100 dpm g^{-1} DW. A 3-factor ANOVA performed as described above, was run to test for differences in the inclination of the profiles (log-transformed), which is likely to reflect mixing of the labelled material (Table 4). There were clear effects of both date and cosm, and the change with time depended on community, indicated by the significant interaction term between date and community. At the start of the experiment there was a difference in D_B between the communities, with a higher D_B in the suspension-feeding community, supported by a significant *F*-value between community and the random factor (cosms within communities). At the end of the experiment D_B had increased in both communities and D_B seemed higher in the deposit-feeding community (Fig. 6), although the *F*-test between community and cosm within community only showed a p-value of 0.11. Apparently, the significant cosm effect was due to very deep penetration in 1 of the boxes (No. 2) in the deposit-feeding community (Fig. 4).

In addition to the parametric ANOVA, we also used a non-parametric approach to explore differences in label redistribution in the 2 communities. When mean activity values from each cosm from the 2 dates from each depth level were treated as paired observations

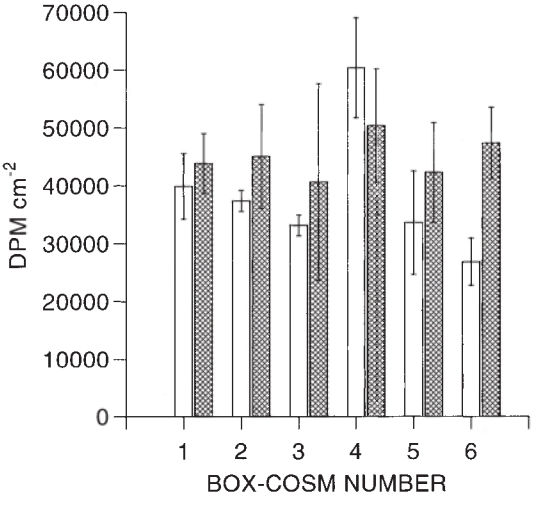

Fig. 5. Activity inventories in the sediment (means ± SE) at the start (open bars) and at the end (cross-hatched bars) of the experiment. Box-Cosm No. 1 to 3: deposit-feeding community; No. 4 to 6: suspension-feeding community.

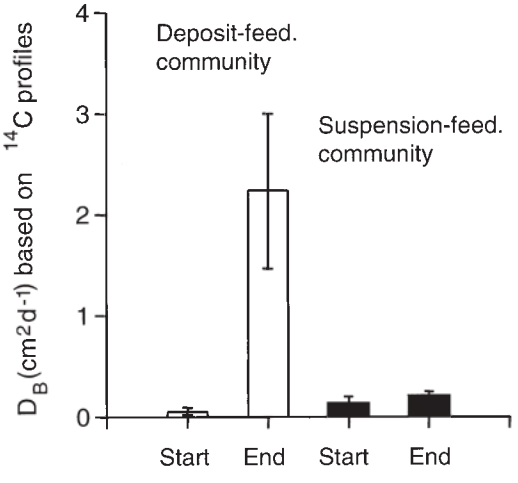

Fig. 6. Bar plot showing mean (±SE) mixing coefficients, D_B (cm^2 d^{-1}), based on label profiles for each community at the start and at the end of the experiment

and testing with a Wilcoxon signed-ranks test, there was a significant increase over time over the depth range 1.5 to 7.5 cm ($p < 0.01$) in the deposit-feeding community whereas there was no significant trend in the suspension-feeding community ($p > 0.05$). Given the lack of evidence for loss of activity in the cosms, this suggests higher mixing rate in the L18 community than in the S3 community. There was a close to significant ($p < 0.06$) positive relationship between D_B based on activity profiles at the end of the experiment and biomass (AFDW) of subsurface deposit feeders, but not with other feeding categories.

Chlorophyll in the sediment

Chl *a* profiles were of different shape in the 2 communities (Fig. 7), with a much steeper exponential decline with increasing sediment depth in the suspension-feeding community. The background level of chl *a*, estimated by the average for the 4 deepest levels at the start and at the end of the experiment, was 50% higher in the deposit-feeding community than the suspension-feeding community ($p < 0.001$, Student's *t*-test). The change in total chl *a* in the sediment over time and between communities was tested with the same method as for ^{14}C activity in the sediment. The response variable was the log of the sum for each inventory of chl *a* in mg cm^{-3} wet sediment (Table 5). There were no effects of date or community, but effect of cosm within communities was just significant ($p < 0.05$). Consequently, and similar to the ^{14}C activity, there was no detectable loss or degradation of chl *a* in the cosms during the experimental period.

