Vol. 105: 291–299, 1994 | MARINE ECOLOGY PROGRESS SERIES Mar. Ecol. Prog. Ser. | Published March 3

Simulated degradation of phytodetritus in deep-sea sediments of the NE Atlantic (47° N, 19° W)

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ABSTRACT: The degradation of phytodetritus in the deep sea was studied in sediment samples of the NE Atlantic in spring and summer 1992 using ^{14}C-labelled algal cells (*Anacystis* sp., Cyanophyceae) fed to the benthic population in ship-board experiments and measuring the liberation of labelled $^{14}CO_2$ over time. The mineralization process showed a 2-step behaviour with an initial rapid rate which later slowed down, indicating the initial attack of easily degradable material of the complex food and the later utilization of less labile matter. The profile of degradation activity with sediment depth showed no clear vertical gradient in March, but in August the activity in the top horizon increased by a factor of 6.1 to 7.8, which was coherent with increased bacterial numbers or biomass (factor of 1.3 to 1.7), respectively, and might be caused by the seasonal input of phytodetritus to the deep-sea bottom. The degradation measured was positively influenced by elevated incubation pressure mostly in summer, indicating that the summer stimulation of microbial activity in 1992 was based on the metabolic activation of the indigenous benthic community, while surface-derived organisms attached to sedimented particles were of lesser importance with respect to consumption of phytodetritus. Several aspects on quality of phytodetritus for nutrition of the deep-sea benthos, seasonality of detritus degradation, and influence of pressure on microbial activity are discussed.

KEY WORDS: Bacteria · Deep-sea · Sediment · Phytodetritus · Barophilism

INTRODUCTION

In the 'ordinary' deep sea the main input of organic matter is provided by the deposition of rapidly sinking 'marine snow', which is composed of coagulated algal remains (phytodetritus) and faecal pellets of grazers (Alldredge & Silver 1988). Approximately 10% of the primary production escapes from the euphotic zone (Angel 1984, Fowler & Knauer 1986), and sinks slowly through the mesopelagial, where it will be be more and more degraded. Only 1% reaches the deep-sea bottom in 4000 to 5000 m depth (Wefer 1989) — compared to up to 50% of the primary production in coastal/shelf areas (Walsh et al. 1981). It was previously assumed that a slow and sparse rain of particulate organic matter (POM) would reach the deep-sea bottom throughout the year (Riley 1964). Investigations during the last decade have altered the concept of slow and constant sedimentation. Studies using sediment traps (Deuser & Ross 1980, Deuser et al. 1981, Honjo 1982) and direct observations (Billett et al. 1983, Lampitt 1985, Rice et al. 1986) indicated a pelago-benthic coupling by fluctuating rates of sinking detritus. In July/August 1988 a mass deposition of phytodetritus was sampled for the first time from a mid-oceanic site in the NE Atlantic at the BIOTRANS station (47° N, 19° W). The 'fluff' covered the bottom with 70 to 390 mg C m^{-2} (Thiel et al. 1988/89) — which seems to be high compared to a total POC deposition of 1 g C m^{-2} yr^{-1} (Honjo & Maganini 1993). Studies at the same station in April/May 1988 showed that faecal pellets of salps also function as vehicles for the vertical flux (Pfannkuche & Lochte 1993), but due to its greater quantity phytodetritus seems to be the most important food source at this locality.

Investigations on pelago-benthic coupling in the open ocean have shown many kinds of responses: increasing biochemical activity (Graf 1989, Pfannkuche 1992, 1993), enhanced oxygen consumption of the sediment community (Pfannkuche 1993), stimulated feeding activity (Billett et al. 1983, Gooday 1988, Lochte & Turley 1988, Turley et al. 1988, Gooday &

Turley 1990), and increased bacterial biomass (Lochte 1992). Unfortunately, investigations on bacterial activity have been performed in different years and with different methods, which makes a comparison very difficult.

