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Phytodetritus on the Deep-Sea Floor in a Central Oceanic Region of the Northeast Atlantic

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Abstract *In a midoceanic region of the northeast Atlantic, patches of freshly deposited phytodetritus were discovered on the sea floor at a 4500 m depth in July/August 1986. The color of phytodetritus was variable and was obviously related to the degree of degradation. Microscopic analyses showed the presence of planktonic organisms from the euphotic zone, e.g., cyanobacteria, small chlorophytes, diatoms, coccolithophorids, silicoflagellates, dinoflagellates, tintinnids, radiolarians, and foraminifers. Additionally, crustacean exuviae and a great number of small fecal pellets, "minipellets," were found. Although bacteria were abundant in phytodetritus, their number was not as high as in the sediment. Phytodetrital aggregates also contained a considerable number of benthic organisms such as nematodes and special assemblages of benthic foraminifers. Pigment analyses and the high content of particulate organic carbon indicated that the phytodetritus was relatively undegraded. Concentrations of proteins, carbohydrates, chloroplastic pigments, total adenylates, and bacteria were found to be significantly higher in sediment surface samples when phytodetritus was present than in equivalent samples collected at the same stations in early spring prior to phytodetritus deposition. Only the electron transport system activity showed no significant difference between the two sets of samples, which may be caused by physiological stress during sampling (decompression, warming). The chemical data of phytodetritus samples displayed a great variability indicative of the heterogeneous nature of the detrital material. The gut contents of various megafauna (holothurians, asteroids, sipunculids, and actiniarians) included phytodetritus showing that the detrital material is utilized as a food source by a wide range of benthic organisms. Our data suggest that the detrital material is partly rapidly consumed and remineralized at the sediment surface and partly incorporated into the sediment. Incubations of phytodetritus under simulated in situ conditions and determination of the biological oxygen demand under surface water conditions showed that part of its organic matter can be biologically utilized. Based on the measured standing stock of phytodetritus, it is estimated that 0.3–3% of spring primary production sedimented to the deep-sea floor. Modes of aggregate formation in the surface waters, their sedimentation, and distribution on the seabed are discussed.*

Keywords Phytodetritus, aggregates, bacteria, benthos, cyanobacteria, deep-sea, marine snow.

Introduction

Food resources for deep-sea organisms have been discussed for more than a century, with the predominating view, until recently, that the ocean floor received a slow and sparse rain of particulate organic matter (POM) (e.g., Riley et al., 1964). A decade ago sediment trap studies provided the first indications for a faster transport and for seasonal fluctuations of POM (e.g., Deuser and Ross, 1980). Additionally, these observations pointed to the occurrence of aggregated particulate matter similar to that observed by divers in ocean surface waters (for review see Alldredge and Silver, 1988).

Large amounts of phytodetritus were first observed on the deep-sea floor at water depths of 1370–4100 m in the Porcupine Seabight by Billett et al. (1983), and further studies in this area indicated that these deposits occurred seasonally from May to August due to sedimentation from the euphotic zone (Lampitt, 1985; Rice et al., 1986). This locality, situated to the southwest of Ireland, is a deep indentation into the continental shelf and is characterized by the interaction of different water masses generating frontal systems in the surface waters. These fronts are generally associated with high phytoplankton abundances (Pingree et al., 1978; Holligan, 1981), which raises the possibility

BIOTRANS publication number 16.

that mass deposition of phytodetritus develops under special hydrographic conditions and may not occur in oceanic regions away from the shelf break.

In our investigations, phytodetritus was found for the first time in a midoceanic region of the northeast Atlantic during July and August 1986. We describe its distribution on the sea floor and its general chemical and biological characteristics. Although this material contained a high proportion of zoogenic detritus, we have maintained the term *phytodetritus* as in earlier publications by other authors.

Materials and Methods

The Study Area

Meteor cruise 3, July 21–August 18, 1986, was part of the program BIOTRANS (*bio*logical vertical *trans*port and energetics in the benthic boundary layer of the deep sea). This long-term project aims to understand biological processes in the deep sea through intensive and repeated sampling, including in situ measurements. The BIOTRANS study area is situated in the northeast Atlantic at 47°–47°30′ N and 19°–20° W) (Fig. 1), and it covers an area of 30 × 60 nautical miles with water depths ranging from 3800–4590 m. Samples selected for this report (Table 1) were taken predominantly at four stations

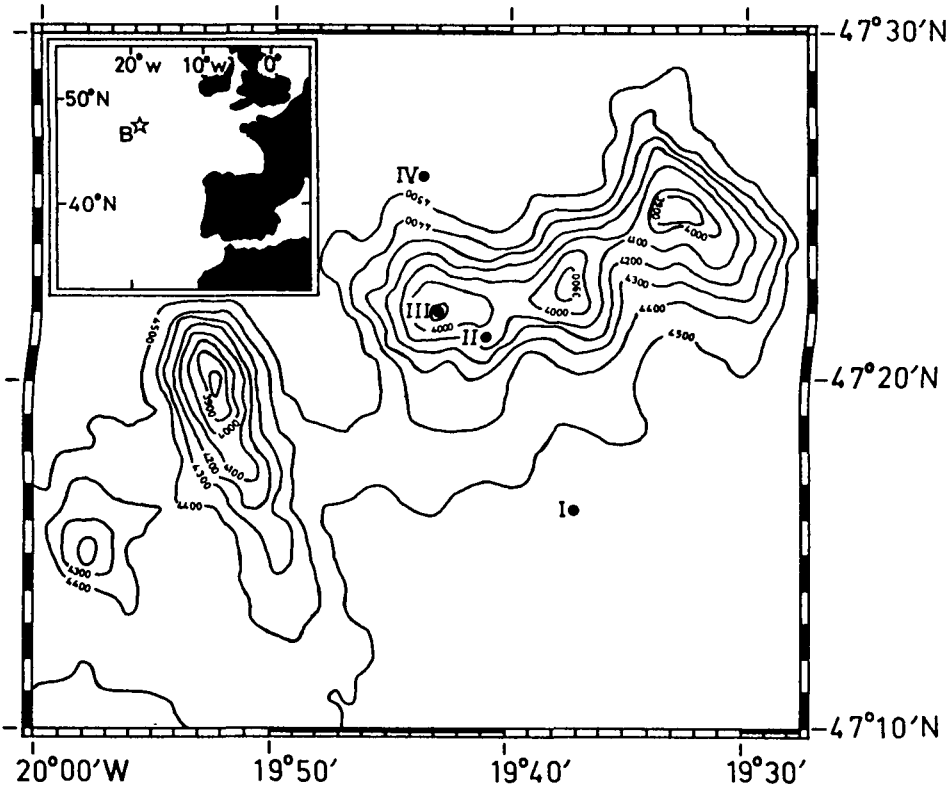

Figure 1. *Map of the investigated area showing the four standard stations (I, II, III, IV) along a* transect crossing the western peak of the deep-sea mountain "Großer Dreizack." Inset: Northeastern Atlantic with B = BIOTRANS area.

Table 1
List of Sampling Stations, Geographical Positions, and Depths

	Date of sampling	Position		Depth (m)
		°N	°W	
Multiple corer no.				
11	06/3/85	47°17.5′	19°38.9′	4540
12	09/3/85	47°05.6′	19°12.8′	4570
15	15/3/85	47°25.7′	19°42.1′	4520
19	23/3/85	47°17.0′	19°45.1′	4480
44	28/7/86	47°26.20′	19°43.08′	4542
45	28/7/86	47°26.33′	19°42.99′	4554
48	02/8/86	47°25.42′	19°42.05′	4551
52	04/8/86	47°20.50′	19°43.40′	4157
56	07/8/86	47°24.71′	19°39.91′	4536
57	07/8/86	47°25.35′	19°39.46′	4508
60	08/8/86	47°24.95′	19°48.21′	4564
63	10/8/86	47°15.16′	19°57.38′	4179
66	12/8/86	47°24.19′	19°46.46′	4546
68	14/8/86	47°26.28′	19°57.02′	4549
Box corer no.				
1138	10/8/86	47°15.31′	19°57.46′	4210
Fotosledge no.				
87	01/8/86	47°30.50′	19°24.40′	4587

along a standard transect crossing one of the three peaks of a seamount called "Großer Dreizack" (Fig. 1) (Heinrich, 1986).

Sampling

Sampling was primarily conducted with a multiple corer (MC) (Barnett et al., 1984), which had already proved suitable for the collection of phytodetritus (Billett et al., 1983; Rice et al., 1986), and to a lesser extent with a box corer. Phytodetritus was removed from the surface of the sediment with wide-mouthed pipettes. For bacteriological samples, sterilized equipment was used. Phytodetritus was found on top of box cores only in small amounts in the form of small gelatinous lumps or loose material entangled on protruding polychaete tubes or other obstacles. The smaller amounts of detritus material in box cores compared to multiple corer samples demonstrate that the bow wave of a box corer, despite an optimized flow of water before and during sediment penetration, still washes away loose, light material.

Benthos standard cameras were mounted on a photo sledge (Thiel, 1970) and on a modified version of the Institute of Oceanographic Sciences epibenthic sledge (Aldred et al., 1976). They were towed at 2 knots and took six photographs per minute. Some larger specimens caught with the bottom net of the epibenthic sledge were analyzed for gut content. Mounted above this bottom net was a 300 μm mesh suprabenthic net, which became clogged by phytodetritus on several occasions. Plankton was collected with a

multiple opening-closing net (Weikert and John, 1981) equipped with nets of 100 μm and 300 μm mesh sizes.

Microscopy

Permanent microscopic glycerine mounts were prepared directly on board. Samples for TEM and SEM were fixed and prepared according to Hemleben et al. (1988), the SEM samples being air-dried, coated with an alloy of Au/Pd, and viewed with a Cambridge Stereoscan 250.

Bacterial and cyanobacterial numbers were determined in samples preserved in 2% buffered, particle-free formalin. They were ultrasonified twice for 5 seconds to disperse detrital clumps prior to counting.

Cyanobacteria were either examined on board by epifluorescence microscopy or the samples were stored in the dark at 5 °C and were counted within 9 weeks after collection. The intense orange-red autofluorescence of the cyanobacterial phycoerythrin (Johnson and Sieburth, 1979) in these deep-sea samples was found to be stable for 14 weeks when stored under these conditions. Autofluorescence was detected using green excitation at a final magnification of $\times 1562$. The mean cell volume of cyanobacteria was determined by classifying >200 cells from one sample into three size classes. Since cyanobacterial cell size was very uniform, this mean cell volume was applied for all samples. Biomass was calculated from total cell numbers, mean cell volume, and a volume to biomass relationship of 0.11 pg C per μm^{-3} (Strathmann, 1967).

Bacterial numbers were determined by the Acridine Orange epifluorescence direct counting technique of Daley and Hobbie (1975), Jones and Simon (1975), and Hobbie et al. (1977). Cell volumes were determined from photographs of the microscopic preparations (Lochte and Pfannkuche, 1987) and carbon was estimated from the biovolumes using a conversion factor of 0.106 pg C μm^{-3} (Nagata, 1986). Comparisons between autofluorescent and nonpigmented bacteria were made on samples stained with 4'6-diamidino-2-phenylindole (DAPI) by viewing them under green excitation (515–560 nm) for autofluorescence of cyanobacteria (orange-red fluorescence) and subsequently under ultraviolet excitation (340–380 nm) for DAPI-stained nonpigmented bacteria (blue fluorescence). Color photographs (see Figs. 12, 13) of these preparations were taken with Kodak Ectachrome Professional P800/1600 film.