A test for changes in the slope of chl *a* profiles was performed in the same way as for ^{14}C activity, with log D_B in Eq. (1) as response variable and assuming a degradation rate constant of 0.03 d^{-1} (Table 6). Background chl *a* was set to the mean concentration of the 4 deepest levels in the sediment for each profile. There were significant effects of community ($p < 0.001$) and date ($p < 0.05$). The interaction between date and community was close to significant ($p < 0.054$). From Fig. 8, which shows D_B by date and by community, it seems clear that the absolute magnitude of change between the start and end of the experiment was the same in both communities. D_B from chl *a* profiles was significantly positively correlated with biomass of sub-surface deposit feeders (Fig. 9, $p < 0.001$, Pearson's product-moment correlation) but not with total biomass.

Table 5. Results of a 3-factor ANOVA with date and community as fixed factors and box-cosm nested in communities as random factor; the response variable was the log of the sum of chlorophyll *a* (µg cm^{-3}) for each inventory

Source	df	MS	*F*-ratio	p
Date	1	0.000	0.00	0.948
Community	1	0.005	1.60	0.213
Date × Community	1	0.010	2.93	0.096
Cosm(Community)	4	0.009	2.77	0.042
Date × Cosm(Community)	4	0.008	2.31	0.077
Error	36	0.003		
Community MS vs Cosm(Community) MS April			0.03	0.878
Community MS vs Cosm(Community) MS June			3.14	0.151

Table 6. Results of a 3-factor ANOVA with date and community as fixed factors and box-cosm nested in communities as random factor; the response variable was the log of the D_B estimated from the chlorophyll *a* profiles assuming a constant degradation rate of 0.03 d^{-1}

Source	df	MS	*F*-ratio	p
Date	1	0.845	6.14	0.019
Community	1	2.302	16.74	0.000
Date × Community	1	0.550	4.00	0.054
Cosm(Community)	4	0.216	1.57	0.207
Date × Cosm(Community)	4	0.080	0.58	0.678
Error	32	0.137		
Community MS vs Cosm(Community) MS April			15.07	0.017
Community MS vs Cosm(Community) MS June			2.29	0.204

DISCUSSION

Differential response to fresh phytodetritus (FPD) by feeding guilds

The differences in activity by weight between individual taxa varied over 2 orders of magnitude (Table 1), and surface deposit feeders showed 1 order of magnitude higher activity, measured as ^{14}C uptake, than subsurface deposit feeders at the end of the experiment. This is in accordance with the view that surface deposit feeders in particular feed on fresh matter, whereas subsurface deposit feeders utilise older food resources to a greater extent. As pointed out by Widbom & Frithsen (1995), the degree of uptake is related to carbon turnover (e.g. growth and respiration) of the species. The present communities were composed of species with highly different C-turnover rates, from slow-growing echinoderms to more rapidly