Several experiments on the response of deep-sea microorganisms on supplementation of organic material had been performed (Altenbach 1992, Meyer-Reil & Köster 1992). While the traditional ways to study microbial activity use artificial food and single labelled substances, which might not be a very representative food source in nature, Lochte & Turley (1988) fed the samples with original phytodetritus. They sampled 'fluff', added it to water of the sediment contact zone of the NE Atlantic, and measured the disappearance of total organic carbon in ship-board incubations. At the same locality Turley & Lochte (1990) fed samples with artificial phytodetritus, and in further studies Lochte (1992) tested the simulation of phytodetritus using ^{14}C-labelled microalgae (*Anacystis* sp., Cyanophyceae). The degradation rates obtained from these investigations were similar, and it can be assumed that intact labelled algae are an appropriate marker for studying the microbial attack of phytodetritus in the deep sea. The present paper presents results of investigations on the degradation of labelled microalgae at the bottom of the NE Atlantic, where this matter should be the most relevant food source for the benthic population. In contrast to previous studies, the samples were taken in the same year (March and August 1992), which allowed the direct comparison of activity in spring and summer and the detection of a seasonally shifting activity.

Moreover, due to pulses of sedimentation it can be expected that the benthic microbial summer population is made up of a greater number of organisms which derive from upper water layers as compared to the spring population. It is likely that indigenous deep-sea organisms show higher activity in experiments performed under *in situ* pressure conditions, while surface-derived bacteria should possess no preference for elevated pressure. We tested to see if the benthic community of the BIOTRANS station would change its range of preferred pressure during the year, because a possible shift should show which of the 2 populations plays a greater role in the degradation of phytodetritus.

MATERIAL AND METHODS

Sampling site and ship-board handling. During the 'Meteor' cruises 21-1 (16 March to 9 April 1992) and 21-6 (26 July to 31 August 1992) sediment samples were taken in the NE Atlantic (BIOTRANS station, 47° 16' N, 19° 35' W, depth 4550 m). The area was marked by 4 transponders (Oceanus, France) enabling controlled sampling in the same 20 × 20 m field both in March and in August. Samples were taken by a multiple corer (Barnett et al. 1984) equipped with 12 plastic tubes (5.5 cm diameter, 50 cm length), which enabled sampling of undisturbed cores. On board, the cores were immediately transferred into a 2°C (*in situ* temperature) cooled experimental container and processed for experiments in order to minimize temperature changes in the samples. During each cruise 2 experiments were performed.

Experimental procedure. The respiratoric remineralization of ^{14}C-labelled algae (*Anacystis* sp., Cyanophyceae, Amersham-Buchler, specific activity 1.96 GBq $mmol^{-1}$ C) was studied according to the method of Lochte (1992). From the 0 to 1 cm, 4 to 5 cm, and 9 to 10 cm horizons, respectively, 200 cm^3 of sediment were pooled and diluted by an equal amount of seawater. After dispensing aliquots of 10 cm^3 in presterilized polyethylene bags, the slurry was supplemented with 1 µCi (= 18.88 nmol C) of labelled algae, and incubated (2 to 4 °C). Parallel samples were incubated at different pressures (1, 150, 300, 460 atm) using pressure cylinders (Wuttke, Hamburg, Germany) and a hydrostatic pressure pump (Hotec GmbH, Remlingen, Germany). Pressurization and depressurization rates were ca 100 atm min^{-1}. The incubations were terminated after 0 (control), 3, 6, 12, 24 and 48 h by shock freezing.

Determination of liberated $^{14}CO_2$. The frozen bags were thawed and 2 subsamples of 3 ml were pipetted from each bag into centrifuge tubes. To these subsamples 6 ml 0.5 N NaOH was added, mixed, and centrifuged [2 °C, 5000 rpm (5530 × *g*), 10 min]. From the supernatant 7 ml was transferred to glass bottles containing CO_2 vials (a mini-vial with a filter paper and 250 µl ethanolamine). The glass bottles were closed by a septum and 1 ml 5 N HCl was injected through the septum. Released CO_2 was immediately bound by the ethanolamine. After 24 h shaking, the CO_2 vials were removed, supplemented with 250 µl ethanol and 5 ml scintillation cocktail (Ultima Gold, Packard), and measured in a Packard Tricarb LSC-counter. The recovery efficiency run with sediment supplemented with $NaH^{14}CO_3$ was between 72 and 77%. The remineralization of algae was calculated from the release of $^{14}CO_2$, recovery efficiency and specific activity of the algal material. The counts per minute (or the amount of liberated CO_2 determined by a calibration test) were plotted against the incubation time. The curve of $^{14}CO_2$ liberation showed a rapid initial phase and a later slower increase. The initial activity (v_1) was calculated by linear regression of the values from 0 to 12 h and the later activity (v_2) by linear regression of the values from 12 to 48 h. In order to relate the measurements