Chemical Analyses

The determinations of particulate carbohydrates (glucose equivalents) and proteins (gamma globuline equivalents), sediment-bound chloroplastic pigments (chlorophyll a, phaeopigments), total adenylates (AMP, ADP, ATP) and electron transport system activity (ETSA) were carried out on board according to the methods described in Pfannkuche and Thiel (1987) and Thiel et al. (1987). For each parameter three replicate subsamples of sediment were taken by cutoff syringes (cross section 1 cm^2) and sectioned into 1-cm thick slices, which were individually analyzed. The data presented in Table 6 are the integrated values of the top 5 cm of sediment. In order to extract only easily soluble protein fractions, sediment samples were hydrolyzed once with 0.5n NaOH at 60 °C for 2 hours. In comparison to a total of six hydrolytic steps, this first hydrolysis extracted on average 25–35% of the total extractable protein. Similarly, only the hot water soluble fraction of carbohydrates (100 °C for 1 hour) is reported here. This fraction represents approximately 10% of the total extractable carbohydrates. Only these relatively labile

fractions were considered because they are likely to represent biologically degradable material.

Analyses of individual chlorophylls and carotenoids in phytodetritus were performed on 2 ml subsamples filtered onto GF/F filters and stored frozen at −20 °C. The pigments were extracted by homogenizing the filters in 2.5 ml 90% acetone, centrifuging residues, and ion-pair derivatizing the pigments with tetrabutyl ammonium acetate prior to analysis using high performance liquid chromatography (HPLC) (Mantoura and Llewellyn, 1983).

Particulate organic carbon (POC) was determined by wet oxidation (Altenbach, 1987) on phytodetritus filtered through precombusted Whatman GF/F glassfibre filters and rinsed with double distilled water.

Biological oxygen demand (BOD) measurements were carried out in order to determine the concentration of organic carbon potentially available for biodegradation. It should be noted that these tests were carried out under conditions that were intended to provide a maximum measure of organic carbon available for biological oxidation. They were not intended to reflect the rate or degree of in situ oxidation. Phytodetritus samples were first centrifuged at 3000 RPM for 5 minutes, the supernatant was discarded, and the residue was dried at 55 °C for 48 hours. Sediment samples were dried immediately. Centrifugation was not carried out with material from MC 60, but the sample weight was corrected for excess salt by comparing sample volumes before and after drying, and assuming that this volume change was due to the evaporation of 35% sea water. BOD was later determined in accordance with the "Standard methods" (Anonymous, 1976). Dried sediment or phytodetritus (10–20 mg) was suspended in 125 ml surface sea water obtained from Galway Bay (Ireland). Incubations lasted for 42 days at 22 °C. Oxygen concentration was determined by the Winkler method (Carritt and Carpenter, 1966). The resulting values were corrected for BOD of the water used. For the calculation of consumption of carbon from BOD, a respiratory quotient (RQ) of 0.85 was selected. RQ values for the decomposition of sedimentary material have been found to fall in the range 0.55–0.96 (Teal and Kanwisher, 1961; Raine and Patching, 1980) for in situ inshore sediments.

Results

Distribution of Phytodetritus on the Sea Floor

First indications of the occurrence of phytodetritus were provided by multiple corer samples. In many cases, the detrital material covered the sediment in some, but not all, of the 12 cores in a layer up to 1 cm thick (Fig. 2). Adjacent cores occasionally contained variable amounts of this material indicating extreme patchiness in the distribution of this material on the sea floor. The cores are arranged to cover the outer edge of an area of 50 × 50 cm with distances between two neighboring tubes of 10 and 20 cm.

Photographic transects confirmed the local variability of detritus distribution. The material was concentrated in the lee of sediment cones (Fig. 3) and in many kinds of depressions, for example, crawling and feeding tracks (Fig. 4), starfish resting impressions (Fig. 5), and biogenic holes. In these photographs (Figs. 3–5) the detritus appears as a fairly homogeneous mass in certain areas, but it may also occur in small, discrete lumps (Figs. 3, 6, 7). In some cases the detritus seems to have been rolled into larger clumps during transport along the seabed by bottom currents. This redistribution of

Figure 2. Multiple corer sample with a layer of phytodetritus and a large gelatinous aggregate on the sediment surface, partly dragged into the sediment by the tube wall.

phytodetritus by currents was also indicated by the fact that it was draped over polychaete tubes and other obstacles (Fig. 6).

The variability between stations was also high. Little detritus was found at station I on the abyssal plain south of the Großer Dreizack, whereas large amounts occurred at station IV on the plain to the north (Fig. 1). Both stations are at the same depth and their bottom slopes are less than at other stations that also yielded moderate amounts of phytodetritus. Previous hydrographic investigations in the region of the Großer Dreizack showed that the bottom currents are strongly influenced by the topography tending to follow the depth contours and forming an anticyclonic circulation above and around the deep-sea mountain ("Taylor column") (Mittelstaedt et al., 1986). These circulation patterns may create more sheltered regions north of the mountain favoring deposition of detrital matter. However, because current speed and direction during the periods proceeding sampling were not measured, the direct causes for the different amounts of phytodetritus at both stations remain unknown.

Macroscopic Appearance

Phytodetritus collected by the multiple corer was variable in appearance and abundance. It was encountered most frequently as coherent gelatinous aggregates up to 10 mm in diameter (Fig. 2). Sometimes it occurred as isolated aggregates, clearly visible against the gray sediment (Fig. 7), or as a more homogeneous layer of looser detrital material covering the sediment to a depth of a few mm to 20 mm. Occasionally, gelatinous sheets with incorporated detrital aggregates were found (Fig. 8). The color of the material varied from greenish (henceforth termed "green" phytodetritus) to yellow and whitish

(henceforth termed "white" phytodetritus). This variation in color may be due to the degree of decomposition (see the following section).

Microscopic Appearance

The detritus consists of phytoplankton, zooplankton, and their skeletal remains (Table 2) embedded within an unstructured matrix consisting of mainly gelantinous and membranous materials. The number of species indicated for each taxon in Table 2 undoubtedly would be much greater if all the organisms could be identified with confidence from their remains. Those that were most obvious when phytodetritus samples were examined microscopically include the tintinnid *Tintinnopsis elegans*, coccolithophorids, silicofla-

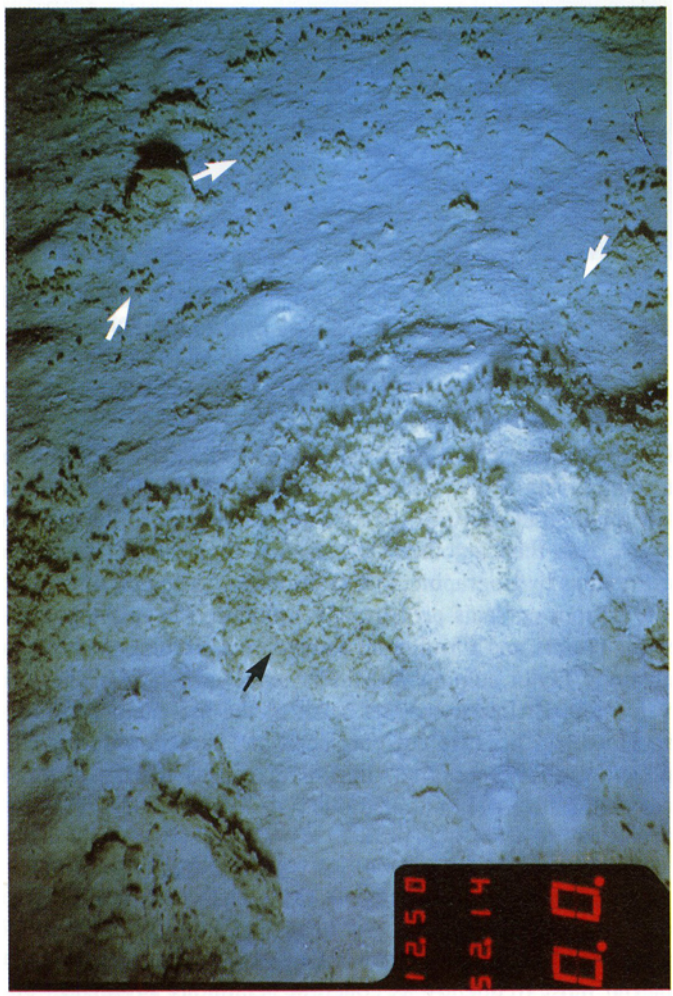

Figure 3. Bottom photograph showing the accumulation of a large amount of flocculent phytodetritus in the lee of a sediment cone (black arrows) as well as small discrete aggregates (white arrows) and an elongated, membraneous large aggregate (lower left). This figure and Figures 4–6 were photographed on August 1, 1986, photosled number 87, depth 4587 m–4600 m; the area covered is approximately 2 m^2.

Figure 4. Bottom photograph showing the accumulation of phytodetritus in a track of an unknown animal and in small depressions. For explanation, see Figure 3.

gellates, dinoflagellates, planktonic foraminifers, and crustacean exuviae (Fig. 9). Also present were diatom species characteristic of the spring bloom: *Bacteriastrum delicatulum, Rhizosolenia bergonii* and *Thalassionema nitzschioides,* and the tintinnid *Dictyocysta elegans.*

In addition to these relatively large planktonic species, greenish cells, 1.6–4.0 μm in diameter, were also present. They had thick cell walls and contained several bodies that displayed the red autoflourescence characteristic of chlorophyll *a*. This suggests that the bodies were chloroplasts and the cells therefore were probably chlorophytes (Fig. 9; see also Fig. 12). These organisms occurred in abundances of approximately 10^4 cells per ml of phytodetritus and thus were several orders of magnitude less abundant than the cyanobacteria (see the following section). It is likely that they are identical with the "chlorellalike cells" described by Silver et al. (1986).

Among the most prominent particles visible within the gelatinous aggregates, in terms of both numbers and volumes, are small, rounded faecal pellets 5–80 μm in

diameter. They are believed to be the waste products of phaeodarian Radiolaria (Riemann, 1989). Similar structures were termed "minipellets" by Gowing and Silver (1985).

Microscopic analyses revealed strong differences between cores from the same locality, e.g., phytodetritus removed from MC 56 cores, categorized as "white" phytodetritus, contained fecal pellets but only few algae. In contrast, samples from MC 57, categorized as "green" phytodetritus, with lumps of greenish gelatinous material comprised small pellets and large numbers of algae about 3 μm in diameter (see Table 8). The pigment analysis of MC 57 also indicates that this detrital material is relatively undegraded (see chlorophylls and carotenoids . . . in the following section).

SEM preparations of "green" material showed recognizable remains of diatoms, whole coccospheres, coccoliths, radiolarians, tintinnids, and amorphous, organic material (Fig. 10). Decomposing chloroplasts, numerous bacteria, and membranous materials

Figure 5. Bottom photograph showing phytodetritus deposited in a resting depression of a starfish, in the lee of sediment cones (e.g., left arrows), and a holothurian fecal cast (right arrow). For explanation, see Figure 3.

Figure 6. Bottom photograph showing phytodetritus caught by a branched obstacle on the sea floor. Discrete smaller aggregates are also visible (arrow). For explanation, see Figure 3.

are shown by TEM (see Fig. 15). On the whole, "green" phytodetritus seems to contain a number of remains of phytoplankton cells and organic components. This is contrasted with SEM pictures of degraded detritus, which was sampled at the BIOTRANS stations in September 1985. This material was recognized as remains of phytodetritus only after evaluation of the 1986 samples. It had a different appearance due to large numbers of siliceous and calcareous skeletons of radiolarians, silicoflagellates, ebriaceans, diatoms, and planktonic foraminifers, in which the preadult forms predominated (Fig. 11). These skeletal remains appear totally devoid of organic matter.