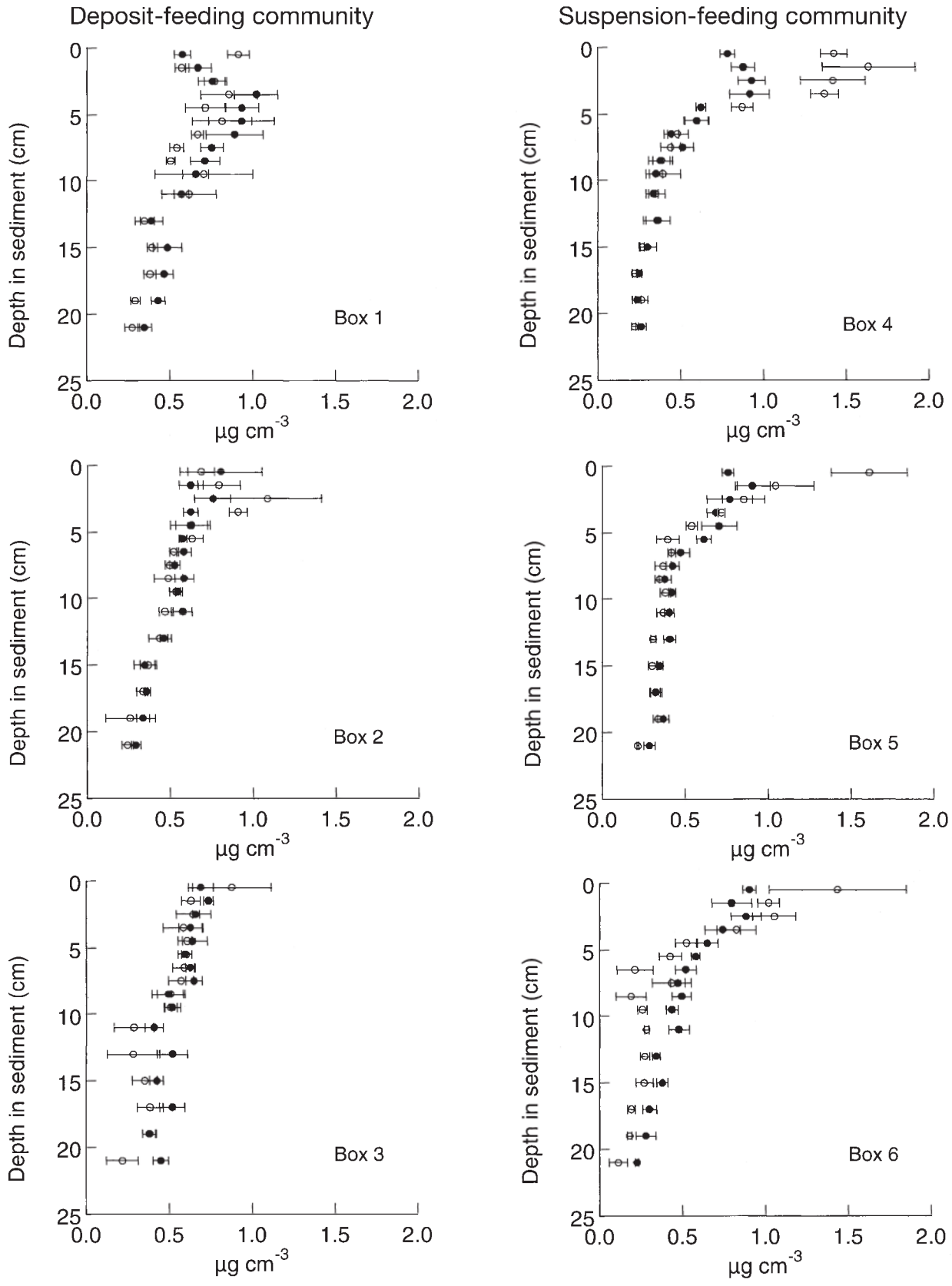

Fig. 7. Sediment profiles of chlorophyll *a*: means (±SE) for cosms 9 h after addition of labelled phytodetritus (○) and after 54 d (●) (µg cm^{-3} wet sediment)

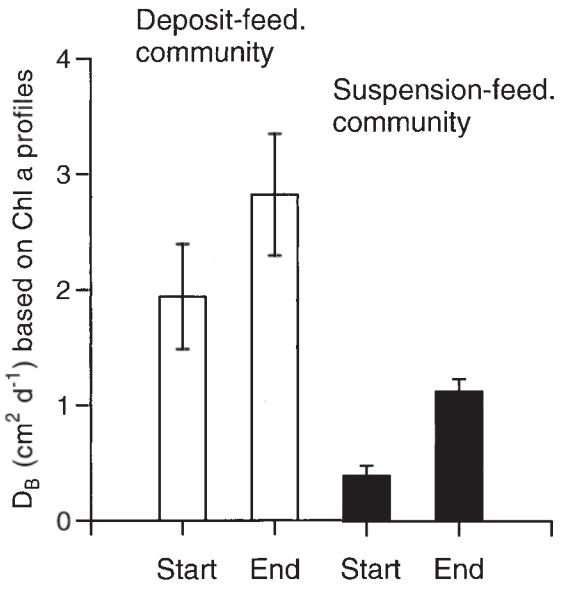

Fig. 8. Bar plot showing mean (±SE) D_B (cm^2 d^{-1}) based on chlorophyll *a* profiles for each community at the start and at the end of the experiment