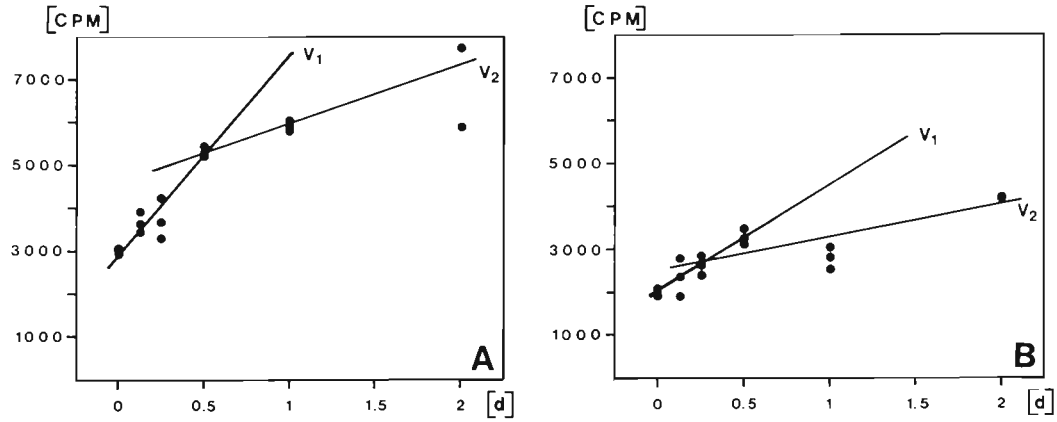

Fig. 1. Time course of ^{14}C-algae degradation measured as liberated $^{14}CO_2$ in the (A) 0 to 1 cm and (B) 4 to 5 cm horizon of deep-sea sediment of the NE Atlantic (19° N, 47° W, March 1992, incubation pressure: 1 atm). An initial rapid phase (v_1) was distinguished from a later slower activity (v_2). The regressions and correlations are (A) $y_1 = 3063 + 4636\,x_1$, $r^2 = 0.987$ and $y_2 = 3492 + 1588\,x_2$, $r^2 = 0.732$ for the 0 to 1 cm horizon, and (B) $y_1 = 2874 + 7705\,x_1$, $r^2 = 0.907$ and $y_2 = 3097 + 2289\,x_2$, $r^2 = 0.636$ for the 4 to 5 cm horizon

obtained from the slurry back to the undiluted sediment, dry weight of slurry and original sediment were determined.

Bacterial counts. Samples for microscopic counts of the total bacterial number (TBN) of the sediment were taken with 3 syringe subcores (diameter: 1.25 cm) from 0 to 10 cm subsurface. The subcore was sectioned in 1 cm horizons. Each horizon was diluted immediately up to 10^{-1} in pre-filtered (0.2 µm) seawater supplemented with formalin (4% final concentration) and stored cool and dark for later analysis. In the laboratory the samples were diluted in filtered distilled water up to 10^{-2}, ultrasonicated for 5 s to separate bacteria from sediment particles, and diluted further up to 10^{-4}. An appropriate volume of 2 to 5 ml was filtered onto a 0.2 µm Nuclepore polycarbonate membrane, stained for 3 min with 0.1% acridine orange (Zimmermann & Meyer-Reil 1974, Daley & Hobbie 1975), washed with citrate buffer (0.056 M Na-Citrate, 0.056 M NaOH, 0.044 M HCl, pH 4) and counted with an epifluorescence microscope. The cell volumes of 50 cells per sample were measured using a graticule grid (New Porton, Tonbridge, UK). From the mean cell volume bacterial biomass was calculated using the conversion factor 0.106 pg C μm^{-3} (Nagata 1989). This factor was choosen because of its conservative character and the lack of verified factors, valid for deep-sea bacteria.

RESULTS

The biological liberation of CO_2 by deep-sea sediment bacteria was simulated by ^{14}C-labelled cyanophyceae (*Anacystis* sp.) in ship-board feeding experiments simulating the degradation of phytodetritus. Three different horizons of sediment cores were tested and measurable activity was found down to 10 cm. The activity rates in August significantly declined with depth of sediment indicating a vertically stratified profile in summer.