Bacteria and Cyanobacteria

Phytodetritus particles were densely colonized by heterotrophic, nonpigmented bacteria and also by photosynthetic, pigmented cyanobacteria. Both groups of organisms were often associated on the detritus and they can be distinguished by the autofluores-

Figure 7. An undisturbed core (6 cm inner diameter) with a thin, irregularly distributed layer of phytodetritus and four small, brown aggregates, an open burrow (nearly in the north), and a burrow surrounded by light sediment covering the phytodetritus layer.

Figure 8. Multiple corer sample showing on the sediment surface a large amount of gelatinous membranes with incorporated phytodetritus. Inner tube diameter: 6 cm.

Table 2
Remains and Intact Cells of Pelagic Organisms Discovered in Phytodetritus

Taxa	Number of species detected
Cyanobacteria	
Dinoflagellates and cysts	5
Silicoflagellates	2
Diatoms	8
Coccolithophorids	5
Chrysophyte cysts	1
Chlorophytes	
Foraminifers	5
Radiolarians	2
Acantharians	1
Tintinnids	3
Pteropods	
Crustaceans	

cence of the cyanobacteria. Under ultraviolet excitation (Fig. 12), nonpigmented bacteria stained with DAPI were found in colonies on the detrital particles. The bacterial cells are morphologically diverse. In the same field of view under green excitation, the phycoerythrin autofluorescence (Fig. 13) shows groups of cyanobacteria also attached to the phytodetritus. Both bacteria and cyanobacteria include numerous dividing cells.

In TEM preparations of phytodetritus cyanobacteria could be recognized by irregular internal membrane structures, thylacoids, which are part of their photosynthetic system (Fig. 14). They also contained polyhedral bodies. Nonpigmented bacteria were numerous in TEM pictures (Fig. 15) and the typical multilayered cell wall of gram-negative bacteria was visible in many cases (Fig. 16). However, a large percentage of the bacterial cells within the detrital sample, which originated from the actinian coelenteron, appear to be in a state of degradation as is indicated by irregular cell shapes and dark (electron-dense) cytoplasm (Fig. 15).

The abundance of bacteria on phytodetritus varied by one order of magnitude between 14×10^6 and 337×10^6 cells/ml of detritus (Table 3). Cyanobacteria ranged between 8×10^6 to 10×10^6 cells/ml of phytodetritus. Together they comprise between 0.5% and 5.0% of the total particulate organic carbon of the phytodetritus (Lochte and Turley, 1988).

A section through a sediment core underneath the phytodetritus shows that more bacterial cells are found within the sediment than in the detritus itself (Table 4). Sediment samples taken in May 1985, before sedimentation of phytodetritus, contained significantly lower bacterial numbers in comparison to the period after the detritus deposition in July/August 1986 (Fig. 17) as tested by independent t-test (t-value = 5.2383, degrees of freedom = 27). An increase in bacterial numbers was detectable in all sediment layers down to 10 cm depth. However, there was no significant difference between numbers of sediment bacteria in July/August and in September (t-value = 1.2651, degrees of freedom = 28).

Chemical Analyses

Chlorophylls and Carotenoids Determined by HPLC Analysis. Phytodetritus samples from MC 57 and MC 66, and the contents of the stomach of a holothurian (*Oneirophanta mutabilis*), give information on the pigment composition and origin of the phytodetritus (Table 5).

Chloropigment concentration in detritus from MC 57 was twice that found in MC 66, but the overall composition was remarkably similar, indicating similar modes of production, sedimentation, and breakdown for the phytodetritus at these two stations.

Phaeophorbide *a* and three unidentified phaeophorbide *a*-like compounds were the principal pigments detected in the detrital material. This is characteristic of faecal pigments from macrozooplankton and/or macrobenthic breakdown of chlorophyll *a* in phytodetritus. Phaeophorbides were even more concentrated in the holothurian stomach (Table 5).

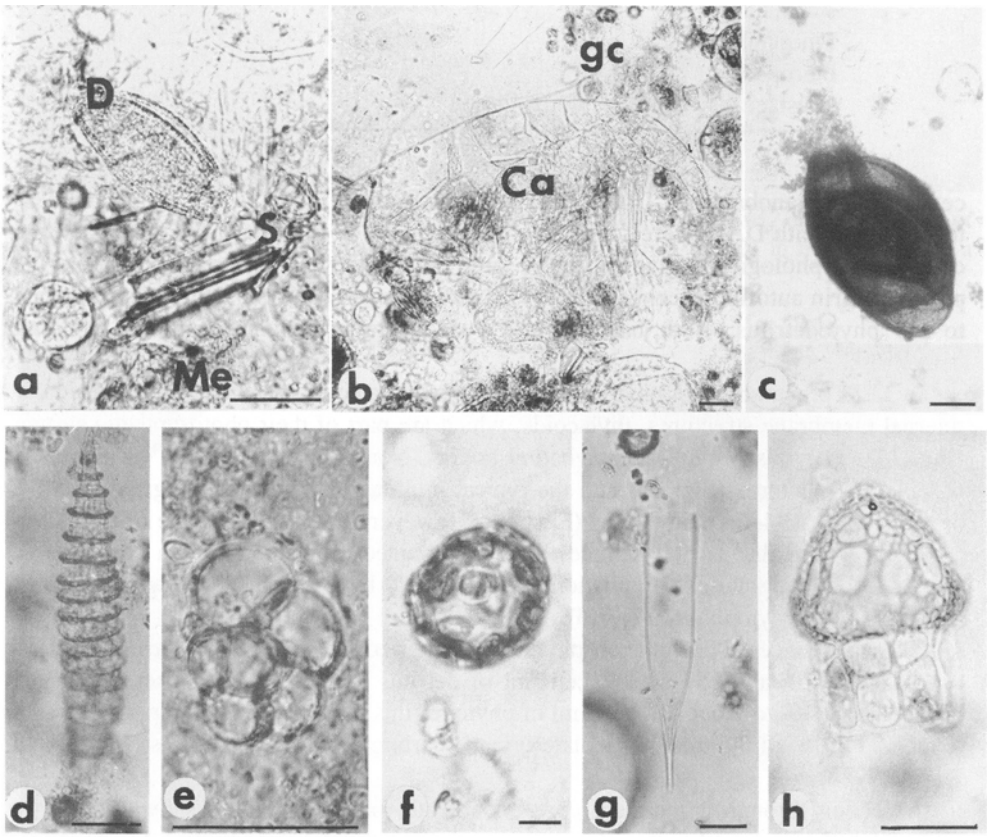

Figure 9. Various organisms occurring in "green" phytodetritus as seen by brightfield microscopy: (*a*) diatoms (D), organic sheets (Me), and a calcitic piece of a spine (S) of a planktonic foraminifer (*Hastigerina pelagica*); (*b*) copepod carapax (Ca), green cells (gc) (probably chlorophytes), and other debris; (*c*) a benthic miliolid foraminifer with attached phytodetritus (*Pyrgo sp.*); (*d*) a nematode of the family Desmoscolecidae obviously feeding on the phytodetritus; (*e*) a juvenile planktonic foraminifer (*Globigerina bulloides*) transported from the photic zone; (*f*) coccosphere of *Emiliania huxleyi*; (*g*) and (*h*) empty tintinnid loricae from the photic zone. All bars 100 μm, except for (*f*) bar = 10 μm.

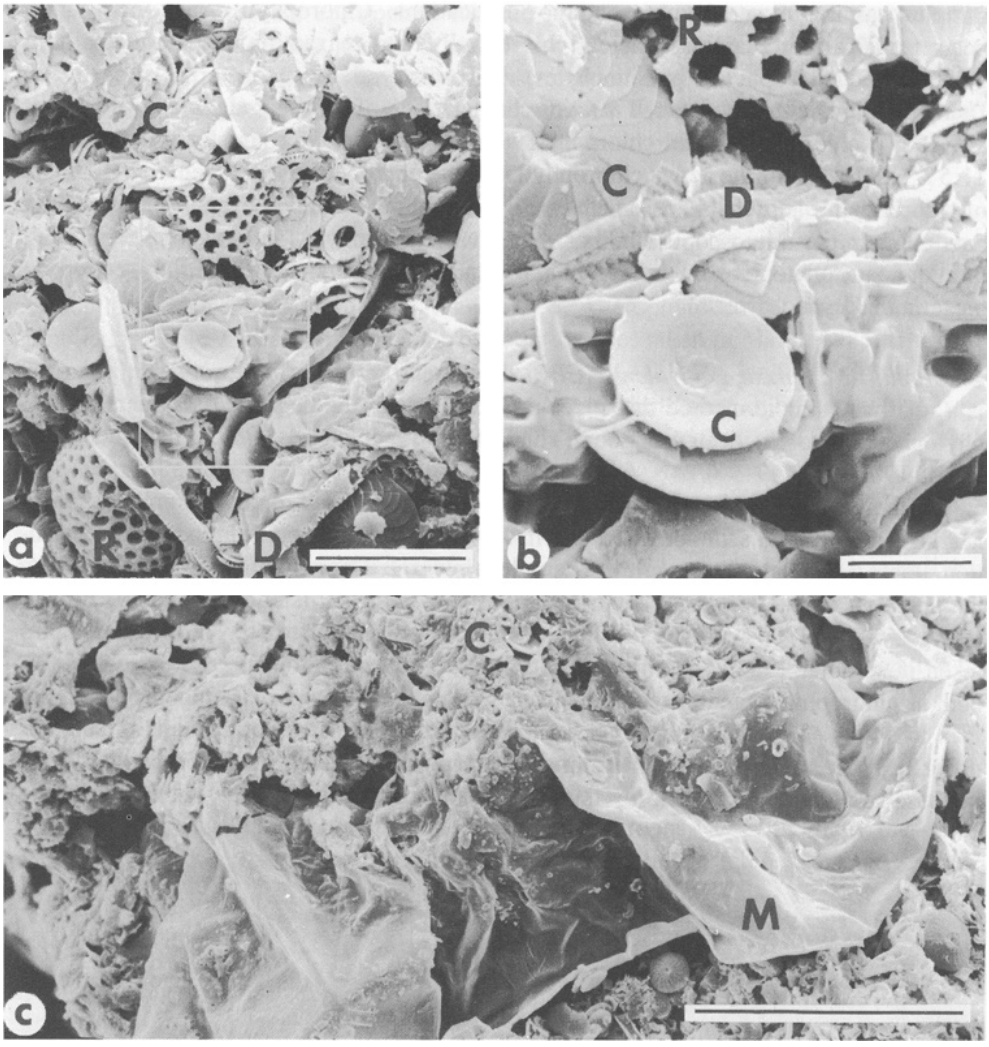

Figure 10. SEM micrograph of "green" phytodetritus: (*a*) showing mostly hard parts of radiolaria (R), diatoms (D), and coccoliths (C); (*b*) higher magnification of frame in (*a*); (*c*) other parts of the green fluff containing membraneous sheets (M) and masses of coccolith debris (C). Bars = 10 μm in (a); 3 μm in (*b*); 40 μm in (*c*).

