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Responses by benthic organisms to inputs of organic material to the ocean floor: a review

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Most of the photosynthetically produced organic material reaching the ocean-floor is transported as settling particles, among which larger particles such as faecal pellets and macroaggregates (marine snow) are particularly important. Recent studies in the northeastern Atlantic have demonstrated that macroaggregates originating from the euphotic zone settle at a rate of approximately 100–150 m d^{-1} to form a deposit (phytodetritus) on the sediment surface. Bacteria and protozoa (flagellates and foraminifers) rapidly colonize and multiply on phytodetritus, while large deposit feeding animals ingest it. Other inputs, for example *Sargassum*, wood and vertebrate carcasses, also evoke a rapid response by benthic organisms. However, the taxa that respond depend on the form of the organic material. The intermittent or seasonally pulsed nature of phytodetritus and many other inputs regulate the population dynamics and reproductive cycles of some responding species. These are often opportunists that are able to utilize ephemeral food resources and, therefore, undergo rapid fluctuations in population density. In addition, the patchy distribution of much of the organic material deposited on the ocean-floor probably plays a major role in structuring deep-sea benthic ecosystems.

Introduction

The presence and persistence of life itself on the ocean-floor can be viewed as a response to organic inputs. The deep sea is a food-limited environment (Dayton & Hessler 1972; Thiel 1979) in which the abundance and biomass of benthic organisms is related directly to the amount of food reaching the sediment surface (Sibuet *et al.* 1984; Sibuet 1987; Tseytlin 1987). This relation applies to the meiofauna (see Thiel 1983), the macrofauna (see Carey 1981; Rowe 1981, 1983; Thiel 1982), and the deposit feeding megafauna (see Lampitt *et al.* 1986; Sibuet *et al.* 1984; Sibuet 1987). Thus, in general terms, benthic biomass is highest near continental margins and under upwelling areas, where primary production is greatest, and decreases towards the oligotrophic central oceanic regions (Hessler 1974; Rowe 1983). Sediment community oxygen consumption also tends to decline with increasing water depth and decreasing surface primary productivity (Smith *et al.* 1983; Smith 1987).

Only a few percent of the primary production generated by photosynthesis reaches the deep-sea floor. The main pathway is provided by particles settling through the water column from the euphotic zone (Rowe 1981; Angel 1984; Fowler & Knauer 1986; Alldredge & Silver 1988; Thiel *et al.* 1990). These particles are of several main types. (1) Large animal remains (mainly vertebrate carcasses); (2) large plant remains (macroalgae, seagrasses, terrestrial material); (3)

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larger particles (faecal pellets, zooplankton carcasses, crustacean moults, skeletal remains of zooplankton and phytoplankton); (4) macroaggregates (marine snow). In addition, turbidity currents and submarine slides may inject significant amounts of organic matter into benthic ecosystems near the base of the continental slope and on adjacent abyssal plains (Griggs *et al.* 1969; Huggett 1987). Upward fluxes of organic matter from the ocean floor may occur also (Smith *et al.* 1989*b*).

Over much of the ocean-floor larger particles (particularly faecal pellets) and macroaggregates originating from surface production, provide the major organic input (McCave 1975; Bruland *et al.* 1989). Considerable data about such fluxes have been obtained from sediment trap and other studies (Fowler & Knauer 1986; Takahashi 1986). These demonstrate a rapid delivery of particles from the photic zone and, in some areas, a distinct seasonal variation in fluxes (reviewed by Tyler 1988). Clear evidence for a seasonal deposition of macroaggregates, consisting largely of plant and animal remains ('phytodetritus'), has been provided recently by time-lapse photography of the sea floor and sediment coring in the northeastern Atlantic (Billett *et al.* 1983; Lampitt 1985; Rice *et al.* 1986; Thiel *et al.* 1990).

A fundamentally different form of organic input originates from hydrothermal vents where hot fluids of volcanic origin are discharged through fissures in the ocean crust. These fluids contain reduced compounds (for example, hydrogen sulphide), which are probably used as an energy source for primary production by chemautotrophic bacteria (Jannasch & Mottl 1985). The high microbial activity and biomass supports a huge animal biomass (Grassle 1986). Similar chemosynthetically based communities have been discovered around cold seeps along tectonically active margins, around brine and hydrocarbon seeps near passive margins (Sibuet *et al.* 1988 and references therein), on turbidity current deposits on the Laurentian Fan (Mayer *et al.* 1988) and on oil-laden whale bones (Smith *et al.* 1989*a*).

Vent communities are of enormous scientific interest, but their impact, if any, on the normal sediment communities that occupy more than 99% of the ocean floor remains largely unknown. For this reason, and because vent communities are well described, we consider only those inputs originating from photosynthetic production. Our discussion is also limited to organisms living in and on the sediment and excludes the near-bottom plankton. The review centres around recent work on benthic responses to phytodetrital deposition in the northeastern Atlantic. For convenience, it is divided into sections dealing with different elements (a mixture of taxa and size categories) of the benthic community. Within each section, we consider responses both to phytodetritus and, where appropriate, to some other kinds of organic input. First, however, we briefly describe the occurrence and nature of phytodetritus.

PHYTODETRITUS

The mass sedimentation of organic detritus to the ocean floor following the spring bloom was first described in detail from the Porcupine Seabight (an area centred around 51° 13′ N; 13° 00′ W in the northeastern Atlantic (*ca.* 51° N, 13° W)). Here phytodetritus is usually present in varying amounts between the spring and late summer at depths of 1000–4500 m (Billett *et al.* 1983; Lampitt 1985; Rice *et al.* 1986). It also occurs in the Rockall Trough, on the Porcupine Abyssal Plain (Barnett *et al.* 1982) and in the northern Bay of Biscay (Sibuet 1985, 1987). Similar material has been collected some 500 miles southwest of the Porcupine Seabight at a more oceanic site (47° 00′–47° 30′ N; 19°–20° W), studied intensively by German scientists under the BIOTRANS (biological vertical transport and energetics of the benthic boundary layer of the deep sea) programme (Lochte & Turley 1988; Riemann 1989; Thiel *et al.* 1990). Material resembling phytodetritus has been recorded on the western side of the Atlantic at bathyal and abyssal depths (Aller & Aller 1986; Grassle & Morse-Porteous 1987) and photographed at 4469 m in the eastern Pacific (Gardner *et al.* 1984). Pigment concentrations in sediments suggest that phytoplankton deposition may occur at bathyal depths in the tropical southwest Pacific and the Arctic (Alongi 1987; Pfannkuche & Thiel 1987).