The liberation of CO_2 typically showed an initial phase (0 to 12 h) of rapid $^{14}CO_2$-production followed by slower release of $^{14}CO_2$ during the period from 12 to 48 h (Fig. 1). For calculating activity rates, rapid and slow degradation were distinguished (v_1 and v_2 in Fig. 1). The rates of the 2 degradation periods were significantly different in the upper horizons (0 to 1 cm layer: v_1 greater than v_2 by a mean factor of 2.9 to 4.4; in 4 to 5 cm: factor of 1.8 to 4.1) but not in the 9 to 10 cm horizon (factor of 1.2 to 2.1). This was caused by the stronger decline of v_1 with increasing depth compared to v_2 (Table 1).

Measurements were performed in March and August 1992 enabling the comparison of a spring and a summer situation. The maximal activity in March was localized in the 4 to 5 cm horizon, while in August the activity increased in the 0 to 1 cm horizon by factors of 0.5 to 1.4 (v_1) and 6.1 to 7.8 (v_2), producing a sharp depth gradient (Fig. 2). The summer activities in the deeper layers showed a nearly unchanged or even decreasing behaviour (v_1: factor of 0.2 to 0.4; v_2: factor of 0.4 to 1.1).

Degradation rates were also measured under various incubation pressures, and the results reflect the influence of this parameter on microbial activity in deep-sea samples (Table 1). Due to the small number of subsamples and low regression coefficients of some incubation series, only tendencies of pressure preferences can be described. The lowest value was determined in the 9 to 10 cm horizon incubated at 1 atm for

Table 1. Degradation rates (pmol C ml^{-1} h^{-1}, ± SD) for ^{14}C-labelled algae in deep-sea sediment under different incubation pressures, r^2, numbers of subsamples (n) and turnover time (d)

Horizon		Pressure (atm) 1	150	300	460
Initial rapid phase v_1 (0 to 12 h)					
March 1992					
0–1 cm	Degradation rate	63.4 ± 2.9	67.3 ± 8.0	100.0 ± 7.1	78.4 ± 3.5
	(r^2, n)	(0.987, 7)	(0.922, 6)	(0.970, 8)	(0.988, 6)
	Turnover time	30	28	19	24
4–5 cm	Degradation rate	207.3 ± 27.2	175.9 ± 24.0	183.3 ± 19.8	110.8 ± 16.7
	(r^2, n)	(0.907, 8)	(0.899, 8)	(0.935, 8)	(0.880, 8)
	Turnover time	9	11	10	17
9–10 cm	Degradation rate	37.1 ± 12.0	67.8 ± 9.3	70.9 ± 20.6	78.5 ± 13.5
	(r^2, n)	(0.615, 8)	(0.898, 8)	(0.664, 8)	(0.849, 8)
	Turnover time	51	28	27	24
August 1992					
0–1 cm	Degradation rate	109.9 ± 21.4	83.7 ± 24.8	41.7 ± 48.4	75.4 ± 41.2
	(r^2, n)	(0.868, 6)	(0.316, 6)	(0.156, 5)	(0.456, 6)
	Turnover time	17	23	45	25
4–5 cm	Degradation rate	25.0 ± 18.1	10.2 ± 7.5	27.2 ± 33.6	29.8 ± 21.7
	(r^2, n)	(0.324, 6)	(0.316, 6)	(0.140, 6)	(0.321, 5)
	Turnover time	75	185	70	63
9–10 cm	Degradation rate	0.14 ± 7.1	20.1 ± 15.8	29.0 ± 13.4	18.3 ± 15.5
	(r^2, n)	(0.001, 6)	(0.288, 6)	(0.537, 6)	(0.259, 5)
	Turnover time	613	94	65	102
Later slow phase v_2 (12 to 48 h)					
March 1992					
0–1 cm	Degradation rate	21.7 ± 4.2	10.6 ± 6.2	17.1 ± 11.0	17.8 ± 1.3
	(r^2, n)	(0.732, 11)	(0.413, 9)	(0.291, 11)	(0.946, 10)
	Turnover time	87	116	84	107
4–5 cm	Degradation rate	61.6 ± 14.7	59.7 ± 7.1	45.1 ± 15.3	60.6 ± 7.5
	(r^2, n)	(0.636, 11)	(0.875, 11)	(0.466, 12)	(0.867, 12)
	Turnover time	31	32	42	31
9–10 cm	Degradation rate	31.5 ± 7.4	41.6 ± 6.8	34.0 ± 3.7	48.3 ± 10.4
	(r^2, n)	(0.642, 11)	(0.787, 11)	(0.894, 11)	(0.681, 11)
	Turnover time	61	45	55	39
August 1992					
0–1 cm	Degradation rate	34.0 ± 27.2	35.4 ± 24.8	212.9 ± 69.5	125.1 ± 24.6
	(r^2, n)	(0.280, 6)	(0.339, 6)	(0.701, 6)	(0.866, 6)
	Turnover time	56	53	9	15
4–5 cm	Degradation rate	32.3 ± 23.0	72.8 ± 12.6	91.4 ± 13.3	24.9 ± 9.1
	(r^2, n)	(0.330, 6)	(0.892, 6)	(0.922, 6)	(0.650, 6)
	Turnover time	58	26	21	76
9–10 cm	Degradation rate	20.0 ± 10.8	34.8 ± 6.8	81.4 ± 15.1	49.9 ± 13.9
	(r^2, n)	(0.461, 6)	(0.868, 6)	(0.878, 6)	(0.762, 6)
	Turnover time	95	54	23	38

