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Transformations of biogenic particles during sedimentation in the northeastern Atlantic

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SUMMARY

The vertical flux and transformation of biogenic particles are important processes in the oceanic carbon cycle. Changes in the magnitude of the biological pump can occur in the north eastern Atlantic on both a seasonal and interannual basis. For example, seasonal variations in vertical flux at 47° N 20° W are linked to seasonal ocean productivity variations such as the spring bloom. The size and organic and inorganic content of phytoplankton species, their development and succession also play a role in the scale and composition of the biological pump. The majority of flux is in the form of fast sinking aggregates. Bacteria and transparent exopolymer particle production by phytoplankton have been implicated in aggregate production and mass flux events. Zooplankton grazing and faecal pellet production, their size and composition and extent of their vertical migration also influence the magnitude of vertical flux. Aggregates are formed in the upper ocean, often reaching a maximum concentration just below the seasonal thermocline and can be a food resource to mesozooplankton as well as to the high concentrations of attached bacteria and protozoa. Attached bacteria remineralize and solubilize the aggregate particulate organic carbon. The degree of particle solubilization is likely to be affected by factors controlling enzyme activity and production, for example temperature, pressure or concentration of specific organic molecules, all of which may change during sinking. Attached bacterial growth is greatest on particulate organic matter collected at 500 m which is the depth where studies of ^{210}Po reveal that there is greatest break-up of rapidly sinking particles. Break-up of particles by feeding zooplankton can also occur. The fraction of sinking POC lost between 150–3100 m at one station in the north eastern Atlantic could supply about 90% of the bacterial carbon demand. Some larger, faster sinking aggregates escape solubilization and disaggregation in the upper 1000 m and arrive in the deep ocean and on the deep-sea bed. Seasonally varying rates of sedimentation are reflected at the deep-sea floor by deposition of phytodetrital material in summer. Approximately 2–4% of surface water primary production reaches the sea floor in 4500 m depth at 47° N 20° W after a sedimentation time of about 4–6 weeks. In this region, concentrations of chloroplastic pigments increased in summer by an order of magnitude, whereas seasonal changes in activity or biomass parameters were smaller. Breakdown of the generally strongly degraded organic matter deposited on deep-sea sediments is mainly accomplished by bacteria. Rates of degradation and efficiency of biomass production depend largely on the proportion of biologically labile material which decreases with advancing decay. It is likely that different levels of organic matter deposition influence the bioturbation rates of larger benthos, which has an effect on transport processes within the sediment and presumably also on microbial degradation rates.

1. INTRODUCTION

Exchanges between ocean and atmosphere are major factors determining the atmospheric CO_2 content. Thus, the rate at which material produced in the upper water column above the seasonal thermocline (10–60 m depth) is lost to the rest of the winter mixed layer and from there through the permanent thermocline (200–900 m depth) is an important question in oceanic biogeochemistry. The North Atlantic is thought to be a major sink for atmospheric CO_2 due to downwelling driven by thermohaline circulation and seasonal decrease of upper ocean CO_2 concentration driven by phytoplankton development (Watson *et al.* 1992). For these reasons the north eastern Atlantic became the focus of investigations by the international JGOFS (Joint Global Ocean Flux Study) programme during the 1989 North Atlantic Bloom Experiment (NABE: Ducklow & Harris 1993) and by BOFS (the Biogeochemical Ocean Flux Study, the U.K. contribution to JGOFS) during 1990 (the Lagrangian Experiment: Savidge *et al.* 1992). The focus of all these studies was the flux of carbon into, through and out of the upper mixed layer of the oceanic water column, along the 20° W meridian. The German programme BIOTRANS (Biologischer Vertical transport und Energiehaushalt in der bodennahen Wasserschicht der Tiefsee) carried out a parallel study of the deep-sea bed in this region since 1985.

Here we examine the current knowledge of vertical particle flux, based mainly on the observations during 1989 and 1990 in the region around 47° N 20° W, its

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magnitude and composition, and its seasonal and spatial variability. This paper focuses on the effect of biological processes on downward transport of CO_2 (the 'biological pump') although it is recognized that this may not necessarily be the dominant process of downward carbon flux on a global scale. Emphasis is placed on the critical biological processes governing transformations occurring during sinking and upon arrival on the deep-sea floor, as we currently see them.