Phytodetritus contains a wide variety of planktonic remains, including those of diatoms, coccolithophorids, dinoflagellates, silicoflagellates, phaeodarians, tintinnids, foraminifers, crustacean eggs and moults, protozoan faecal pellets ('minipellets'), nano- and picoplankton cells (chlorophytes, cyanobacteria and bacteria), embedded in a gelatinous and membranous matrix (Billett *et al.* 1983; Lochte & Turley 1988; Riemann 1989; Turley 1990; Thiel *et al.* 1990). The colour variation of phytodetritus, from green to white, together with variations in its planktonic constituents, indicates that several pulses may be deposited during the late spring and summer (Billett *et al.* 1983; Lochte & Turley 1988; Thiel *et al.* 1990). The presence of relatively undegraded algal cells and viable cyanobacteria reflect its rapid sedimentation (Lochte & Turley 1988).

The organic carbon content of phytodetritus varies from 0.56–7.8% and this variation probably arises from differences in the degree of degradation of individual samples (Lochte & Turley 1988). On the sea-floor, phytodetritus often occurs in biogenic depressions, tracks and holes (Billett *et al.* 1983; Rice 1983; Rice *et al.* 1986) and accumulates behind sediment mounds (Thiel *et al.* 1990). For example, during *Cyana* dives in the Bay of Biscay (2000 m), Sibuet (1987, p. 127) observed centimetre to decimetre sized areas of brown phytodetritus that had accumulated in hollows caused by bioturbation. This material was present for only a few months during the summer. Time-lapse photography showed that it can be resuspended by bottom currents (Lampitt 1985). Thiel *et al.* (1990) suggested that pieces may snowball into larger lumps as currents roll them across the sea-floor. The extremely patchy sea-floor distribution of phytodetritus, resulting from microtopography and current activity, is also reflected in the chemical variability of sediments collected during the summer compared with those collected before the spring bloom (Thiel *et al.* 1990).

In the following discussion we mention results based on material collected during *Meteor* cruise 3 (1986) (Thiel *et al.* 1990) in the abyssal BIOTRANS area (4550 m water depth), and at a much shallower bathyal site in the Porcupine Seabight (51° 36′ N, 13° 00′ W; 1340 m depth) which was sampled intensively during *Challenger* cruises 6/82 and 10/82. Most of the material was collected using a multiple-corer (Barnett *et al.* 1984). This gear collects samples of sediment and overlying water in which the sediment surface is virtually undisturbed and, therefore, is ideal for sampling light, flocculent material such as phytodetritus.

BENTHIC RESPONSE

(*a*) *The community*

A very quick community response to the deposition of phytoplankton blooms occurs in some shallow water environments, for example, the Kiel Bight (Graf *et al.* 1983, 1984; Meyer-Reil 1983). On theoretical grounds, Martin & Bender (1988) concluded that seasonal variations in fluxes of labile organic compounds, such as those resulting from phytodetrital deposition, may have sufficient amplitude at middle and high latitudes to evoke a similar response in the deep sea. Evidence for such a response is provided by the data of Smith & Baldwin (1984) and Smith (1987), who found that sediment community oxygen consumption was highest in early summer and lowest in late autumn and winter along a transect from the euphotic eastern to the oligotrophic central North Pacific (1300–5900 m). Initially, these variations were attributed to seasonality in the supply of sinking organic material (Smith & Baldwin 1984). However, Smith (1987) subsequently failed to detect consistent seasonality in particulate fluxes measured concurrently with sediment community oxygen consumption and concluded that his results did not confirm the previously suspended direct coupling between these two parameters.

Using a novel experimental approach, Cahet & Sibuet (1986) conducted *in situ* incubations in the Bay of Biscay (2000 m). They found that the benthic communities (bacteria, nanobiota, meiofauna) responded in less than three hours when ^{14}C labelled glucose solution and particulate organic substances (carbohydrate mixed with ^{14}C labelled algae) were injected into the sediment–water interface from the submersible *Cyana*. After 24 h incubation on the ocean floor, 84 % of the ^{14}C radioactivity was incorporated into the benthic biota whereas only 4 % was incorporated during the same period under surface conditions (1 atm†, 4 °C). These results demonstrate that a substantial degree of organic degradation occurs very rapidly in the deep sea and also emphasize the need for more *in situ* experimentation.

(*b*) *Bacteria*

(i) *Responses to phytodetritus*

Rice *et al.* (1986) studied cores from different parts of the Porcupine Seabight and the adjacent abyssal plain. There were no significant differences between total counts and biomass estimates for bacteria in phytodetritus, superficial sediment beneath phytodetritus, and sediment not overlain by phytodetritus. However, the significantly higher frequency of dividing cells, and the larger mean cell volumes in both the phytodetritus and the underlying sediment, indicated that microbial activity was greater within and immediately beneath the detrital aggregates than in normal sediments.

BIOTRANS phytodetrital samples were colonized by dense, active populations of heterotrophic, non-pigmented bacteria and larger, but less abundant photosynthetic, pigmented cyanobacteria (Lochte & Turley 1988; Thiel *et al.* 1990). The *Synechococcus*-like cyanobacteria were still viable and likely to have originated in the euphotic zone. Together, these procaryotes accounted for 0.5–5.0 % of the total particulate organic carbon in the phytodetritus. When incubated under *in situ* temperatures and pressures, the bacteria quickly multiplied, doubling approximately twice per day, converting some of the detritus into bacterial carbon and respiring the remainder as CO_2. It is estimated that about 1.8 % of detrital particulate organic carbon was degraded each day by this microbial activity such that the detritus would be consumed within two months of reaching the sea floor (Lochte & Turley 1988; Suess 1988).