v_1 (0.5% activity of the highest rate of this series). Because the activities found in the surface layer raised in summer, especially in incubation series of elevated pressure, the range of preferred pressure of the top horizon shifted toward *in situ* conditions. For example, for v_2 (which should be the activity rate of greater ecological relevance than v_1; see 'Discussion') the highest summer rates were found at 300 or 460 atm, while in March no optimum was found. No further significant optimal pressure conditions were found when comparing activity rates in other horizons.

The bacterial abundance increased in the top 5 cm of the sediment between March and August (Table 2). Summarized over 10 cm sediment depth, the cell number increased in summer by a factor of 1.3 and the biomass by a factor of 1.2.

DISCUSSION

Quality of phytodetritus for nutrition of deep-sea benthos

Possibly the most important limiting factor in deep-sea environments for heterotrophic life is the availability of degradable matter (Gage & Tyler 1991). Except for the oases of hot vents or cold seeps, all production at the deep-sea bed is fuelled by the sedimentation of detrital matter derived from the euphotic zone. Recent investigations on the quantification of this processes in the temperate NE Atlantic indicated a seasonally pulsed mass sedimentation of phytodetritus with a maximum in late July, about 6 wk after the spring algal bloom (Rice et al. 1986, Thiel et al. 1988/89, Pfannkuche 1993). The sedimentation of particulate matter during the rest of the year is presumably small and sparse. Occasional depositions are given also through the rapid sinking of faecal pellets from swarm-building salps, but their absolute amount is much lower than the carbon deposition in summer (Pfannkuche & Lochte 1993). This supports the theory of a pelago-benthic coupling in the open ocean mediated by phytodetritus as dominant factor.