Chlorophyll *a*, which is associated with intact phytoplankton cells, accounts for a surprisingly high proportion(26.0% and 23.1%, respectively) of the phytodetritus pigments in the two samples. This indicates that a significant percentage of the material sampled at both stations was undegraded. The same conclusion can be drawn from the molar ratio of phaeophorbide *a* plus phaeophorbide *a*-like substances to chlorophyll *a* (R). This ratio is small for relatively undegraded material. Values of R = 1.64 (MC 57) and R = 2.04 (MC 66) indicate relatively fresh phytodetritus compared to a value of R = 42.1 in the holothurian stomach. Such high value implies an advanced state of chlorophyll breakdown in the holothurian gut (Table 5). The presence of chlorophyll *b* and chlorophyll *c* further substantiates that the phytodetritus is relatively undegraded.

The occurrence of chlorophyll *b*, chlorophyll *c*, fucoxanthin, and zeaxanthin in both

samples has important chemotaxonomic implications. Chlorophyll *c* and fucoxanthin occur principally in diatoms, whereas chlorophyll *b* and zeaxanthin occur principally in green algae (chlorophytes, prasinophytes) and prokaryotic cyanobacteria, respectively. Using the pigment to chlorophyll *a* ratios characteristic of different algal taxa (Burkill et al., 1987), chlorophyll *c* and chlorophyll *b* containing cells account for an average of 11.5% and 61.7% of the active chlorophyll *a* in the phytodetritus. The remaining 26.8% of chlorophyll *a* is probably associated with zeaxanthin containing cyanobacteria. These data confirm the microscopic findings that small chlorophytes and cyanobacteria were the dominant phytoplankton cells containing intact pigments (see preceding section on bacteria and cyanobacteria).

Chloroplastic Pigment Equivalents (CPE). The measurement of chloroplastic pigments is a relatively simple method that gives an indication of the degree of sedimentation of phytoplankton to the deep-sea floor (Thiel 1978; Pfannkuche, 1985; Pfannkuche and Thiel, 1987).

In Table 3 CPE concentrations are given for individual sediment samples taken in March 1985 prior to sedimentation and in July/August 1986 after phytodetritus deposition. Table 6 compares four sediment samples (integrated from 0 cm to 5 cm depth) from the deep-sea plains north and south of the Großer Dreizack (stations I and IV, Fig. 1) taken in spring 1985 with four sediment samples (integrated from 0 cm to 5 cm depth) taken in summer 1986. The chloroplastic pigment concentrations presented in Table 6, both as chlorophyll *a* and phaeopigments as well as the CPE sum, are higher in summer than in spring. The independent t-test shows that the means of both groups of samples differ significantly. The ratio of summer to spring data is 18.5 for chlorophyll *a*. This increase in pigments is caused by the phytodetritus deposition on the sea floor and the

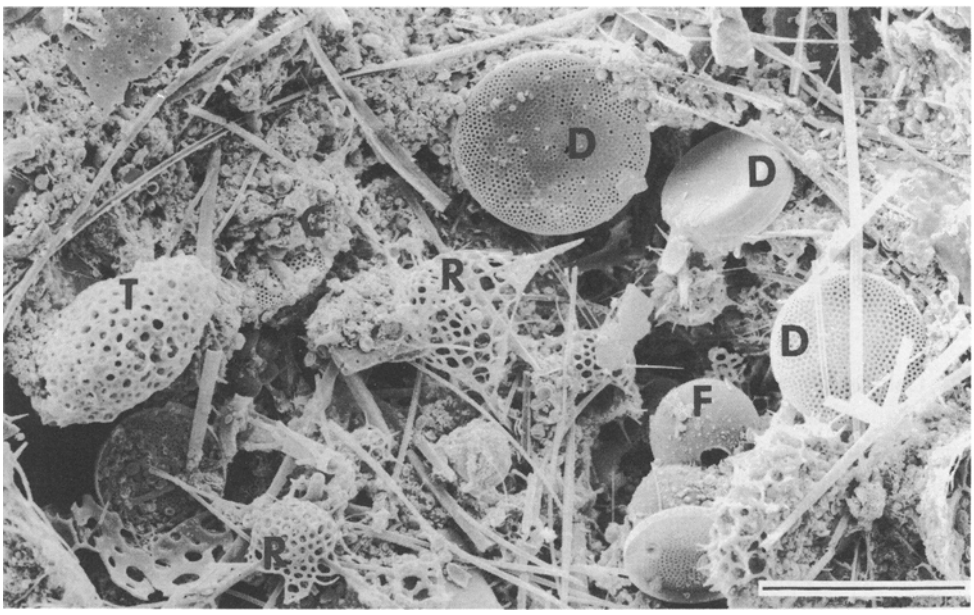

Figure 11. Degraded detritus sampled in September 1985 at the BIOTRANS site containing almost only hard parts of tintinnids (T), diatoms (D), radiolarians (R), and foraminifers (F); coccolith debris constitutes the background (C). Bar = 100 μm.

particularly high ratio for chlorophyll *a* again indicates that the material is relatively undegraded. Phaeopigments and CPE are higher by factors of 2.87 and 3.22, respectively. From our photographic and visual observations, highly variable concentrations are to be expected. Standard deviations presented in Table 6 are especially high for chlorophyll *a* with 100% in spring and even 129% in summer samples.

Chemical Components and Activity Measurements. Concentrations of particulate organic carbon (POC), carbohydrates (CH), protein (P), total adenylates (TA), and electron transport system activity (ETSA) were measured in various sediment samples down to 5 cm depth. Measurements from July/August 1986, when phytodetritus was present, are compiled in Table 3 together with data from four samples taken in March 1985, when no phytodetritus was present. Table 6 compares values of CH, P, TA, and ETSA in samples with and without phytodetritus. Generally, the measurements were significantly higher in summer compared to spring as shown by t-test, with the exception of ETSA. CH and P were approximately twice as high in summer and TA was 5.5 times higher. These increased concentrations are a clear indication of higher organic content and living matter in the sediment down to 5 cm depth when phytodetritus is present. In contrast, ETSA was not significantly different in spring and summer. Since ETSA is an activity measurement, warming and decompression during sampling may have adverse effects on the values of this parameter. The very low values of carbon equivalents calculated from ETSA in comparison to other measurements listed in Table 8 may also be indicative of sampling artifacts.

Standard deviations for all measured parameters are high in summer. It indicates that small-scale variability influences the summer data to a larger extent than the spring data, as already noted for CPE concentrations. This is probably caused by the irregular distribution of phytodetritus as shown by the seabed photographs. It seems likely that sedimentation and transport by bottom currents result in strong patchiness on the seabed. Biological activities (e.g., feeding, bioturbation, biodeposition) may subsequently distribute the detrital material further.

Biological Oxygen Demand (BOD). BOD of detritus from MC 60 gave extremely variable results between replicates that were probably due to inhomogeneity of degradable organic matter between the subsamples (Table 7). Subsequently, the remaining samples were thoroughly homogenized and greater uniformity between replicates was obtained (Table 7).

The degradable organic content of phytodetritus was higher than that of deeper sediment horizons when estimated on a dry weight basis. The surface sediment layer yielded intermediate values that may be due to the burial of detrial components and/or to our inability to separate adequately the phytodetritus from the sediment. However, when the higher water content of the phytodetritus and the top sediment layers are taken into account, the degradable carbon content per unit sample volume increases with sediment depth (Table 7; layers 2–3 cm compared to 10–11 cm). It should be noted that, in addition to detrital organic carbon, any benthic animals or bacteria inhabiting the phytodetritus would be included in the BOD measurements.

Phytodetritus Inhabitants and Consumers

The detrital material contains 0.9–7.9% POC per dry weight unit (Table 3) of which 5–32% is probably degradable as shown by BOD measurements (Table 8). Therefore,

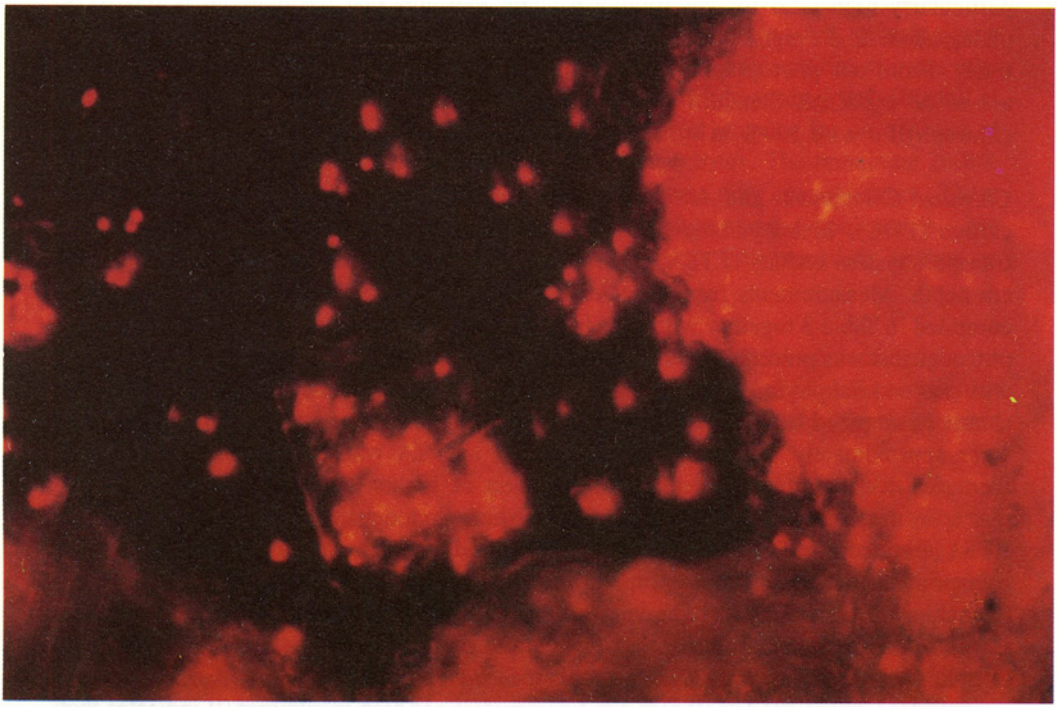

Figure 12. Microscopic view (magnification 1250×) of DAPI stained phytodetritus under UV-excitation showing numerous bacteria (blue fluorescence), cyanobacteria (yellow), and chlorophyll *a* containing microalgae (red). Note the presence of dividing cells and formation of clusters or microcolonies.

phytodetritus presumably has a nutritive value for many of the deep-sea organisms. Consequently, we investigated it for living organisms that might have invaded it or used it as a food source.

Foraminifera. Fresh, green aggregates contained large populations of benthic foraminifers (Gooday, 1988). Briefly, the phytodetritus assemblages were dominated by two major taxa, the allogromiins, which have a thin, flexible, organic test wall, and the rotaliins in which the wall is rigid and calcereous. The three most abundant species are an undescribed allogromiin (possibly a species of *Tinogullmia* Nyholm) and two rotaliins, *Epistominella exigua* (Brady) and *Alabaminella weddellensis* Earland. Two multichambering agglutinating species, *Adercotryma glomeratum* (Brady) and *Trochammina* sp., are also fairly common. Numerous foraminifers inhabit the underlying sediments and the assemblages are more diverse than in the phytodetritus. However, the three main phytodetritus-dwelling species occur only sporadically in the sediment. As a result, the sediment samples contain relatively fewer allogromiins and rotaliins and a relatively greater proportion of other taxa, particularly saccamminids and tubular astrorhizaceans.