To see if this was a microbial response by benthic, rather than by surface derived bacteria, Turley & Lochte (1990) undertook a second study in which sterilized phytodetritus was incubated with sediment contact water from the BIOTRANS site. Rapid bacterial colonization and growth was observed under surface and deep-sea conditions, in both cases leading to a

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† 1 atm ≈ 10^5 Pa.

doubling time of about one day. However, the rate of bacterial decomposition was significantly faster at 450 atm, indicating that at least some components of this deep-sea microbial community were barophilic.

Turley *et al.* (1988) and Thiel *et al.* (1990) presented data on bacterial abundances in a multiple-corer sample overlain by phytodetritus. Bacteria were considerably more abundant in all sediment layers studied (down to 10 cm) than in the detritus itself, with a subsurface peak in the 4–6 cm layer (Thiel *et al.* 1990). Bacterial abundances also were significantly higher in sediments collected during July–August 1986 and September 1985 than before the deposition of phytodetritus in May 1985 (Thiel *et al.* 1990). They suggest that the infaunal bacterial response resulted from the rapid incorporation of organic material into the sediments. Presumably, this was caused by the activities of burrow-dwelling organisms such as sipunculans (Romero-Wetzel 1987).

Aller & Aller (1986) examined the distribution and abundance of organisms around burrows at the high energy benthic boundary-layer event (HEBBLE) site on the Nova Scotia Rise (4820 m). Most of the burrows were filled with anoxic detritus rich in diatoms which apparently had arrived recently from the euphotic zone. Bacteria and meiofauna (nematodes and foraminifers) were significantly more abundant around and within the borrow infills than in the surrounding sediments. Aller & Aller (1986) speculated that bacteria and other organisms could respond, in a matter of hours or days, to the rich energy source provided by undecomposed detrital material.

(ii) *Responses to inputs of organic material other than phytodetritus*

Except in the region of hydrothermal vents, rates of microbial activity are slower in the deep sea, mainly as a result of low temperature (Jannasch & Wirsen 1984). Nevertheless, there is growing evidence that indigenous deep-sea bacteria can react quickly to a variety of organic inputs. Highly labile substances, such as flesh and bread, were consumed or decayed within ten weeks when held in perforated double containers 5 m above the ocean-floor at 5200 m depth (Sieburth & Dietz 1972). Similarly, Seki *et al.* (1974) reported that normally rare barophilic bacteria quickly multiplied when brought into contact with dissolved organic nutrients just above the floor of the subarctic Pacific (5207 m). There was little activity when the experiment was conducted under surface conditions. Refractory substances, such as wood, were also colonized by dense populations of bacteria, some of them filamentous, when exposed on the sea floor for periods of several months (Kohlmeyer 1980; Gardener *et al.* 1983; Desbruyères *et al.* 1985). Recently, particular emphasis has been placed on the importance of organic-rich microenvironments, such as those provided by freshly settled particles (for example, pelagic faecal pellets), benthic faeces, animal burrows, decaying invertebrate carcasses and particularly animal guts, as sites of intense microbial activity in the deep sea (for example, Yayanos *et al.* 1981; Sibuet *et al.* 1982; Deming & Colwell 1982, 1985; Deming 1985, 1986; Jannasch & Wirsen 1984; Meadows & Tait 1985). These results, together with Lochte & Turley's (1988) observations on phytodetritus, indicate that some populations of deep-sea benthic (or near benthic) bacteria fluctuate according to the relative abundance of organic material on the ocean-floor. Other kinds of barophilic bacteria, which are adapted to growing slowly, steadily and efficiently in low nutrient conditions, may also inhabit deep-sea sediments (Deming 1986).

Most of the organic matter arriving on the ocean floor is rapidly utilized by benthic communities and only a small proportion enters the sedimentary record (Khripounoff *et al.*

1985; Khripounoff & Rowe 1985; Riemers 1989; Turley & Lochte 1990). *In situ* experiments conducted by Cole *et al.* (1987) indicated that 50–85% of fresh, surface produced material was decomposed each year at their abyssal station (3856 m) in the Panama Basin. The incubation experiments of Turley & Lochte (1990) support the notion of rapid benthic decomposition. They found that the phytodetrital decay rate was logarithmic with approximately 28% of the material being decomposed within the first three weeks of its arrival on the sea floor. Direct visual evidence for very rapid decomposition is provided by time-lapse photographs taken in the abyssal (4873 m) eastern Pacific that show the disappearance, in about two weeks, of a mucus sheath abandoned by an enteropneust (Paul *et al.* 1978; Thorndike *et al.* 1982). Faecal pellets also decomposed more rapidly than expected at a nearby site (Gardener *et al.* 1984). Bacteria (and their predators) probably play a central role in these decomposition processes (Jumars *et al.* 1989). Rowe & Deming (1985) estimated that bacteria are responsible for 15–30% of benthic remineralization in the deep sea. Smith *et al.* (1987*a*, see also Smith *et al.* 1987*b*) concluded that microbial metabolism in the sediments and overlying nepheloid layer accounted for more than 70% of the carbon remineralization in the Santa Catalina Basin (1300 m).

The studies reviewed above indicate that organic material deposited at the sediment–water interface is subjected to intense microbial activity, resulting in high respiration and remineralization rates. It is likely, therefore, that anthropogenic inputs of organic material, such as sewage sludge, would initially stimulate a similar biological response, leading to high utilization of O_2 and production of CO_2. The degree of deoxygenation of the benthic boundary layer would also depend on the amount of material deposited, its degree of dispersion on the sea floor and the exchange of oxygen between the benthic boundary layer and overlying water.