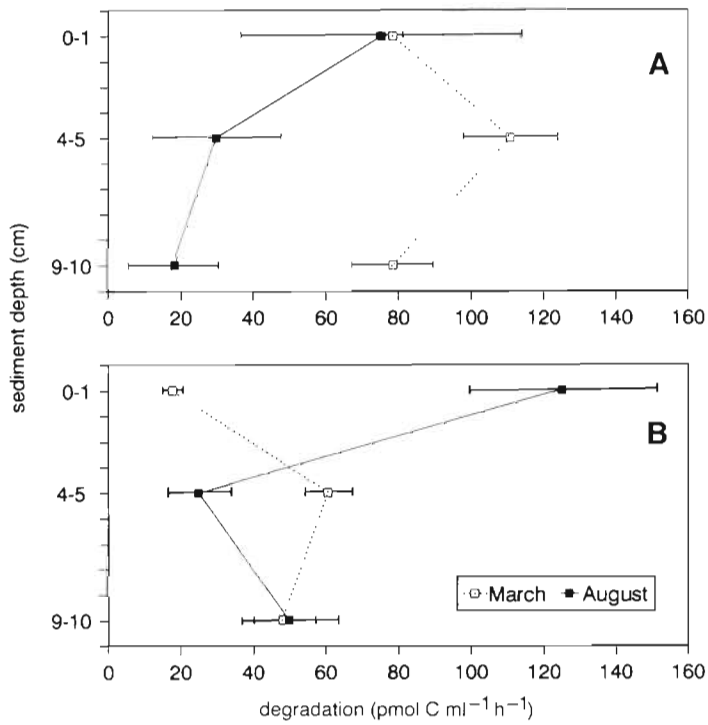

Fig. 2. Degradation rate (± SD) in deep-sea sediment using ^{14}C-labelled algae in March and August 1992; incubation pressure: 460 atm. The initial rapid activity v_1 (A) was distinguished from the second slow phase v_2 (B). The total amount of added carbon was 1880 pmol C ml^{-1} Each experiment was carried out twice

Table 2. Microbial abundance (± SD) in sediment of the BIOTRANS area in April (n = 2) and August (n = 3)

	Sediment depth (cm)	Total bacterial number (× 10^9 cells cm^{-3})	Mean cell volume (µm^{-3})	Bacterial biomass (mg C cm^{-3})
March 1992	0–1	3.55 ± 1.86	0.0390	0.0147 ± 0.008
	1–2	5.79 ± 2.26	0.0365	0.0224 ± 0.008
	2–3	4.41 ± 0.79	0.0500	0.0219 ± 0.004
	3–4	4.83 ± 1.87	0.0382	0.0196 ± 0.008
	4–5	2.46 ± 1.90	0.0479	0.0125 ± 0.010
	5–6	4.43 ± 3.59	0.0342	0.0160 ± 0.013
	6–7	3.75 ± 2.89	0.0304	0.0121 ± 0.009
	7–8	4.43 ± 2.73	0.0247	0.0116 ± 0.007
	8–9	5.19 ± 3.29	0.0308	0.0169 ± 0.011
	9–10	3.41 ± 1.36	0.0386	0.0139 ± 0.006
	0–10	4.1952 × 10^{14} cells 10 cm^{-1} m^{-2}		1.62 ± 0.84 g C 10 cm^{-1} m^{-2}
August 1992	0–1	5.62 ± 3.29	0.0375	0.0223 ± 0.012
	1–2	8.57 ± 4.43	0.0420	0.0382 ± 0.019
	2–3	6.85 ± 5.21	0.0325	0.0236 ± 0.018
	3–4	7.87 ± 4.73	0.0349	0.0291 ± 0.018
	4–5	8.98 ± 5.53	0.0287	0.0273 ± 0.017
	5–6	3.01 ± 1.96	0.0319	0.0102 ± 0.007
	6–7	3.87 ± 2.85	0.0282	0.0116 ± 0.008
	7–8	4.49 ± 2.77	0.0400	0.0190 ± 0.012
	8–9	3.03 ± 1.95	0.0345	0.0111 ± 0.007
	9–10	1.93 ± 0.72	0.0193	0.0039 ± 0.002
	0–10	5.4217 × 10^{14} cells 10 cm^{-1} m^{-2}		1.96 ± 1.2 g C 10 cm^{-1} m^{-2}

In this study, a method to simulate phytodetritus and its mineralization was applied using ^{14}C-labelled microalgae as food source in ship-board experiments. The labelled algae were added to sediment suspensions although this approach might be susceptible to a number of experimental artifacts. Preparations of slurries could destroy the fine structure of the microenvironment, as well as microbial aggregates and particle-bound biofilms (Hall et al. 1972, Meyer-Reil 1978, 1986, Novitsky 1983). Therefore some authors preferred the core-injection technique (Meyer-Reil 1986), which might be appropriate for water-soluble diffusable substrates but not for particulate algae cells, which should be the more typical food source in the deep sea.

Incubations of deep-sea sediment samples fed with this substrate showed a 2-step kinetic of respiration of algal detritus. These findings are similar to the observation of Lochte (1992), and were expected to be caused by the initial attack on easily degradable compounds of the complex biological material (e.g. monomeric and oligomeric substances), and a later degradation of less labile components (e.g. macromolecules). Also Westrich & Berner (1984) showed that natural planktonic material can be divided into fractions of distinctly different biological lability, decomposability, and reactivity, and therefore different degradation rates in marine sediments can be calculated by first-order kinetic analysis.