Foraminifers appear to have colonized the phytodetritus since they occur embedded within the aggregates rather than merely being loosely associated with them. The fact that some species have green cytoplasm suggests that they are feeding on the phytodetritus (Gooday, 1988). Samples of phytodetritus from a shallower water site in the Porcupine Seabight (51° 36′ N, 13° 00′ W, 1349 m) are also inhabited by benthic foraminifers

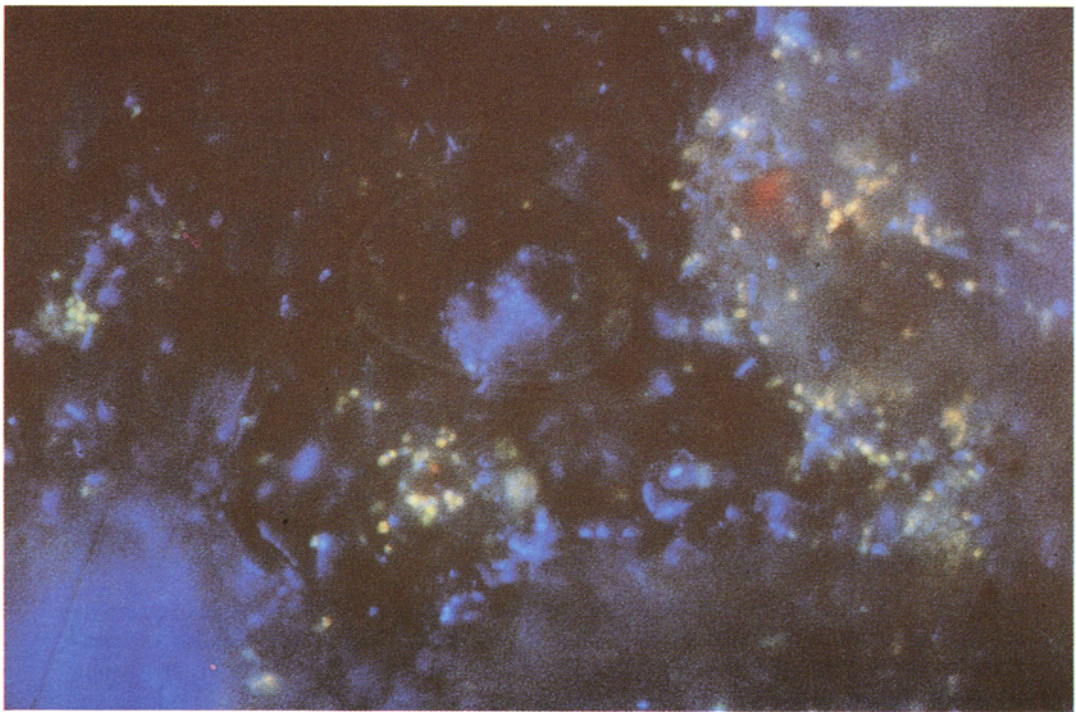

Figure 13. The same field of view as shown in Figure 11 under green excitation showing the specific orange-red autofluorescence of cyanobacteria.

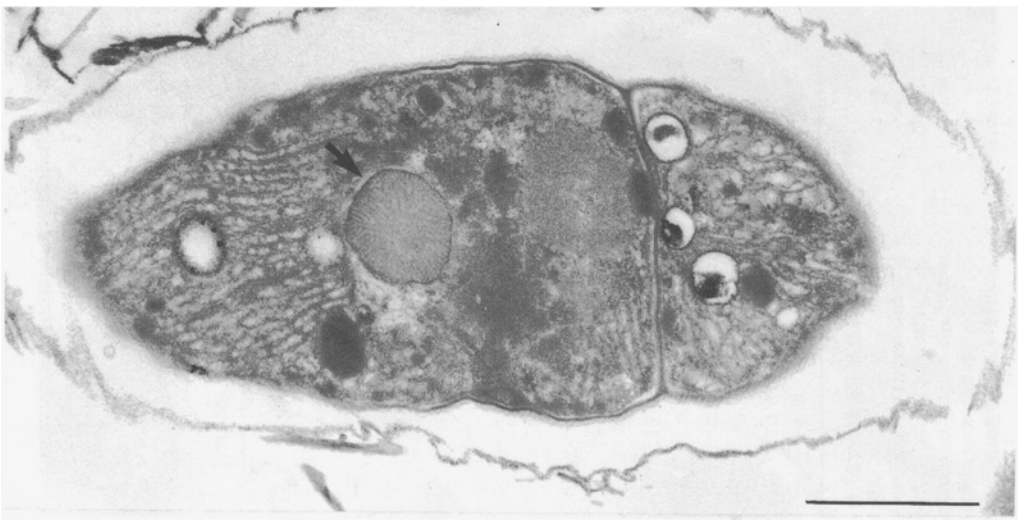

Figure 14. TEM micrograph of a cyanobacterium with thylacoids randomly distributed in the cytoplasm and a polyhedral body (arrow) from "green" phytodetritus. Bar = 1 μm.

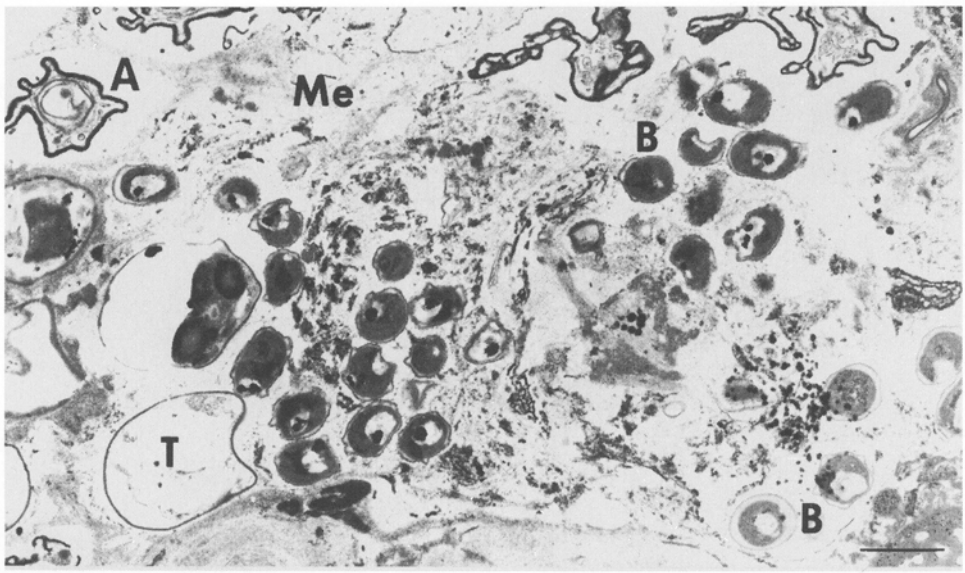

Figure 15. TEM micrograph of "green" phytodetritus isolated from the coelenteron of an actinia showing degrading bacteria (B), thecate algal cells (T), strongly degraded algal cells (A), membraneous sheets (Me), and debris; the calcareous components are dissolved during the preparation procedure. Bar = 1 μm.

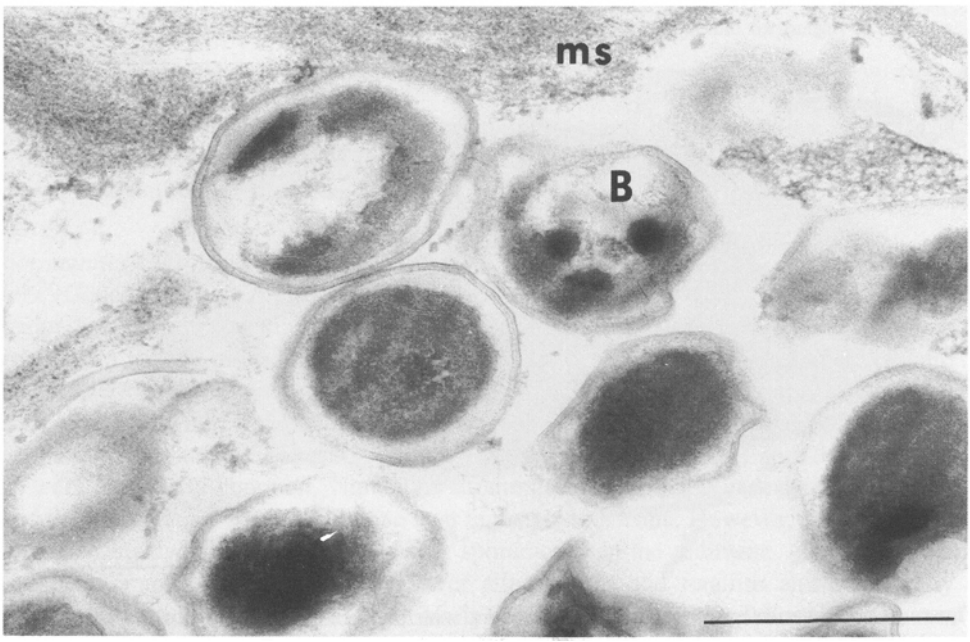

Figure 16. TEM micrograph of bacteria (B) and mucous sheets (ms) from "green" phytodetritus already strongly degraded. The typical three-layered cell wall of gram-negative bacteria is clearly visible. Bar = 0.5 μm.

Table 3

Chemical Composition, Activities, and Bacterial Numbers in Sediment Surface Samples (integrated from 0 to 5 cm) Taken in March 1985 Devoid of Phytodetritus (MC 11 to 19) and in July/August 1986 with Phytodetritus (MC 44 to 68, KG 1138)

MC (KG)[a] no.	DW[b] (mg cm^{-3})	CPE[c] ($\mu g\ cm^{-3}$)	Protein[d] (total) ($\mu g\ cm^{-3}$)	CH[e] (total) ($\mu g\ cm^{-3}$)	POC[f] ($\mu g\ C\ cm^{-3}$)	Total adenylates (ng cm^{-3})	ETSA[g] ($\mu l\ O_2\ cm^{-3}$)	Bacteria ($\times 10^6$ cells cm^{-3})
				March 1985				
11	n.d.*	0.419	165.7	18	n.d.	2.20	0.227	n.d.
12	n.d.	0.475	126.8	21	n.d.	1.67	0.241	n.d.
15	n.d.	0.367	169.1	29	n.d.	1.41	0.313	n.d.
19	n.d.	0.589	161.5	15	n.d.	2.06	0.556	n.d.
				July/August 1986				
44	2.03	1.662	169.8	30	159.4	6.41	0.368	336.9
45	36.20	n.d.	n.d.	n.d.	317.1	n.d.	n.d.	218.2
48	9.20	1.028	n.d.	n.d.	92.8	n.d.	n.d.	86.1
52	21.01	2.324	364.5	70	391.6	11.78	0.196	261.7
56	3.55	0.640	314.3	16	71.4	18.10	0.104	138.6
57	11.46	0.590	430.1	28	164.6	6.73	0.301	242.4
60	n.d.	1.725	434.7	60	n.d.	10.50	0.146	n.d.
63	n.d.	1.768	341.4	50	n.d.	11.38	0.238	n.d.
KG 1138	n.d.	0.818	312.5	56	n.d.	10.30	0.243	n.d.
66	3.36	n.d.	n.d.	n.d.	72.8	n.d.	n.d.	13.6
68	n.d.	1.219	207.5	39	n.d.	9.00	0.269	n.d.

[a]MC = sampled by multiple corer; KG = sampled by box corer.
[b]Dry weight.
[c]Chloroplastic pigment equivalents.
[d]As gamma globulin equivalents.
[e]Carbohydrates as glucose equivalents.
[f]Particulate organic carbon.
[g]Electron transport system activity.
*Not determined.