(*c*) *Flagellates*

Responses to phytodetritus

Lochte & Turley (1988) reported that a population of barophilic flagellates developed when phytodetritus was incubated under 450 atm at 2 °C. In a separate study, which integrated descriptive and experimental approaches, Turley *et al.* (1988) described a similar flagellate, identified as *Bodo* sp., which flourished when sterile phytodetritus was incubated under the same *in situ* conditions with sediment contact water from 4500 m depth. After a lag of 16 days, growth was exponential with a mean doubling time of 2.11 days. When corrected for temperature differences this was within the range for shallow-water flagellates living at approximately 15–20 °C (Turley *et al.* 1988). No growth occurred at 1 atm. Like other bodonids, this flagellate ingested bacteria. An estimated 75–83% of the bacterial carbon consumed was dissipated by respiration and excretion and the remaining 17–25% converted into flagellate biomass. The flagellate probably lives in superficial deep-sea sediments and flourishes when able to graze on detrital bacterial populations. Lochte & Turley (1988) suggested that grazing by *Bodo* sp. reduced the size of the bacterial populations that developed in their pressurized incubations. The development of large populations of flagellates and amoebae in the western Coral Sea may also be related to the deposition of phytodetritus (Alongi 1987).

The growth of populations of bacterivorous flagellates on phytodetritus suggests that parallels exist between microbial communities on detritus in shallow and deep water. Flagellates, including bodonids, are important consumers of bacteria attached to decaying

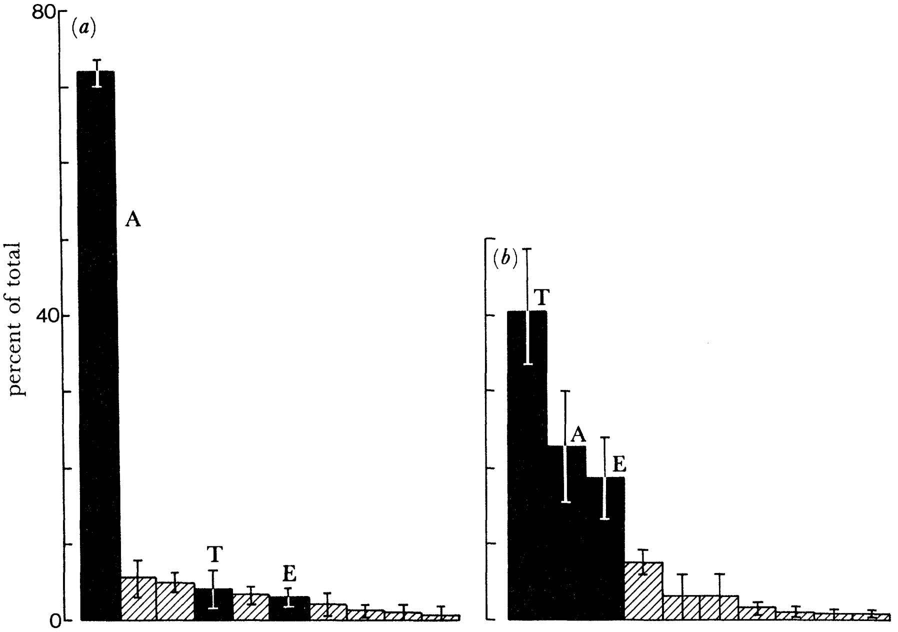

Figure 1. Percentage abundances of foraminiferal species in phytodetrital samples from the northeastern Atlantic. For (*a*) the Porcupine Seabight site (1340 m), each bar represents the mean of six samples (total of 979 rose Bengal stained specimens); for (*b*) the BIOTRANS site (4550 m), each bar represents the mean of five samples (total of 1100 stained specimens). Locations are given in the text. Species occurring at both sites are shown in black: A, *Alabaminella weddellensis*; E, *Epistominella exigua*; T, *Tinogullmia* sp.nov.

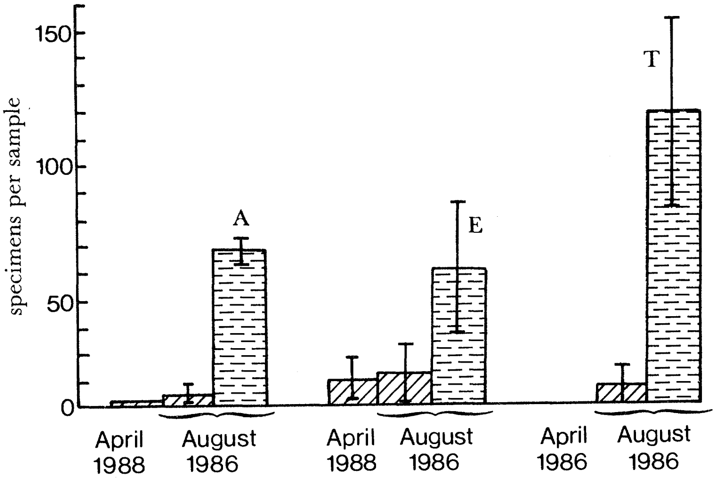

Figure 2. Abundance of three foraminiferal species in phytodetrital and sediment samples from the BIOTRANS site (4550 m). Bars represent the mean number of rose Bengal stained specimens in two (April 1988) and five (July 1986) subsamples (0–1 cm depth, 3.46 cm^2 surface area). In July, specimens occurred in both phytodetritus (horizontal dashed shading) and sediment (oblique shading). Phytodetritus was not present during April. A, E, T as figure 1.