It is likely that natural phytodetritus just deposited at the deep-sea bottom lacks easily degradable monomers, because these should be consumed during the approximately 6 wk sinking to the sea floor. Investigations on the microflora settled on phytodetritus showed that fluff particles of near-surface water (Caron et al. 1982, Prezelin & Alldredge 1983, Alldredge et al. 1986, Davoll & Silver 1986) and deep-sea samples (Silver & Alldredge 1981, Alldredge & Youngbluth 1985, Thiel et al. 1988/89) harbour numerous microorganisms which include bacteria, algae and protozoa and commonly occur in concentrations 2 to 5 orders of magnitude higher than in the surrounding water. The attachment seems to stimulate biological activity, as associated bacteria possess strong extracellular enzymatic activity (Amy et al. 1987, Smith et al. 1992, Hoppe et al. 1993) and have been identified as local 'hot spots' of metabolic activity (Alldredge & Silver 1988). This suggests that easily degradable compounds of algal material should be largely utilized/respired, whereas more refractile algal materials mainly reach the deep-sea bed. Applying these considerations to the results of our experiments, the degradation rates for the more refractory residual compounds measured between 12 and 48 h would be more relevant for the description and comparison of deep-sea mineralization rates. It can be assumed that the rate of CO_2 release would have declined further during the period after 48 h, and that this period would also possess more relevance for deep-sea ecology. On the other hand, results from prolonged incubations would not reflect as much initial events of mineralization of pulses of sedimented materials in the deep-sea environment.

Despite possible artifacts derived from the decompression of the material during the sampling or the destruction of the sediment's fine structure through the experimental preparation of slurries, some assumptions of the C consumption may be made: linear integration of respiration rates from 0 to 10 cm results in a respiration rate of 1.33 ± 0.2 mg C m^{-2} d^{-1} in March and 1.65 mg $\pm$ 0.42 mg C m^{-2} d^{-1} in August. The difference between March and August is not significant because the summer activity increased only in the uppermost horizon while it decreased in deeper layers. Assuming the efficiency with which detrital organic carbon was converted into bacterial biomass as 10% (as suggested by Turley & Lochte 1990), the total carbon consumption accounts for 1.46 ± 0.22 mg C m^{-2} d^{-1} in March and 1.82 ± 0.46 mg C m^{-2} d^{-1} in August. Pfannkuche (1993) assumed, on the basis of his *in situ* respirometer measurements, a deposition of 4.4 to 9.3 mg C m^{-2} d^{-1}. But the comparison of these 2 measurements is difficult, because Pfannkuche's *in situ* oxygen consumption data were obtained from unfed sediment communities, while the values presented here derive from laboratory experiments on a fed community.

Vertical and seasonal aspects of phytodetritus degradation

The degradation assays were performed with samples of the surface horizon down to 10 cm sediment depth. Microbial activity was detected in all layers, and the values decreased with depth as expected. Mineralization rates varied between 0.2 to 11% d^{-1} (v_1) and 0.9 to 11% d^{-1} (v_2) of the total added organic carbon. A possible stimulation of activity caused by the food supply can not be excluded, because the supplemented fresh food might be more labile than material commonly found in the sediment. Any assay using added labelled substrate will be confronted with this problem. But an artificial stimulation of activity should be limited to the first hours of the experiment, and by the quantitatively insignificant fraction of the added material compared to the total organic carbon in this sediment.

The vertical profiles of activity found in different seasons vary in that in August the maximal respiration

was found at the top horizon, while in March the highest activity was found in the intermediate layer (4 to 5 cm). Following the theory of a seasonally pulsed POM deposition in the deep sea and a simultaneously shifting microbial activity (e.g. Graf 1989, Lochte 1992, Pfannkuche 1992), the summer peak at the sediment's surface should be a reaction to the presence and availability of freshly deposited POM, which had supported a microbial activity 6.1- to 7.8-fold higher than the March level. Graf has shown a similar increase in ATP concentration sediment cores of the shallow 'Hausgarten' area in the Baltic Sea (Graf 1987) and the Norwegian continental margin at 1430 m depth (Graf 1989). He described rapid uptake of chlorophyll *a* into the sediment due to bioturbation, lag times of 8 d for benthic response to food pulses, and vertical profiles of heat production indicating metabolic activity down to approximately 8 cm depth. In the study presented here, such a deep-reaching effect was not observed.