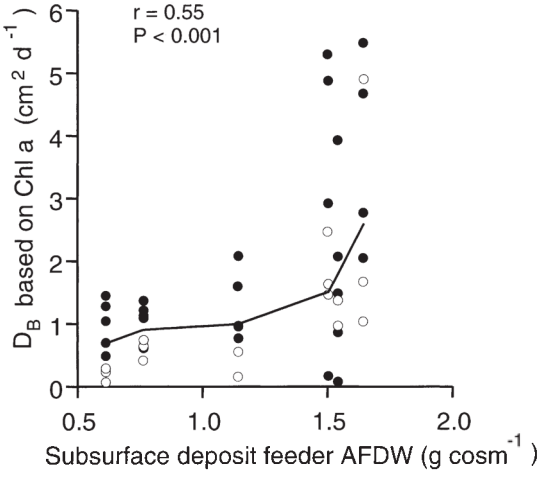

Fig. 9. Plot of D_B obtained from chlorophyll *a* profiles at the start (○) and at the end (●) of the experiment against ash-free DW of subsurface deposit feeders, echinoids excluded. D_B was estimated assuming a reaction rate constant of 0.03 d^{-1}. r is the Pearson-r. A line for LOWESS smoothing averages is indicated with a tension factor of 0.5

growing polychaetes. However, in addition to the statistical test for the whole communities (Table 2) we also performed the same ANOVA analysis on polychaetes only. Judging from compiled P:B ratios (Brey 1999), this class is assumed to be fairly homogeneous with respect to C-turnover, and we got exactly the same result as for total fauna. Furthermore, since the incubation time was ca. 2 mo, much longer than most gut passage times (on the order of a few hours to 1 d), we can reject the possibility that activity in the animals mainly originated from gut contents. Therefore, we feel confident that the different uptake of label between feeding categories was real.

There are, to our knowledge, not many studies of the pathways of fresh phytodetritus at the species level in natural marine benthic assemblages (but see Widbom & Frithsen 1995). It is unclear whether differential use of FPD is related to functional differences in terms of feeding depth in the sediment. We hypothesised *a priori* that traditional surface deposit feeders should be the feeding category that most readily would utilise the FPD in our experiment, as the FPD was deposited on the sediment surface, and indeed the results support this expectation. This role of deposit feeders has rarely been demonstrated experimentally before for coastal macrofauna. Widbom & Frithsen (1995) reported high uptake of FPD in surface-deposit-feeding macrofauna in an enrichment experiment with added ^{14}C. A differential response of meiofauna to FPD related to feeding depth in the sediment has been reported by some investigators (Rudnik 1989, Gullberg et al. 1997), but others (e.g. Olafsson et al. 1999) did not find a difference between feeding depths. Although the statistical test clearly showed that there were differences in species specific uptake of label between traditional feeding guilds in our experiment, which was similar across communities, there were in some instances substantial differences in uptake between species within guilds. One notable example was the maldanid polychaete *Maldane sarsi*, which had a high ^{14}C body burden. In the past, maldanids have been generally considered to be head-down subsurface deposit feeders, but recent studies have shown that some of them are able to acquire surface deposits by hoeing, and were suggested to contribute to subduction of FPD within a few days, a so-called non-local transport (Blair et al. 1996, Levin et al. 1997, 1999). Hoeing of label from the surface can possibly also explain the 5-fold higher weight-specific activity in *Rhodine loveni* in Cosm No. 2 compared to activity in the same species in the other cosms, and the increased sediment activity at the *R. loveni* feeding depth (>15 cm) in this cosm. There are no other possible candidates in this cosm to explain this deep injection of label. Another example is the normally deep-dwelling bivalve *Mysella bidentata* which lives in the burrow of the ophiuroid *Amphiura filiformis*. This bivalve showed 1 order of magnitude higher weight-specific activity compared to its host. Possible transport mechanisms for FPD into the sediment are irrigation of the burrow or active hoeing of surface material into the burrow by the host. The indication of high uptake of FPD by *M. bidentata* is in

accordance with field observations showing very high densities of this species in frontal areas with a high vertical input of FPD to the bottom (Josefson & Conley 1997). More difficult to explain are differences in uptake between related species feeding at the sediment-water interface. Among the surface deposit-feeding terebellomorph polychaetes, the ampharetids (*Anobothrus gracilis*, *Amphicteis gunner* and *Melinna cristata*) showed very high uptake, while the terebellids (*Terebellides stroemi* and *Pista cristata*) had a much lower uptake of label (Table 1) . Differences in uptake of *Skeletonema costatum* between related species from the same feeding guilds is in agreement with data of Olafsson et al. (1999) using the same diatom species to feed meiofauna. Reasons for differences within guilds may be food selection, although there is no information to support this. Anyhow, we should bear in mind that *S. costatum* is only one of several potential algal food species that sediment to the sea floor in spring, and lack of response to this species is not necessarily representative of a response to a normal spring bloom.