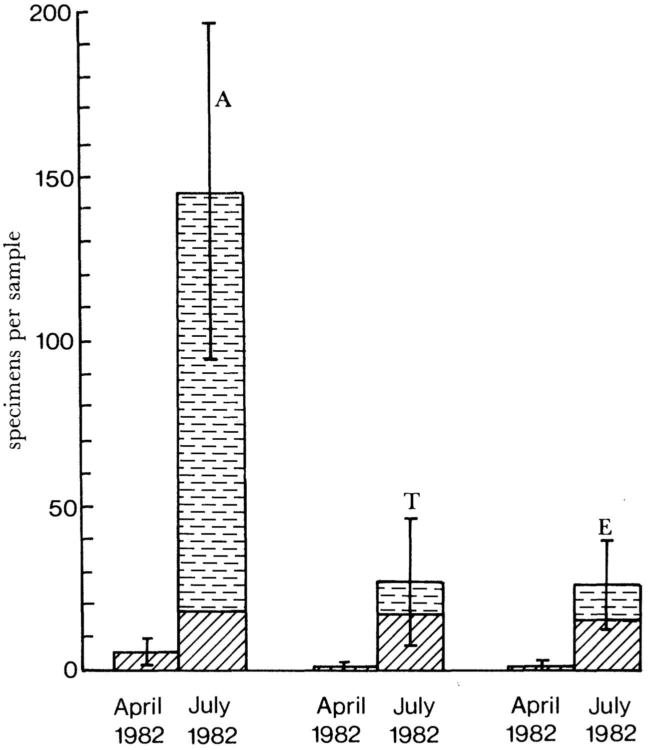

FIGURE 3. Abundance of the three foraminiferal species in phytodetrital and sediment samples from the Porcupine Seabight (1340 m). Bars represent the mean number of rose Bengal stained specimens in eight (April 1982) and five (July 1982) subsamples (0–1 cm depth, 3.46 cm^2 surface area). In July, specimens occurred in both phytodetritus (horizontal dashed shading) and sediment (oblique shading). Phytodetritus was not present during April. A, E, T as figure 1.

aquatic vegetation in coastal waters (Fenchel & Jorgensen 1977) and to detrital aggregates in the ocean plankton (Caron 1987).

(d) *Foraminifera*

(i) *Response to phytodetritus*

Like bacteria, some foraminiferal species responded directly to phytodetritus. Samples from the BIOTRANS and Porcupine Seabight sites were inhabited by numerous specimens (mostly 50–200 μm in size) representing some 10–11 species (figure 1), considerably fewer than in superficial sediment samples taken directly beneath the phytodetritus (Gooday 1988; Gooday & Lambshead 1989). In the BIOTRANS material, detrital aggregates collected in August 1986 were dominated by three species, *Epistominella exigua*, *Alabaminella weddellensis* and *Tinogullmia* sp.nov., which were much less abundant in the sediment populations. Two surface sediment samples obtained in April 1988, before the spring bloom in the BIOTRANS area, yielded fewer specimens of these species (figure 2), indicating that populations diminish drastically with the dispersal of the ephemeral phytodetritus habitat towards the end of the summer.

Detrital populations from the Porcupine Seabight, sampled during July 1982, were dominated by *A. weddellensis* (75 % of specimens) (figure 1). Also present were small numbers of *E. exigua* and *Tinogullmia* sp.nov. (Gooday & Lambshead 1989). All three species were also fairly common in the 0–1 cm layer of sediment directly underlying the phytodetritus. They were significantly more abundant in these sediments than in similar samples collected in the same area during April 1982, before the deposition of phytodetritus. At both the bathyal and abyssal sites, therefore, certain foraminiferal species flourish during the summer, apparently as a direct response to phytodetritus.

Several observations indicate that these foraminifers feed on phytodetritus (A. J. Gooday & C. M. Turley, unpublished work). First, the distinctive green protoplasmic colouration of the calcareous species (*E. exigua*, *A. weddellensis*, *Bulimina* sp., *Pyrgoella* sp.) is probably due to the ingestion of small eucaryotic algae (chlorophytes), which are a component of the detritus (Thiel *et al.* 1990). In transmission electron microscopy sections of *E. exigua*, the protoplasm contains numerous 2–3 μm diameter bodies which are believed to be chlorophytes. Secondly, the three dominant phytodetritus-dwelling species all display bright orange autofluorescence, characteristic of phycoerythrin-containing cyanobacteria, when examined using epifluorescence microscopy (green excitation 450–490 μm). Finally, feeding on bacteria is indicated by preliminary incubation experiments conducted under *in situ* conditions (A. J. Gooday & C. M. Turley, unpublished work). An allogromiin incubated for five days consumed bacteria-sized fluorescent microspheres. This specimen resembled the phytodetritus-dwelling *Tinogullmia* sp.nov., which has unpigmented protoplasm and, therefore, is assumed not to ingest green algae.

We hypothesize that when the phytodetritus arrives on the sediment surface in the late spring and early summer, it is colonized by benthic foraminifers that feed on the detritus and associated organisms. They subsequently reproduce rapidly and build up large populations. The colonizing species, which represent a small proportion of the total foraminiferal diversity in the sediments, display some opportunistic characteristics. These include the ability to utilize a transient habitat, a large population size, and population fluctuations due to rapid reproduction followed by large-scale mortality (Grassle & Grassle 1974). At least one of the colonizing species (*E. exigua*) has a widespread distribution, another feature of opportunists (Grassle & Saunders 1973). Interestingly, the protoplasm of *E. exigua* specimens from BIOTRANS samples collected in April 1988, before the spring bloom (see above), contained numerous small green cells, presumably planktonic algae. It seems likely that small amounts of phytodetritus continue to settle from the euphotic zone throughout the year and sustain small populations of this (and other) species during periods of relative famine following the disappearance of obvious detrital deposits from the sea bed.

Unlike the bacterial populations referred to above, there is no evidence that infaunal foraminiferal assemblages respond rapidly to phytodetritus. The vertical distributions of both total populations and individual species was broadly similar in the top 5 cm of horizontally sectioned subcores collected during April and July in the Porcupine Seabight (A. J. Gooday, unpublished observations). That is, there was no obvious upward relocation of infaunal foraminifers following detritus deposition. These species are probably utilizing a different source of organic carbon than those inhabiting phytodetritus. This implies the existence of a trophic segregation between surface and infaunal species, similar to that observed in mesocosm studies of soft-bottom communities (Rudnick 1989).

A foraminiferal response to phytodetritus may occur on the continental shelf and slope. In the North Sea (Fladen Ground, 117–141 m) Faubel *et al.* (1983) recorded a tenfold increase in foraminiferal population density within six weeks of the arrival of the spring bloom on the sea floor. The metazoan meiofauna, on the other hand, reacted much more slowly and did not reach maximum development until the winter. On the outer Arctic shelf (northern Barent Sea, at 240 m and 320 m), Pfannkuche & Thiel (1987) found large numbers of benthic foraminifers associated with sediment-bound chlorophyll and phaeopigments. These populations were dominated by a small, spherical agglutinated species which may have been responding opportunistically to the deposition of phytodetritus.