Table 4
Bacterial Direct Counts in 2 cm Layers
of a Sediment Core Taken at Station IV

Sediment depth (cm)	Dry weight (g cm^{-3})	Bacterial numbers (cells $cm^{-3} \times 10^8$)	(cells $g^{-1} \times 10^8$)
0 (phytodetritus)	0.0362	2.2	60.2
0–2	0.5113	14.73	28.81
2–4	0.5700	10.48	18.38
4–6	0.6404	15.57	24.31
8–10	0.6944	12.99	18.71

(Gooday, unpubl. observation) and hence this may be a widespread phenomenon. Indeed, TEM micrographs of cytoplasm of a miliolid foraminiferan (*Pyrgo* sp.) shows partially degraded phytodetritus (Hemleben, unpubl. observation).

The "white" phytodetritus, which is probably more degraded material merging into the underlying sediment, lacks a distinctive benthic foraminiferal fauna. It yields occasional specimens that belong to species also found in the sediment.

Nematoda. Some of the detrital aggregates on the sediment surface were colonized by nematodes. The highest densities encountered were 29 specimens in a detritus aggregate

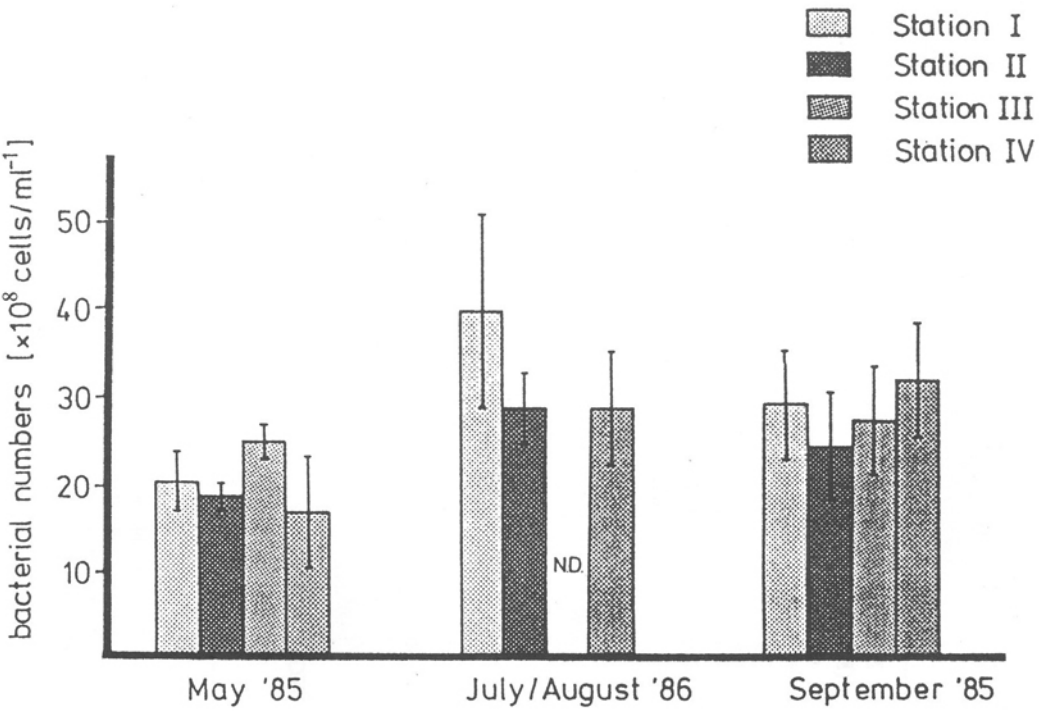

Figure 17. Bacterial numbers averaged over the top 6 cm of sediment at the four standard stations (Fig. 1) at various seasons. The data are compiled from investigations in 1985 and 1986. The bracketed lines show the standard deviation.

Table 5
Chlorophyll and Carotenoid Pigments in Phytodetritus and Holothurian Gut Contents

	Pigment concentrations and % compositions								
	MC 57			MC66			Holothurian gut		
	ng cm^3	pmol cm^3	%	ng cm^3	pmol cm^3	%	ng cm^3	pmol cm^3	%
Chlorophyll *a*	407	456	26.0	206	230	23.1	130	146	2.1
Chlorophyll *a* allomer	154	172	9.8	76	79	8.0	74	82	1.2
Chlorophyll *a'*	<	<	<	7	8	0.8	<	<	<
Polar Chlorophyll *a*	34	38	2.2	19	21	2.1	152	171	2.5
Chlorophyllide *a*	53	86	4.9	5	9	0.1	<	<	<
Phaeophorbide *a*	168	282	16.2	116	195	19.6	641	1082	15.9
Phaeophorbide *a*-like	276	466	26.6	162	275	27.7	3004	5066	74.4
Phaeophytin *a*	127	146	8.3	92	106	10.7	<	<	
Pyrophytin *a*	89	105	6.0	59	76	7.7	223	265	3.9
Tot. Chloropigments *a*	1274	1752	100.0	736	993	100.0	4224	6812	100.0
Chlorophyll *b*	134	148		45	50		<	<	
Chlorophyll *c*	10	16		6	10		<	<	
Fucoxanthin	85			70			*	*	
Zeaxanthin	57			23			*	*	
R[a]	1.64			2.04			42.1		

[a]Molar ratio of phaeophorbide *a* + phaeophorbide *a*-like substances to chlorophyll *a*.
< = Below detection limit of 5 ng cm^{-3}.
* = Not detected.

Table 6

Summarized Data from Four Sediment Samples Taken in March 1985 (MC 11, 12, 15, 19) and Four Sediment Samples Taken in July/August 1986 (MC 44, 60, 63 and KG 1138) Collected in the Deep-Sea Plains North and South of the Groβer Dreizack at Stations of Similar Water Depths

	Chloro-phyll *a* (μg cm^{-3})	Phaeo-pigment (μg cm^{-3})	CPE (μg cm^{-3})	Protein (μg cm^{-3})	CH (mg cm^{-3})	TA (ng cm^{-3})	ETSA (μl O_2 cm^{-3})
				March samples			
$\bar{x}$	0.010	0.453	0.462	157.5	0.021	1.76	0.343
±s.d.	0.010	0.141	0.146	39.3	0.007	0.41	0.148
%s.d.	100.0	31.1	31.6	25.0	33.0	23.3	43.1
n	12	12	12	11	11	12	12
				July/August samples			
$\bar{x}$	0.185	1.301	1.486	312.5	0.048	9.64	0.249
±s.d.	0.239	0.599	0.705	119.8	0.013	3.31	0.131
%s.d.	129.2	46.0	47.4	38.3	27.0	34.3	52.6
n	12	12	12	12	12	10	12
				Comparison of July/August with March samples			
ratio	18.5	2.9	3.2	2.0	2.3	5.5	0.7
t-value	2.5356	4.7705	4.9250	4.1341	5.9149	8.4133	1.6422
df	22	22	22	20	20	18	22
sign.	0.0188	0.0001	0.0001	0.0005	0.0000	0.0000	n.s.

Note. Data represent the integrated values from 0 to 5 cm sediment depth. For abbreviations of measured parameters, see text. Table abbreviations: $\bar{x}$ = mean, s.d. = standard deviation, n = number of observations (3 or 2 syringe subsamples were available per MC or KG), ratio = ratio of means of July/August to March samples, t-value = calculated value of t in test for difference between means, df = degrees of freedom, sign. = level of significance, n.s. = not significant.

Table 7
Results of BOD Experiments with Phytodetritus and Underlying Sediment Horizons

Sample	Subsample type	Horizon (cm)	BOD (mg O_2 g^{-1})	BOD (mgC g^{-1})	Mean BOD (mgC g^{-1})	Mean BOD (mgC cm^{-3})
MC 60	Phytodetritus	—	13.94	4.45	2.37	0.03
			0.89	0.28		
	Phytodetritus core	Surface	3.41	1.09	1.25	0.40
			4.42	1.41		
		2–3	2.29	0.73	0.78	0.48
			2.57	0.82		
		10–11	3.41	1.09	0.75	0.56
			1.28	0.41		
	Control core	Surface	2.88	0.92	1.13	0.43
			4.27	1.36		
		2–3	2.56	0.82	0.57	0.37
			1.01	0.32		
		10–11	1.89	0.60	0.67	0.49
			2.32	0.74		
MC 66	Phytodetritus	—	6.19	1.90	2.09	0.02
			7.12	2.27		
MC 68	Phytodetritus	—	12.20	3.89	3.34	0.02
			8.74	2.79		

Note. The control is a core without phytodetritus coverage. See text for high variability between the replicates in MC 60. Results are expressed both per gram dry weight (corrected for excess salt, see Chemical Analyses section in text) and per volume of sample; organic carbon contents are calculated assuming a respiratory quotient of 0.85.

of approximately 0.3 ml volume picked from a box corer sample (KG 1140). In another sample, 77 specimens were found in about 1 ml of more flocculent detritus from MC 56. In contrast, other samples had densities of about 10 nematodes per ml or less. Hence, patchiness appears to be high. A preliminary determination of species in seven samples showed that monhysterids and chromadorids predominate. The presence of many individuals of a *Monhystera* species in three samples is remarkable as this genus is usually confined to coastal and sublittoral regions (Lorenzen, 1979) and occurs, for instance, in great numbers in rotting seaweeds along the shore line. Therefore, we suggest that the related deep-sea species may be adapted to feeding on the phytodetritus. Two nematodes demonstrated that they had been feeding on detrital particles since characteristic small green cells, found in phytodetritus, were detected in their intestines (Fig. 18).

Harpacticoida and Kinorhyncha. Harpacticoids and kinorhynchs were discovered in phytodetritus samples, but no obvious differences in abundance could be detected compared with sediment samples without phytodetritus. The number of harpacticoids varied between 23 and 3 per 25 cm^2 sediment surface area, and species abundance in the

Table 8

Summary Table of Chemical and Biological Variables Determined in Phytodetritus Samples (see Table 3) and Standardized for 1 m^2 of Seabed by Assuming a Thickness of the Phytodetritus Layer of 1 cm and a Coverage of the Seabed of 10%

Variable	Range	Mean	n	MC 56	MC 57	MC57/ MC 56
Dry weight mg cm^{-3}	2.03–36.20	12.40	7	3.55	11.46	3.2
Organic carbon mg C m^{-2}	71–392	181	7	71	165	2.3
BOD* mg C m^{-2}	17–25.5	19.6	3	n.d.	n.d.	n.d.
Proteins mg C m^{-2}	85–217	162	8	157	215	1.4
Carbohydrates mg C m^{-2}	6–28	18	8	6	11	1.8
Bacterial biomass mg C m^{-2}	0.2–7.6	3.2	7	1.7	4.2	2.5
Cyanobacterial biomass mg C m^{-2}	0.2–0.4	0.3	4	0.4	n.d.	n.d.
Total adenylates μg m^{-2}	6.4–18.2	10.5	8	18.2	6.7	0.4
ETSA* mg C m^{-2}	0.047–0.168	0.106	8	0.047	0.137	2.9
CPE mg m^{-2}	0.6–2.3	1.3	9	0.6	0.6	0.9
Total chloropigments a^+ mg m^{-2}	0.7–1.3	1.0	2	n.d.	0.7	n.d.