2. PARTICLE FORMATION AND ESCAPE FROM THE UPPER MIXED LAYER

(*a*) *Rationale and approach*

Particulate flux due to gravitational settling may be assessed by two principal ways. Sediment traps attached to fixed or drifting moorings (Martin *et al.* 1987) collect vertically settling material for prolonged periods of time to give a time-series of samples. Alternatively, concentrations of various radionuclides which are scavenged by particles can be used to model the flux of other components of the material (Buesseler *et al.* 1992). Both techniques have uncertainties associated with them when applied to the upper mixed layer and often give results which are quite different (Buesseler *et al.* 1994).

Losses from the upper mixed layer (UML) may be expressed in terms of the components of the material or as percentages of primary production in the euphotic zone. Relationships between primary production and losses of particulate organic carbon (POC) determined by sediment trap studies have been described in the past. The relation determined by Betzer *et al.* (1984, see figure 1A) (POC flux = 0.409 Primary Production$^{1.41}$/depth$^{0.628}$) appears to describe losses from the 1989 JGOFS NABE well in the deeper water column but with more scatter in the upper layers. The proportion of primary production leaving the upper 150 m during the entire 1989 JGOFS NABE studies was about 11% (Lochte *et al.* 1993) using sediment traps but higher when using the ^{234}Th model (Buesseler *et al.* 1992). In May 1990, losses at 100 m, measured using sediment traps, were between 10–40% of primary production, but a clear decrease with depth was found only in one of the three deployments (see figure 1*b*). As during the NABE (see figure 1*a*), agreement with the Betzer curve improves with depth and, furthermore, temporal variability at greater depths appears to be reduced.

(*b*) *Mechanisms and pathways*

There are several pathways involved in the biological pump: (i) sinking of aggregated plant and animal remains; (ii) detrainment of particles during pycnocline shallowing; (iii) active downward transport caused by feeding, defaecation, respiration and reproduction; and (iv) mortality by migrating zooplankton. Downward advection and diffusion of dissolved organic carbon (DOC) produced in the UML by decomposition, leakage of cells and excretion may also be a significant contribution to the export flux (Ducklow, this volume). A critical parameter in particle flux is not only the concentration of particles but also their sinking rate. Experimentally determined sinking rates of individual phytoplankton cells of 0.1–2 m d^{-1} (e.g. Smayda 1970) may have little bearing on the real transport rates in the system. Trends in productivity are manifest at depth after an interval which implies sinking rates of about 60–500 m d^{-1}. The reason is simply that the majority of the flux is in the form of fast sinking aggregates, commonly referred to as 'marine snow' (Alldredge & Silver 1988). Despite this high rate of sinking, the particles will be subject to chemical and biological transformations during their downward passage. The clearest justification for this assertion is that there are populations of bacteria and plankton which reside in the mesopelagic realm and rely on this food source for sustenance. For example, the fraction of sinking POC lost between 150–3100 m at the NABE site was found to be capable of supplying about 90% of the bacterial carbon demand in these waters (Turley & Mackie 1994).

(*c*) *Aggregate distribution and formation*

Marine snow is most abundant in the surface of the ocean decreasing sharply in the top 100 m (Alldredge & Silver 1988; Gardner *et al.* 1993; Lampitt *et al.* 1993*b*). Recently, sub-surface peaks, just below the pycnocline, have been repeatedly recorded in the northeastern Atlantic (Lampitt *et al.* 1993*b*). The relation of these peaks to the physics and biology of the water column poses some difficult questions. If this physical boundary were simply a barrier reducing the sinking rates of the particles produced above, one would expect the peak to be on or just above it. A simple explanation would be that the pycnocline is a region of greatest rate of production due to the physical processes of turbulent shear which are likely to be greatest here (Osborn 1974). This may cause aggregation of smaller particles by enhanced contact (McCave 1984). Field observations indicate that turbulence may also cause break-up of marine snow (Riebesell 1992). Laboratory experiments have shown, however, that natural levels of turbulence in the ocean would be insufficient to cause break-up and that biological processes are more likely to dominate destruction (Alldredge *et al.* 1990).