The increased activity in summer was coherent with the higher bacterial numbers at this time (Table 2) compared to March. In March a very small vertical gradient of both parameters was found, while in August the seasonal effect was located in the upper 5 cm of the profile, where the cell numbers increased by nearly 2 times in some layers. In horizons deeper than 5 cm no stimulation could be detected. Martin & Bender (1988) concluded on their modeling studies that most sedimenting material would be buried too slowly to produce seasonal signals of seasonal decomposition pulses in the sediment column. The relatively small or missing shift of bacterial biomass and mineralization rate in deep layers of the sediment found in the present study supports this thesis, and indicates that only the sediment surface is affected by environmental variations as seasonal sedimenting events, and therefore plays the dominant role in benthic metabolism.

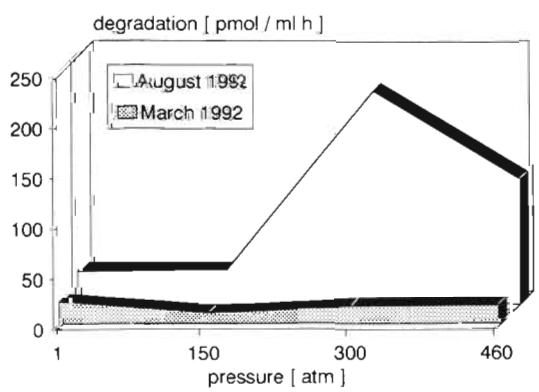

Fig. 3. Influence of incubation pressure on algae degradation by the benthic community of the surface horizon. No significant pressure preference was found in March, while the values in August were significantly higher under elevated pressure

Moreover, the mean cell volume of the sediment bacteria found here is surprising, because in shallow-situated sediments the bacterial cell volume is mostly greater than in the water column. Similar low values of deep-sea sediment bacteria were reported also from Lochte & Rheinheimer (1990). Maybe a reduced cell size is an adaption of the organisms to the sparse nutrition supply of this environment.

Effect of pressure on phytodetritus degradation

The effects of pressure on microorganisms in general and on deep-sea bacteria in particular are multiple and not sufficiently understood. While only a small number of viable obligate barophilic organisms have been found (e.g. Dietz & Yayanos 1978, Yayanos et al. 1979, 1982, Deming et al. 1981, Turley et al. 1988) several reports on the barophilic behaviour of a whole microbial community have been published in recent years (e.g. Deming & Colwell 1985, Lochte & Turley 1988, Turley & Lochte 1990, de Angelis et al. 1991, Lochte 1992). In the present study, the samples were incubated under different pressures ranging from surface (1 atm) to *in situ* condition of 460 atm (Table 1). A comparison of the activities in the different layers showed that a significant influence of pressure on activity could be detected mostly with the v_2 values in summer, while the v_2 rates in March were not affected by the pressure conditions during the incubation (Fig. 3). Moreover, the summer values in 1 atm series were only 1.6× higher than in March, while at 460 atm a 7.0-fold seasonal increase was observed. A possible explanation is that barophilic indigenous organisms benefit more from the seasonal food supply than bacteria which originate from upper water layers. Pfannkuche (1992, 1993) assumed that the carbon utilization of microorganisms within the freshly settled phytodetritus would account for 60 to 80% of the summer increase of the total benthic carbon consumption. Although it is not clear how much cells were damaged during the sampling process in 1992 or if the original benthic population and the organisms attached to settled particles can sufficiently be distinguished by their baroresponse, the benthic community's seasonal shift from barotolerance to barophilism provides evidence that the indigenous population in 1992 was more important for the utilization of phytodetritus than surface-derived organisms.

Acknowledgements. Thanks to the crew of the RV 'Meteor' and all the scientific staff for their helpful support. I especially thank K. Lochte for acquainting me with the assay of respiratoric algae degradation in sediment samples and K. Jeskulke for skillful technical assistance. The manuscript benefited

from the comments by G. Graf, H.-G. Hoppe, K. Lochte, B. Karrasch, W. Koeve, and 2 anonymous reviewers. This work was supported by grant MUF 03F0565A from the Bundesministerium für Forschung und Technik, Germany. This is BIOTRANS publication no. 33.

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This article was presented by G. Rheinheimer, Kiel, Germany

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Manuscript first received: June 5, 1993
Revised version accepted: November 12, 1993