Possible fossil analogues of these modern phytodetrital assemblages have been described by Caralp (1984) from the northeastern Atlantic (2000–2600 m). Three foraminiferal species, *Bulimina exilis*, *Melonis barleeanum* and *Chilostomella* sp., occur abundantly in Holocene and Pleistocene deposits rich in radiolarians and diatoms (indicators of productivity). Caralp (1984) proposed that these species flourished in the presence of rapidly deposited organic matter of high nutritive quality. More recently, Caralp (1989) has concluded that *B. exilis* favours fresh organic material deposited from upwelling waters, whereas *M. barleeanum* (an infaunal species, Gooday 1986) prefers more degraded material.

(ii) *Responses to organic inputs in other areas*

Foraminifers are an important component of the meiofauna and macrofauna in many deep-sea areas (Thiel 1983; Gooday 1986; Alongi & Pichon 1988). Geological studies have established that food supply, as reflected in the organic carbon content of the surface sediments, is a major factor influencing their broad scale distribution patterns (van der Zwaan 1982). Dense foraminiferal assemblages may develop in areas of the outer shelf and upper slope subject to intense upwelling; for example, off southwest Africa (Basov 1976) and northern Florida (SenGupta *et al.* 1981). A similar relation exists between foraminiferal biomass and oceanic fluxes in deep water off northwest Africa (Altenbach & Sarnthein 1989). Here, Lutze *et al.* (1986) identified a 'high productivity group' of species whose occurrence in cores reflected periods of more intense upwelling and hence delivery of organic material to the sea floor. Lutze (1980) and Lutze & Coulbourne (1984) emphasized the correspondence between the distribution of 'high productivity' species, such as *Uvigerina peregrina*, and organic carbon in modern sediments in the same area of the northeastern Atlantic. A correlation between foraminiferal species and food availability was also described by Mackensen *et al.* (1985) in the Norwegian Sea. These studies indicate that for some species (e.g. *Uvigerina peregrina*), distribution patterns are controlled by the quantity and quality of available organic material rather than by bottom water masses as commonly supposed (Corliss *et al.* 1986). The nature and origin of the organic material is unspecified. However, in upwelling areas and the Norwegian Sea it is likely that much of the input would be delivered as phytodetritus.

(*e*) *Metazoan meiofauna*

Response to phytodetritus

There is no difference in the gross taxonomic composition and density of metazoan meiofaunal populations in sediment samples collected in the Porcupine Seabight before (April) and after (July) the deposition of phytodetritus (A. J. Gooday & O. Pfannkuche, unpublished work). The vertical distribution of the organisms is also virtually identical in the two sets of samples. These data indicate that, in general, small metazoans react less vigorously than small foraminifers to detrital inputs.

However, there is evidence that particular metazoan taxa respond to phytodetritus. BIOTRANS samples contained nematodes, harpacticoid copepods, and occasional kinorhynchs

(Thiel *et al.* 1990). The nematodes were most abundant, occurring in densities of less than 10 to about 100 per ml of detritus. Monhysterids and chromadorids predominated and a species of *Monhystera* was particularly abundant (Thiel *et al.* 1990). Members of this genus are usually confined to coastal and sublittoral environments and thrive in rotting seaweed stranded on the shore-line. Harpacticoids were as abundant in phytodetritus as in the underlying sediments. However, the exuviae of adults and nauplii were significantly more abundant in the detritus. Many of these exuviae belonged to the Ectinosomatidae, although live specimens of this family were not encountered in the detrital aggregates. This may indicate that ectinosomatids colonise the phytodetritus and feed, moult and reproduce in it. Alternatively, the exuviae may have been incorporated passively into the aggregates during their sedimentation or after their arrival on the sea bed (Thiel *et al.* 1990).

(*f*) *Metazoan macrofauna and megafauna*

(i) *Response to phytodetritus*

Echinoderms often dominate the deposit-feeding megafauna in the deep sea and it was suggested, more than a hundred years ago, that some abyssal species may feed on phytoplankton remains (Castracane degli Antelminello 1886). One important group, the holothurians, feed selectively using their prehensile oral tentacles and some deep-sea species can select organic-rich particles (Khripounoff & Sibuet 1980; Sibuet *et al.* 1982; Sibuet 1984, 1987). Evidence that certain holothurians feed on superficial sediment, rich in organic material, is provided by Billett *et al.* (1988). The gut contents of four species from the Porcupine Seabight were compared with superficial sediment collected with a multiple-corer from the same area. Pigment analyses revealed the presence of chlorophylls and their degradation products in the guts of all four species. Billett *et al.* (1988) concluded that some holothurians feed 'readily and indiscriminately on the detritus' when it is homogeneously distributed, a view supported by bottom photographs (Billett *et al.* 1988, fig. 6), which showed one of the species studied (*Benthogone rosea*) apparently browsing on phytodetritus. The patchy distribution of *B. rosea* in the Bay of Biscay may be related to heterogeneity in the food content of the superficial sediments (Sibuet 1987). Bottom photographs indicate that other echinoderms, notably the ophiuroid *Ophiomusium lymani* (Billett & Hansen 1982, fig. 6B), and the echinoid *Echinus affinis* (Grassle *et al.* 1975; Billett *et al.* 1983; Lampitt 1985; Rice *et al.* 1986, fig. 2B; Grassle & Morse-Porteous 1987, p. 1913; Lampitt & Billett 1988), are also attracted to patches of detritus. There is recent evidence that *E. affinis* feeds mainly on freshly deposited phytodetritus during the summer (de Siquiera Campos *et al.* 1990). Finally, large concentrations of the holothurian *Kolga hyalina* may be related to detrital accumulations (Billett & Hansen 1982).