Magnitude of uptake compared to total label added

To compare the uptake by the fauna with the available amount of labelled detritus, the following calculation was made. The total ^{14}C-activity at the start of the experiment in the top 1 cm of the sediment should reflect the potential of the labelled food resource for, in particular, surface deposit feeders, which obtain their food which solely from the sediment surface. Total activity in the top 1 cm per box-cosm was calculated from dpm g^{-1} sediment DW assuming a water content of 50% and a specific gravity of dry sediment of 2.5. This was compared to the total amount of activity potentially ingested, calculated from the activity (dpm) in all surface deposit feeders in the box-cosm and assuming a growth efficiency (GE) of 50% (Fig. 10). The activity in surface deposit feeders was fairly similar between the 6 box-cosms (ca. 2 to 3 $\times 10^6$ dpm $cosm^{-1}$). The assumption of 50% GE is an approximation based on the literature, where the respired portion of ^{14}C-labelled fresh algal detritus assimilated by macrofauna ranges from 60% in *Diporeia* sp. (Fitzgerald & Gardner 1993) to ca. 30% in *Nereis diversicolor* (Kristensen et al. 1992) and larvae of *Chironomus riparius* (Gullberg et al. 1997). If these results apply to our study, the fraction of labelled material ingested by surface deposit feeders may be less than 10% of the total label available from the beginning in the top 1 cm of the sediment (Fig. 10), and this may explain why we did not find a significant loss of $^{14}CO_2$ despite the faunal activity.

Comparing the ^{14}C-uptake of the total fauna with total activity in the cosms, the animal portion was lower, maybe less than 5%. These findings agree with some previous work that added fresh phytodetritus to animal systems. In a study adding labelled microalgae to micro-cosms with macrofauna, Andersen & Kristensen (1992) found that 60 to 70% of the label was left in the sediment after 21 d. Their study was conducted at a higher temperature (15 to 23°C compared to our at 7 to 10°C, which may have influenced the microbial activity. They also concluded that there was no effect of macrofauna on the release of $^{14}CO_2$. Similarly, Widbom & Frithsen (1995), enriching meso-cosm systems (MERL) with ^{14}C-labelled phytodetritus, found that after 2 to 5 mo only 9 to 25% of the total label was bound in animal tissue, while 75% or more was still in the sediment. In a micro-cosm experiment with Baltic Sea amphipods and using ^{14}C-labelled *Skeletomema costatum* van de Bund et al. (2001) showed that 49 to 66% of the label remained in the sediment and 1 to 11% was incorporated into animal tissue after 2 mo. Thus, in a 2 mo period only a small fraction of the labelled material has been assimilated by macrofauna, in spite of being high quality fresh algal matter. How can this be? Because of their high content of fatty acids and lack of cellulose, diatoms constitute a high-quality food for benthic animals (e.g. Lopez & Levinton 1987). To some extent, the assimilated portion is dependent on the total amount of matter added. We do not know the absolute amount of labelled C added, but it is clear from the chl *a* measurements that the addition of chl *a* was small relative to the amounts of chl *a* already