Note. In this case 1 m^2 contains 1000 cm^3 of phytodetritus. Carbohydrates are originally determined as glucose equivalents and are recalculated in this table as mg carbon (6 moles carbon per mole of glucose). Protein measurements are converted into carbon equivalents by assuming a conversion factor of 0.5 (Schneider unpubl. data). n = number of analyzed samples; n.d. = not determined; * = conversion to C_{org} based on RQ of 0.85; $^+$ = from HPLC measurements.

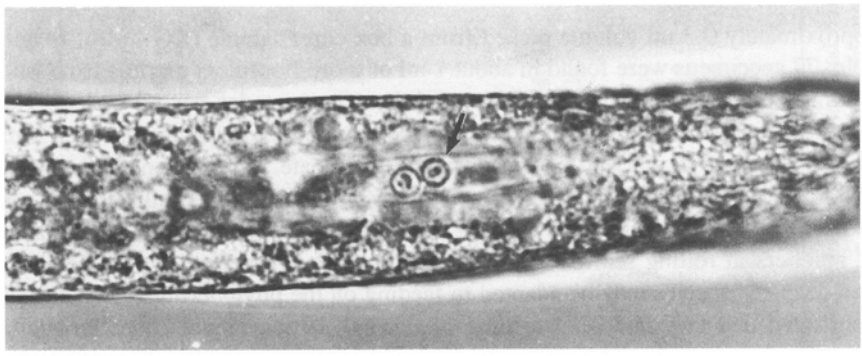

Figure 18. Two algal cells (arrow) in the intestine of a nematode, genus *Monhystera*. Cell diameter is 3 μm.

detritus mass with about 10 species was not higher than in the sediment. Generally, in deep-sea samples males are rare, and in these samples no males were found. About 20% of the females were egg producing or egg bearing. Significant differences between phytodetritus and sediment are shown by the number of adult and nauplii exuvia, which mainly were shed by members of the family Ectinosomatidae. Within three detrital samples, adult exuvia were 1.7, 3.1, and 7.3 times more numerous than in samples without this material. Similarly, nauplii exuvia were more abundant than nauplii in phytodetritus.

Several species of the family Ectinosomatidae are known to live on the sediment surface. However, no living individuals of this family were discovered in the phytodetritus. From these observations it is not clear whether ectinosomatids invaded the detritic mass and moulted therein. Such invasion of the newly settled material, feeding on the organic components, moulting and egg production would be an appropriate reaction of opportunistic species. A seasonal input of phytodetritus might stimulate an annual reproductive cycle. However, the shed exuvia might also have been collected and aggregated by phytodetritus on the sea floor. As ectinosomatid species also live in surface waters and specific identification of shed exuvia is not possible, sedimentation as part of phytodetritus aggregates may be a further explanation for their occurrence.

A small number of kinorhynchs were discovered in phytodetritus but none in sediment samples.

Macro- and Megafauna. Equal size fecal pellets (400 × 700 μm) within a large phytodetrital aggregate (approximately 2 cm^3) were discovered next to an amphipod, and they were presumably produced by it. The SEM photographs (Fig. 19) of a squashed fecal pellet indicate that phytodetritus had served as a food source for the amphipod. Furthermore, phytodetritus could be recognized visually in the guts of holothurians, asteriods, sipunculids, and actiniarians caught with a trawl.

The foregut of *Oneirophanta mutabilis* (Holothuria) contained a mixture of sediment and greenish phytodetritus. This material had a higher proportion of phaeophorbide *a* and related components as compared to phytodetritus material (Table 5). The ratio of phaeophorbide *a* and phaeophorbide *a*-like substances to chlorophyll *a* was 42.1, which is higher than in phytodetritus (R = 1.6 to 2.0). Although the holothurian caught in the trawl and the phytodetritus collected by the multiple corer were not from the same location, the much higher ratio in the gut material indicates pigment breakdown by this megabenthic organism. Similar observations were made on two species of holothurians by Billett et al. (1988) who showed that major degradation probably occurs in the stomach.

The coelenteron of actiniarians contained phytodetritus and what we interpret to be degrading algal cells, bacteria, and cyanobacteria (Fig. 15). In the deep sea, such sessile organisms must utilize all opportunities to gather food. Therefore, passive food collection of sinking or resuspended phytodetritus by bottom-living specimens may be important for their nourishment (Aldred et al., 1979).

Discussion

Oceanic Phytodetritus

For several decades observations have been made in both shallow and deep water on various kinds of particulate matter in the water column that are likely eventually to form

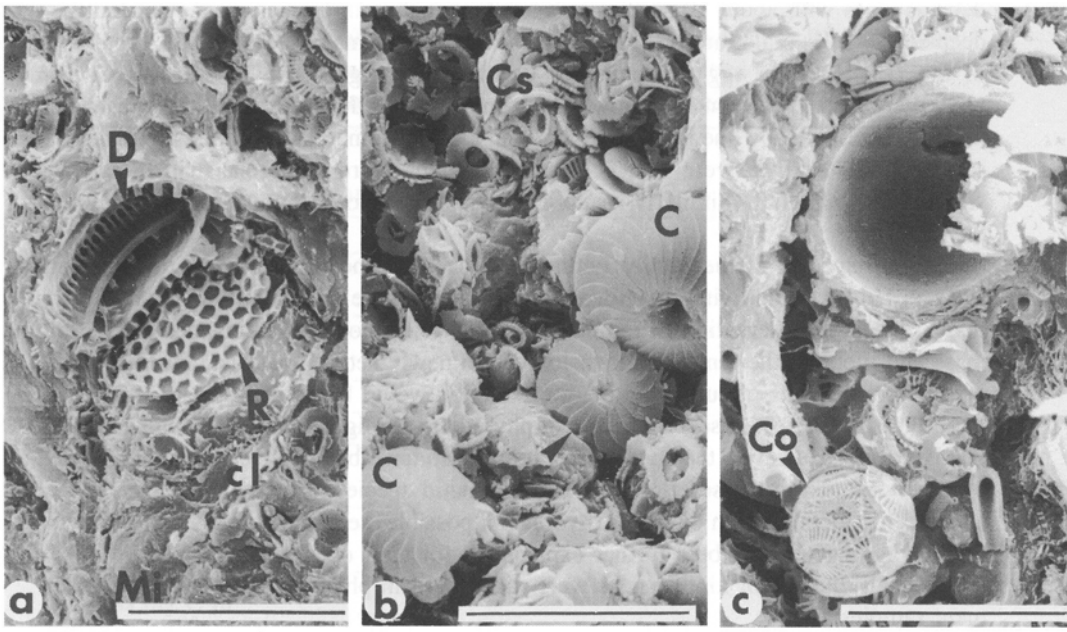

Figure 19. SEM micrographs showing the contents of an amphipod faecal pellet; the amphipod was feeding on "green" phytodetritus: (*a*) a diatom (D) and pieces of a radiolarian (R) are embedded into a rather compact matrix of coccolith ooze, clay (cl) and mica (Mi); (*b*) larger coccoliths (C) are partially dissolved (arrow) and are surrounded by small coccolith debris (Cs); (*c*) other parts are well preserved showing an undisturbed coccosphere (Co), membranous sheets, and other siliceous debris. Bars = 10 μm.

the phytodetritus aggregates on the seabed. These include the following categories of material, partly compiled by Trent (1985):

Snow: marine, sea, or plankton snow (Inoue et al., 1953; Suzuki and Kato, 1953; Peres and Picard, 1955; Honjo, 1978; Silver et al., 1978; Shanks and Trent, 1979; Silver and Alldredge, 1981; Alldredge and Cox, 1982; Davoll and Silver, 1986; Asper, 1987; Alldredge and Silver, 1988).

Aggregates: organic, micro- and macro- or large amorphous aggregates (Riley, 1963; Johannes, 1967; Bishop and Marra, 1984; Bishop et al., 1977, 1978, 1980; Trent et al., 1978; Caron et al., 1982, 1986; Honjo et al., 1984; Alldredge and Youngbluth, 1985; Beers et al., 1986; Kranck and Milligan, 1988).

Flocs and flakes: mucus and macroflocs, flocculent organic matter (Gordon, 1970; Coles and Strathmann, 1973; Krank and Milligan, 1980; Hunt, 1983).

Particulate matter (McCave, 1975; Wakeham and Canuel, 1988).

From the data available today based on direct observations by divers, sediment trap content, and material photographed and collected from the sea floor, it is apparent that all these different types of particles represent various aspects of particulate matter aggregation.

Studies on the vertical flux of oceanic particulate material using sediment traps (see reviews by Alldredge, 1984; Angel, 1984; Honjo, 1980, 1982; Smetacek, 1985) have revealed that such fluxes vary seasonally and involve the sinking of detrital aggregates containing particles of diverse origin. The discovery of organic detritus arriving season-

ally over an extensive area of the floor of the Porcupine Seabight, forming a layer a centimeter thick or more (Billett et al., 1983; Lampitt, 1985; Rice et al., 1986), indicated that there is an important mechanism for the rapid transfer of material from the euphotic zone to deep water. As these observations were confined to the Porcupine Seabight, however, there was the possibility that hydrographic and topographic features may have been responsible for enhanced sedimentation or downward slope transport.

Our discovery of phytodetritus in a midoceanic region, approximately 400 nautical miles from the continental shelf, indicates that seasonal sedimentation of organic material is a more widespread phenomenon than could be hitherto assumed. Influences from either shelfbreak fronts or the shelf slope are probably minimal in this region of the northeast Atlantic. Therefore, the observations are evidence for a rapid sedimentation of particulate mater originating from surface waters in the open ocean during certain times of the year. The spatial and temporal extent of such deposition of organic matter is still unresolved.

A cold core eddy has been described from the BIOTRANS region (Beckmann et al., 1987; Lochte and Pfannkuche, 1987; Mittelstaedt, 1987) and hence special hydrographic conditions may also be involved in triggering sedimentation events in this area. Mittelstaedt (1987) and Klein (1987) give evidence that cold core eddies may extend downward close to the seabed and may create abyssal storms. Since vertical transport at the edges of cold core eddies can have a downward component, this may enhance sedimentation. A high concentration of the euthecosomatous pteropod *Limacina retroversa* was recorded in the eddy core down to 400 m by Beckmann et al. (1987). Their fecal pellets probably contributed to the downward flux of detritus, as observed by Bathmann (1988).

Formation of Phytodetritus

Planktonic organisms incorporated in the detritus indicate that it originated in the surface waters. The species present included some that are typical of the spring bloom in the oceanic euphotic zone. Continuous Plankton Recorder data (J. M. Colebrook, Institute for Marine Environmental Research, Plymouth, U.K., personal communication) show that in 1986 the bloom occurred during May in the BIOTRANS area, and maximum development took place in the second half of this month.

Assuming a sinking rate of 100–150 m per day (Billett et al., 1983; Alldredge and Silver, 1988), the detritus would have reached the sea floor at 4500 m during late June or early July, leaving a period of 4–8 weeks between the times it arrived and was sampled. An even shorter residence time of some aggregates on the sea floor is suggested by the presence of coccolithophorids and cyanobacteria characteristic of summer production. This is also substantiated by the relatively high pigment and organic carbon contents of the phytodetritus (see earlier section on chemical analyses). Hence it is possible that more than one sedimentation event occurred and that these are represented in our samples. These could correspond to the "white" and "green" phytodetritus of which the white material seems to be in a more advanced state of degradation and is presumably older. It also has to be noted that the detrital material may be advected from different regions by lateral transport.