Thiel *et al.* (1990) observed an amphipod inside a phytodetrital aggregate from the BIOTRANS site. Scanning electron microscope examination of associated faecal pellets showed that the amphipod had ingested phytodetritus. This material was also found in the guts of holothurians, asteroids, sipunculans and actinians from the same area (Thiel *et al.* 1990). 'Flocculent organic material', possibly phytodetritus, was ingested by ophiuroids in the Rockall Trough (Pearson & Gage 1984). In two species (*Ophiocantha bidentata* and *Ophiocten gracilis*) it was more abundant during the summer, when phytodetritus might be expected to occur on the sea floor.

Tyler (1988), Tyler *et al.* (1982) and Harrison (1988) developed the hypothesis that a direct link exists between the deposition of phytodetritus and the seasonal patterns of reproduction observed in some deep-sea macrofaunal and megafaunal animals. Seasonal reproduction is best documented among echinoderms, but species belonging to a wide spectrum of other taxa, including isopods, bivalves, brachiopods, scaphopods, actinians, decapods and macrurid fish, apparently also display this phenomenon (Tyler 1988; Harrison 1988). The sudden influx of food either ensures the survival of planktotrophic larvae or fuels the process of vitellogenesis which is observed during the summer and autumn in some echinoderm species, for example, *E. affinis* (Tyler & Gage 1984; de Siquiera Campos *et al.* 1990). The delivery of phytodetritus may also be responsible for seasonal growth, evidence for which is provided by rings and banding in bivalve and brachiopod shells, the skeletal plates of crinoids and echinoids, and fish otoliths (Duco & Roux 1981; Gage 1987; Tyler 1988). Merrett (1987) has suggested that distinct differences between abyssal demersal fish populations in different regions of the northeastern Atlantic are related ultimately to a switch from the seasonal delivery of organic material (presumably phytodetritus) north of the Azores to a lack of seasonality in the more oligotrophic region to the south.

The link between phytodetritus and seasonal growth and reproduction is presumably trophic (Tyler 1988). Despite its low organic carbon content, phytodetritus recovered from the BIOTRANS site had carbon:nitrogen ratios and plant pigment concentrations characteristic of relatively undegraded material (Lochte & Turley 1988; Thiel *et al.* 1990). Deposit feeders that ingest this material are probably utilizing easily degradable organic compounds (lipids and proteins) and bacteria (Sibuet *et al.* 1982). The large populations of bacteria ($3-165 \times 10^6$ cells mg^{-1}) and cyanobacteria ($2-4 \times 10^6$ cells mg^{-1}) together comprised 0.5–5% of the total particulate organic carbon in BIOTRANS samples of phytodetritus (Lochte & Turley 1988). The results of Sibuet *et al.* (1982) and Deming & Cowell (1982) indicate that some holothurians harbour barophilic bacterial populations in their hindguts. These may convert more refractory organic compounds, not absorbed in the foregut, into molecules that can be assimilated by the host.

Foraminifers undoubtedly are ingested by consumers of phytodetritus but may have little nutritive value (for example, Buzas *et al.* 1989 and references therein). The deep sea isopod *Amuletta abyssorum* apparently actively selects foraminifers as food items (Wilson & Thistle 1985) and scaphopod molluscs feed almost exclusively on these protozoans (Davies 1987). Scaphopods are fairly abundant among the macrofauna in box-cores collected in the Rockall Trough (Davies 1987). In two species, *Cadulus cylindratus* and *Pulsellum lofotense*, the buccal pouch contained more foraminifers in summer months (May to September) than winter. The ratio of planktonic to benthic tests was also higher during the summer. Many of the planktonic foraminifers contained protoplasm and, therefore, were of potential nutritive value. The seasonal sedimentation of planktonic foraminifers has been described by Thunnell & Reynolds (1984). *Cadulus cylindratus*, in addition to showing a seasonal variation in the quantity and identity of ingested food items, also had a seasonal cycle of gamete production. Hence, this species appears to display both a trophic and a reproductive response to food pulses.

(ii) *Responses to organic material other than phytodetritus*

Deep sea benthic metazoans display a broad spectrum of ecological strategies and trophic requirements and hence a wide variety of responses to organic inputs. Here, we highlight a few important studies which illustrate a range of macrofaunal and megafaunal responses to different kinds of input.

Wolff (1979) has reviewed the numerous records of associations between animals and plant material including seagrasses, macrophytes (for example, *Sargassum*) and a wide variety of terrestrial material such as twigs, branches and fruit. Such material may provide food, a substrate for attachment or shelter for benthic organisms. Deep-sea animals known to ingest plant material include sipunculans, echiuroids, polychaetes, gastropods, bivalves, isopods, amphipods, asteroids, echinoids and possibly polyplacophorans, ophiuroids and fish (Wolff 1979). Perhaps the most specialized herbivores are deep-sea boring bivalves of the family Pholadidae, subfamily Xylophagainae. Members of this diverse taxon (3 genera, 40 species, Turner 1981) have long been known to bore into wood and other plant remains (Knudsen 1961). Turner (1973) was the first to investigate their ecology in any detail. She described how species of *Xylophaga* and *Xyloredo* responded dramatically to the presence of wood panels placed on the sea floor off the Bahamas at 1830 m for 104 days. When recovered, the wood was riddled with borings. The bivalves had settled as larvae and grown to maturity during a three month period. The adults contained enormous numbers of eggs. These species showed all the characteristics of opportunists, including rapid growth, early maturity, an efficient larval dispersal mechanism and the ability to utilize a transient food resource (Turner 1973).