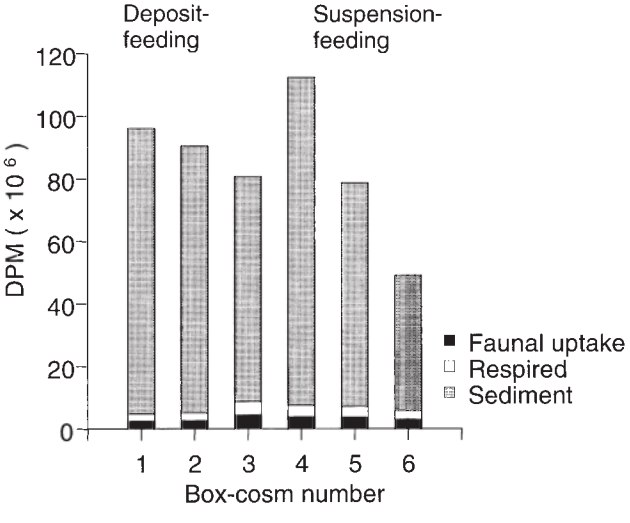

Fig. 10 Composite bar-plot showing, for each cosm, the amount of ^{14}C activity taken up by surface deposit feeders after 54 d, the portion respired assuming 50% growth efficiency, and the total ^{14}C activity in the top 1 cm of the sediment at the start of the experiment

present in the cosms. p was 0.905 in a 2-way ANOVA for effect of time between field inventories (3 to 5 per community) and the inventories taken in the cosms at the start of the experiment (9 per community).

There could be several reasons for this: (1) *Skeletonema costatum* is not very palatable; when alive, the heavy silica shells protect the algae from being digested; this is probably not the whole truth, since it has been shown that this particular species may be a useful food item for marine invertebrates (e.g. Guillard 1975). (2) The labelled material could rapidly have been been removed (mixed down) from the sediment-water interface, where the likelihood of its being ingested probably is highest. Label had certainly been removed from the top 1 cm in the deposit-feeding community, as indicated by the marked decrease in the top 1 cm of the sediment (Fig. 4). This was also statistically supported by using the same ANOVA as in Table 3 with the activity in the top 1 cm as the response variable instead of the whole inventory. The p-value was then 0.05 when testing the MS of community against the MS of the random factor (cosm within communities) at the end of the experiment.

Mixing as opposed to degradation

Added labelled FPD was removed from the sediment surface in several ways. Already early in the incubation, that is 9 h after addition of labelled phytodetritus, a significant portion of label was found below the top layer (Fig. 4) especially in the suspension-feeding community. Differences between D_B in communities in April was greater than variation in the random factor cosms (Table 4) and D_B was higher in the suspension-feeding community. This can partly be explained by the pushing down of material with the corer, but the difference between communities could well result from both passive transportation aided by irrigation or active dragging of the material into the burrow by the ophiuroid *Amphiura filiformis* in the S3 community. The latter mechanism has been described by Rosenberg et al. (1997), who observed that after addition of food material, the ophiuroids immediately became active and dragged the material into the burrows.

Although initially there was a rapid transport of FPD down to ca. 5 cm in the suspension-feeding community, there were over the course of the experiment several indications of a higher and deeper mixing of algal matter into the sediment in the deposit-feeding community: (1) The significantly higher background levels of chl *a*; (2) the higher D_B (based on chl *a* profiles assuming the same constant degradation rate) in the deposit-feeding community; (3) the increase in ^{14}C-activity at depth over the experimental period as indicated by the results of the Wilcoxon test (above) as well as a Student's *t*-test, where each of the 5 samples in each box-cosm were regarded as random samples that showed a highly significant difference of D_B ($p < 0.01$) between the 2 communities. However, testing the MS of communities against the MS of the nested-factor box-cosm within communities with respect to D_B based on activity in June, did not show a significant result ($p = 0.11$: Table 4). This indicates that the variation between box-cosms was of similar magnitude as the variation between communities. A part of the between-cosm variation in D_B in June apparently was due to high values in Box-Cosm No. 2, in which a large portion of label appears deeper than 15 cm in the sediment (Fig. 4). As discussed earlier, this was probably due to a non-local transport event like hoeing caused by the maldanid polychaete *Rhodine loveni*. Local transport of label, that is, downward transportation of surface matter at a lower rate, for instance through defecation on the surface, was evident in all box-cosms from the deposit-feeding community (Fig. 4). It seems, therefore that part of the variation between box-cosms resulted from different mechanisms of subduction, both occurring in the deposit-feeding community.

The chl *a* profiles (Fig.7) and statistical testing of inventories show clearly that the reactive chl *a* pool did not decrease substantially over the experimental period. This suggests a very low degradation rate, most likely far below the 0.03 d^{-1} commonly used in the literature (e.g. Boon & Duineveld 1998). A low degradation rate was also supported by the test of change in total ^{14}C-activity over the period, which did not show a significant result.