Evidence concerning the formation of phytodetritus in surface waters is provided by two small aggregates (about 1 cm diameter) caught with a multiple closing net (100 μm mesh) at 150 m and 350 m depths. They were composed of a mucus material loaded with small green algal cells, diatoms, dinoflagellates, tintinnids, juvenile planktonic foraminiferans, and masses of minipellets, similar to those observed by Gowing and Silver

(1985) and found in the detrital mater on the seabed. They also contained acantharian tests (without fecal pellets) and needles of phaeodarian Radiolaria. The aggregate from 350 m contained an almost intact phaeodarian within the mucoid matrix (Riemann, 1989). Although these aggregates may have been artifacts created mechanically within the net (Swanberg et al., 1986), similar ones have been observed and collected in shallow waters by divers (Beers et al., 1982; Alldredge and Youngbluth, 1985). Because we found the same planktonic components embedded in a gelantinous matrix on the surface of undisturbed sediment samples as well as in the plankton haul, such aggregations must occur abundantly as a natural phenomenon.

Mucus production is not well understood, but it is an important factor in aggregate formation. It was observed when diatoms are aging under conditions of nutrient depletion (Degens and Ittekot, 1984; Smetacek, 1985). Senescent cells are reported to be stickier than those of growing populations, and other particles easily adhere to them.

On one occasion we observed a "marine snowstorm" on the sea surface, at first accusing the ship's engineers of having pumped out the waste water tanks while the ship kept its position on station. However, we discovered subsequently that the white, mostly elongated flakes were made up of some sort of mucus, containing minipellets, acantharians, dinoflagellates, coccolithophorids, masses of gliding pennate diatoms and other cells (Riemann, 1989). Observing the "snowstorm" around the ship, it became apparent that the flakes seemed to originate from where the bow thrusters drew air below the sea surface. Translucent mucus flakes or invisible aggregates must have been drifting in the surface layer and became visible only from tiny trapped air bubbles. This observation indicates the possible widespread occurrence of mucus flakes, which may participate in the formation of aggregates (Riemann, 1989).

Seabed Accumulation

The aggregates presumably do not arrive on the seabed in the form of the large clumps recovered by multiple corer and documented by photographic records. The size of sedimenting particles was recorded via a camera attached to sediment traps by Asper (1987). He found the most abundant size class of aggregates to be 1.4–1.9 mm, which settled on average faster than larger aggregates (4–5 mm). In our benthic photographs, isolated aggregates about 1 cm in diameter were visible on the sea floor (Fig. 3) and they may be an indication of the predominant size of the phytodetritus during settling in the lower part of the water column.

The appearance and distribution of phytodetritus seen in most sea floor photographs may be due to bottom currents concentrating and further aggregating the material. Lampitt (1985) observed resuspension of phytodetritus at current speeds higher than 7 cm sec^{-1}. In the BIOTRANS area most frequently current speeds of 2–6 cm sec^{-1} were observed 10 m above the bottom, although abyssal storms with velocities up to 27 cm sec^{-1} also occurred (Mittelstaedt et al., 1986). In approximately 31% and 11% of the time, the current velocities exceeded 7 cm sec^{-1} and 10 cm sec^{-1}, respectively. Therefore, the light detrital material is likely to be resuspended and transported frequently. During these times it reaggregates, incorporating benthic components, and settles and concentrates behind mounds, in depressions, and other biogenic structures. Similar observations are reported by Novell and Jumars (1984) and Allev and Allev (1986). This process may also be a mechanism for the dispersal of small benthic organisms that attach to the resuspended material.

As shown both by Lampitt (1985) and by our own results, current transport can

modify the distribution of the phytodetritus, and this process will be repeated as long as the material is neither ingested, decomposed by microorganisms, nor incorporated into the sediment or trapped in depressions. Fast incorporation into the sediment of part of the material was suggested by our chemical data. The small-scale patchy distribution of food resources may thus become important for organisms on and in the seabed.

Phytodetritus as a Food Resource

Phytodetritus is assumed to play an important role in the nutrition of deep-sea organisms per se, and this may be enhanced by the presence of bacteria and their biochemical transformation of the material. We have found that some benthic meiofauna, principally foraminifers, nematodes, and possibly harpacticoid copepods, colonize the detritus. Billett et al. (1983) noted that large, deposit-feeding invertebrates were attracted to detrital patches and recent evidence suggests that some holothurian species feed readily on this material (Billett et al., 1988). Our observations on the gut content of animals support the notion that megafaunal invertebrates utilize phytodetritus as a food source. However, Silver et al. (1986) describe the presence of sporopollenin in the thick cell walls of chlorellalike cells, which are probably identical to the abundant small chlorophytes found in our investigations. This may be an indication for poor digestability of these particular cells and for some limits in the utilization of phytodetritus as a food source.

In previous investigations indirect evidence has been accumulated for a rapid biological breakdown, e.g., a disappearance of sedimented detritus within a short period of time (Rice et al., 1986). When phytodetritus was present, we observed a rise in chloroplastic pigment equivalents, proteins, carbohydrates, adenylates down to 5 cm depth, and an increase in bacterial numbers down to 6 cm depth (Table 6, Fig. 17). This implies that the detritus was to some extent incorporated into deeper sediment layers within a few weeks. On the other hand, macro- and megafaunal consumption of detritus and bacterial degradation obviously occurs rapidly and is partly localized at the sediment surface. Therefore, it is likely that mineralization of fresh phytodetritus at the sediment surface as well as incorporation of detrital components into the sediment occurs parallel. Rapid bioturbation rates have already been shown in shallow water sediments (Graf, 1987; Mahaut and Graf, 1987).

Rapid degradation of phytodetritus by heterotrophic bacteria was observed in incubation experiments under simulated in situ conditions. Approximately 1.8% of detrital POC was dissipated per day by microbial action (Lochte and Turley, 1988). This breakdown of phytodetritus as well as conversion of recalcitrant organic molecules to more easily degradable components may, therefore, be an important pathway for the final consumption of the material. The rise in bacterial numbers within the sediment during the time of phytodetritus deposition (Fig. 17) is an indication of benthic response to increased organic matter input.

The summary Table 8 provides an overview of the quantitative data giving the range from all analyzed phytodetritus samples. Additionally, the results from MC 56 and MC 57 are listed, since in these two cases the most complete sets of analyses are available. In order to relate these data to the primary production in the euphotic zone, they were normalized to 1 m^2 of seabed assuming an average phytodetritus coverage of the seabed of 10% (based on seabed photography) and a material thickness of 1 cm.

Because of the heterogeneous nature and irregular distribution of phytodetritus, the quantification of the detrital material is a problem. For instance, in the case of MC 56 and MC 57 the latter has consistently higher values, probably caused by the lesser

water content in comparison to MC 56 as indicated by their respective dry weights. The material on MC 57 was categorized on board as "green," whereas that from MC 56 was "white," and a higher age and/or stronger degradation was hypothesized for the whitish material (see earlier sections on macroscopic and microscopic appearances). However, the ratios between the two sets of data are fairly similar, which leads to the conclusion that both samples contained phytodetritus of similar "quality" but different in quantity.

The total particulate organic carbon content of phytodetritus reported by Rice et al. (1986) ranged from 0.56 to 0.85% of the detrital dry weight on the slope and 1.28% on the Porcupine Abyssal Plain, Billett et al. (1983) reported 6% from sediment traps, Deuser and Anderson (1981) measured 5% and Honjo (1980) 6.5–12.5%. The mid-Atlantic phytodetritus had an organic carbon content of 0.9–7.8% of dry weight (mean 2.3%). It appears that the detrital material collected in the mid-Atlantic was more recently deposited and may have had a higher nutritional value than that retrieved from the Porcupine Seabight. The pigment analyses support this conclusion.

The total organic carbon is, as expected, on average 10 times higher than the amount of biologically degradable carbon, although the small number of BOD samples limit this comparison (Table 8). It has to be noted that the BOD tests were carried out under conditions intended to maximize the biological oxidation of organic material and that it involves decomposition of the detrital material by bacterial communities alien to the deep sea and under incubation conditions totally different from the deep-sea environment. Therefore, it remains an open question whether degradation in situ would yield similar results or whether deep-sea adapted bacteria may utilize the detrital material further. Material from the 10–11 cm sediment horizon still contained biodegradable organic carbon, though at a lower concentration than the phytodetritus. The ultimate fate of refractory organic carbon would be burial in the sediment. Degens and Mopper (1976) estimate that in oceanic sediments, 0.2–0.6 g C $m^{-2}a^{-1}$ of the input of organic matter is permanently buried in this way.

Smetacek (1984) has remarked that little is known of the digestibility of sedimenting material. It may be assumed, however, that the biodegradation of phytodetritus since its formation at the surface results not only in a progressive decrease in its organic content, but also in an increase in the proportion of refractory organic material. Although it is not possible to relate protein- and carbohydrate-carbon (Table 8) directly to POC measurements, due to uncertainties in the applied calibrations (e.g., protein is calibrated against gamma globulin, which may not be representative for detrital matter), it appears that a high proportion of the total carbon consists of easily degradable proteins. Water soluble carbohydrates may constitute up to 10% of the organic components.

Organisms that invaded the detrital mass or developed within it, as observed for foraminifers (Gooday, 1988), nematodes, bacteria, and flagellates (Lochte and Turley, 1988; Turley et al., 1988), increase the proportion of cellular carbon. Thus not all organic matter within the phytodetritus is of surface water origin, but may have been contributed by deep-sea organisms. The same consideration applies for some of the other chemical components.

In some cases no visible detritus was found on top of the particular sediment core (MC 44), but it was present in the immediate vicinity and the measured values of CPE, proteins, CH, POC, TA, and bacterial numbers (Table 3) indicated the influence of detritus. Incorporation of phytodetritus into the sediment by bioturbation or diffusion of dissolved components may have bound some of the organic matter to the sediment before the bulk of the loose material had been removed by near bottom currents.

Phytodetrital Flux from the Euphotic Zone to the Deep-Sea Bed

Primary production in the BIOTRANS area is assumed to be in the range of 50–100 g C $m^{-2}a^{-1}$ according to Koblentz-Mishke et al. (1970), and 25% of this may be produced during the spring phytoplankton bloom, i.e., 12.5–25 g C $m^{-2}a^{-1}$. The organic carbon of the phytodetritus (71–392 mg C m^{-2}; Table 8) would therefore represent minimally 0.25% and maximally 3.1% of the spring "new" primary production. These estimates, which are based only on the amount of phytodetritus present on the sea floor, imply a sedimentation of around 0.3–3% of surface water spring primary production down to 4500 m. The primary production data assumed here are to be considered only as a guideline and will have to be adjusted when more detailed measurements are available from this region of the northeast Atlantic.

Although the percentage of surface water primary production reaching the deep-sea bottom is small, its role in the nutrition and maintenance of the deep-sea ecosystem is certainly of crucial importance. The above budget calculations neglect the possibility of prolonged sedimentation or several sedimentation events. Furthermore, they do not take into account the possibility that the analyzed phytodetritus had already been resting and consumed on the sea floor for some time. Therefore, more detailed seasonal studies are needed to evaluate the total energy input into the deep-sea benthic boundary layer by sedimentation. At this stage of the investigations, the fate of the phytodetritus in the form of biomass production by various organisms, respiration, burial of recalcitrant matter in the sediments, and removal of material by currents cannot be quantified. However, many independent observations on the microscopic scale and by chemical analysis, as presented above, indicate that the seasonal pulse in sedimentation induces measurable changes in the deep-sea environment and its living community. In order to quantify and understand these phenomena, more detailed studies are required.

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