Grassle & Morse-Porteous (1987) studied the abundance of macrofaunal animals in relation to three kinds of organically enriched samples: (1) box-corer with decomposing *Sargassum*; (2) azoic sediments with added organic material (ground fish) in experimental sediment trays; (3) cores taken around experimental wood blocks. Certain species were found to be common in the enriched samples but not in the background community. Prominent among these were capitellid and spionid polychaetes. Capitellids occur in other organic-rich deep sea microhabitats, for example, among faecal pellets lining the burrows of dead xylophagid bivalves (Turner 1977). Another polychaete, *Ophryotrocha*, which occurred in very high densities in cores with rotting *Sargassum* (Grassle & Morse-Porteous 1987), has also been found in a piece of *Xylophaga*-bored pine log from the North Atlantic (1831 m) (Wolff 1979), petroleum saturated sediments near hydrothermal vents in the Guaymas Basin (2000 m, Gulf of California) (Grassle *et al.* 1985; Grassle 1986), on slate recruitment panels placed within vent communities on the East Pacific Rise (van Dover *et al.* 1988) and in sediment trays deployed for six months at 2160 m in the Bay of Biscay (Desbruyères *et al.* 1980). In the latter case, the development of dense macrofaunal populations dominated by three opportunistic polychaete species, *Ophryotrocha puerilis*, *O.* sp. and *Prionospio* sp., probably represented a response to the presence of large organic aggregates within the sediment trays (Desbruyères *et al.* 1985). A number of other macrofaunal species, including *Leptamphopus* sp., *Harpinia propinqua* (amphipods), *Yoldiella dissimilis* and *Thyasira croulinesis* (bivalves), were also associated with decaying *Sargassum* in the samples of Grassle & Morse-Porteous (1987). Like the xylophagid bivalves referred to above, these polychaetes and other invertebrates are, at least to some extent, opportunists.

In visual terms the most dramatic benthic response to food inputs from surface waters is that evoked by large food falls. These are quickly consumed by dense aggregations of highly mobile scavengers (see, for example, Ingram & Hessler 1983, and references therein). The most voracious scavengers are demersal amphipods (family Lyssianassidae) and fish, for example, brotulids, macruroids, sablefish and, particularly, hagfish. Ophiuroids, polychaetes and a variety of other crawling epibenthic invertebrates are also attracted to carrion. Smith & Baldwin (1982) have shown that two species of scavenging deep-sea amphipods display elevated rates of oxygen consumption when exposed to bait odour, a physiological adaptation that enables them to arrive at the bait within a matter of hours or less.

Sieburth & Dietz (1972) suggested that disruption of flesh by carrion feeding amphipods would facilitate its decomposition by bacteria. However, experiments conducted in the Santa Catalina Basin (1310 m) by Smith (1985, 1986) showed that the organic content of food falls is almost totally utilized by scavengers. Bacterial counts, CHN (carbon, hydrogen, nitrogen) analyses and meiofaunal abundances all indicated that little food is left over to benefit the sediment community. The main impact on the sediment community is caused by disturbance due to the frenzied feeding activities of the scavengers. The area disturbed during Smith's (1986) experiments contained fewer macrofaunal species than undisturbed areas (see also Grassle & Morse-Porteous 1987) but was rapidly repopulated by three species (two polychaetes common in the background community and one normally rare cumacean).

(*g*) *Importance of organic inputs for community structure*

Grassle & Morse-Porteous (1987) and Grassle (1989) have emphasized the crucial role played by organic inputs in deep-sea ecology. Deposits of the kinds discussed above (phytodetrius, wood and other large plant remains, animal carcasses, etc.) create a mosaic of organic rich patches on the ocean floor. In the absence of large-scale physical disturbances (usually rare in the deep sea), this mosaic pattern persists, although the patches themselves are ephemeral. Together with small-scale physical disturbances, for example, caused by the feeding activities of scavengers (Smith 1986), patchiness of organic input helps to maintain the diversity of deep sea sediment communities and increases their heterogeneity (Grassle 1989).

Conclusions

The deep-sea sediment ecosystems are finely balanced, highly diverse and contain organisms of great ecological and taxonomic interest. Particularly in central ocean regions, their existence depends largely on sedimented organic material ranging from flocculent phytodetritus to large vertebrate carcasses. This review, of the responses of benthic organisms to these inputs, leads us to the following conclusions.

1. A wide variety of benthic organisms (from bacteria to fish) respond in hours, days or weeks to organic inputs to the food limited ocean-floor. These responses serve to emphasize that deep-sea ecological processes may operate more rapidly than commonly assumed.

2. Different taxa respond to different inputs. For example, bacteria, flagellates and foraminifers colonize and multiply on phytodetritus; scavenging amphipods and fish congregate around and consume vertebrate carcasses; boring xylophagid bivalve larvae settle and grow on wood. Thus, finely particulate material is degraded by bacteria, whereas large carcasses are utilized by scavengers so efficiently that bacteria are excluded to a large extent from the decomposition process.

3. Opportunistic life-styles facilitate the rapid utilization of organic inputs (see also Jumars *et al.*, this Symposium). Such organisms include boring bivalves, capitellid, spionid and dorvileid polychaetes, foraminifers, bodonid flagellates and possibly the nematode *Monhystera* and echinosomatid harpacticoid copepods. Bacteria are perhaps the pre-eminent deep-sea opportunists.

4. Seasonal organic pulses, for example the deposition of phytodetritus, may regulate the population dynamics of bacteria and some protozoans (flagellates and foraminifers) and the reproduction and growth cycles of some metazoans.

5. A variety of patchily distributed organic inputs probably play a major role in structuring ocean-floor communities, for example, by helping maintain high species diversity and increasing population heterogeneity.

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Discussion

J. A. ALLEN (*University Marine Biological Station, Millport, Isle of Cumbrae, U.K.*). Have dinoflagellate cysts been found in the phytodetritus?

A. J. GOODAY. Dinoflagellates are commonly present in phytodetritus collected during the summer (July and August) (Billett *et al.* 1983; Rice *et al.* 1986; Riemann 1989) and their cysts have been observed in material from the BIOTRANS area (Thiel *et al.* 1990, table 2).

Note added in proof (*10 January 1989*). Since this manuscript was submitted two important papers have been published on benthic responses at bathyal depths in the Norwegian Sea. Graf

(1989) described how the benthic community reacted within days to a pulse of phytodetritus. By measuring the ATP content of the protoplasm, Linke (1989) detected a physiological response to food inputs among several species of benthic foraminifera.

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