The results thus indicate a low overall rate of degradation of chl *a* despite the presence of abundant macrofauna. The macrofauna was apparently active, as evidenced by the significant mixing of labelled matter and observations of feeding activity on the sediment surfaces of the cosms (faecal pellets, mounds, tracks from tentacles etc.). Furthermore, surface deposit feeders had apparently ingested and assimilated a portion of the ^{14}C-labelled material from the sediment surface, and a portion had been transferred to the next trophic level as evidenced by high activity in several predators. The uptake apparently was similar or of greater magnitude than that reported by Widbom & Frithsen (1995) in a similar experiment, who found-weight specific activities ranging from 0.5 to 7 million dpm g^{-1} AFDW after a 5 mo period compared to our data (0.1 to >100: Table 1).

Thus it seems that the initial fate of the added FPD was essentially burial rather than respiration and incorporation into biomass. We estimate that over the 2 mo period may be more than 90% of added label was buried into and left in the sediment rather than being

consumed by the macrofauna. The result of no significant loss of $^{14}CO_2$ may seem unrealistic, but could due to most of the added material being buried more or less intact. Because of the relatively low temperatures (7 to 10°C), impact by other heterotrophs (meiofauna and bacteria) might be low. The low degradation rate of chl *a* in the cosms, of which a major part was present before addition of labelled diatom-C, agrees with the findings of Webb (1993), who found no effect of the surface deposit-feeding bivalve *Macoma balthica* on sedimentary chlorophyll.

The D_B calculated from chl *a* profiles (Fig. 9) is high compared to biodiffusion coefficients reported in the literature. For example, coefficients from ^{234}Th analysis in marine coastal areas typically range between 0.01 and 0.5 $cm^2\ d^{-1}$ (Matisoff 1982, Sun et al. 1991, 1994). The λ constant we used (0.03 d^{-1}) may have been far too high, since there were no detectable losses of chl *a* or label over the course of the experiment. We do not, however, have access to independent estimates of D_B for the investigated area. Using the literature maximum value of D_B (0.5 $cm^2\ d^{-1}$) in Eq. (1), we get ranges for λ of 0.065 to 0.013 for the suspension-feeding community and as low as 0.012 to 0.003 for the deposit-feeding community.

Implications for the fate of the spring bloom

The labelled phytodetritus was added as 1 pulse and allowed to settle on the sediment surface in still water. The addition was made in spring when water temperatures was low, and we used *Skeletonema costatum*, which is a dominant spring-bloom diatom in Scandinavian coastal waters and elsewhere. Therefore, we expected the experiment to mimic a real-post-spring bloom event on the bottom. We do not know, however, exactly how much C was added, nor do we know how much natural-spring bloom material there was in the sediments at the beginning of the experiment. We do know, however, that the added amount, equal between cosms, was enough to cause an equal or greater weight specific activity in fauna than reported earlier in similar experiments (e.g. Widbom & Frithsen 1995). In any case the experiment does show the fate of spring bloom material arriving at these kinds of sediments in April. The sediment profile images showed a significantly deeper depth distribution of the RPD at Stn L18 than at Stn S3. Thus, a deep RPD is associated with high infaunal bioturbation and irrigation activity deep in the sediment, as indicated by the high mixing rates at the former station. The oxic conditions prevailing deep in the sediment also indicate that the annual input of organic material to these environments is assimilated and remineralised. The remineralisation of the buried phytodetritus is probably not associated with anaerobic degradation involving sulphur, as no black sulphidic spots appear in the sediment profile images.

Our findings of rapid burial and initially low degradation rates of the bloom material is in contrast to the findings of Graf et al. (1982), who reported that a great part of the bloom was rapidly respired. They agree, however, with results from several studies: Kanneworff & Christensen (1986) concluded, from benthic respiration measurements, that the bloom remained for several months in the sediments of Øresund, which was attributed to rapid burial into the sediment. Likewise van de Bund et al. (2001) concluded that burial slows mineralization. Also, Hansen & Josefson (2001), in the Øresund, demonstrated that 3 mo after the spring bloom event, a great part of the sediment chlorophyll consisted of live cells of spring bloom diatoms in roughly the same proportions as during the bloom peak. An implication of our results is that the spring phytoplankton bloom, by being rapidly buried, may serve as a food buffer for the benthos over an extended period over the year, rather than being instantly respired.

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