Several reviews of processes and mechanisms involved in aggregate formation are available (Alldredge 1986; Turley 1992). However, we would like to specifically address two fairly new issues here: (i) the potential of transparent exopolymer particles (TEP) (Passow & Wassmann 1994) and sub-micron particles (Koike *et al.* 1990) as precursors of aggregates; and (ii) the role of bacteria in aggregate formation.

TEP are highly sticky, particulate polysaccharides formed by abiotic coalescence of dissolved (< 0.4 μm) polysaccharides most likely exuded by diatoms (Passow & Wassmann 1994). TEP were found to be numerous at the peak of a diatom bloom and an important agent of diatom flocculation. They may be involved in dynamic

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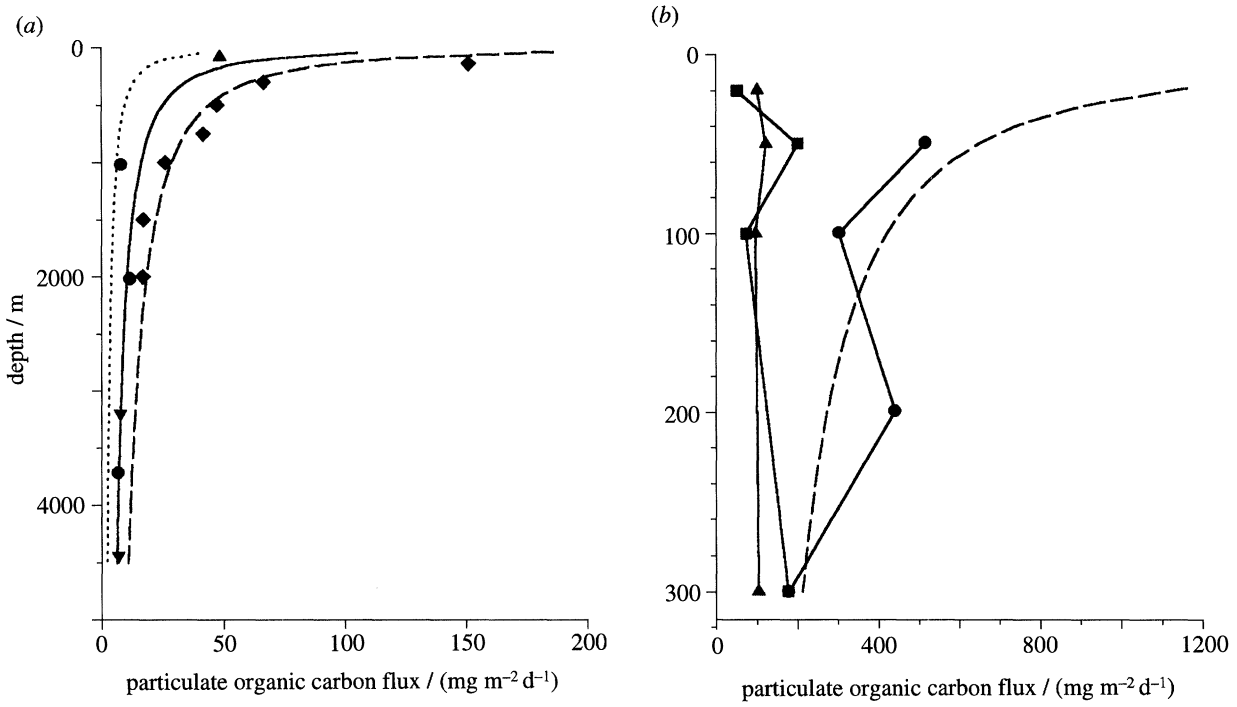

Figure 1 (*a*) POC flux predicted using the equation of Betzer *et al.* (1984) relating primary production to flux at depth. Three profiles are presented based on production levels of 400 (dotted line), 800 (solid line) and 1200 (dashed line) mg organic carbon m^{-2} d^{-1}. These figures cover the range of estimates of primary production which may be derived for the 11 May 1989. Key to symbols: inverted triangles, Newton *et al.* (1994); diamonds, Martin *et al.* (1993); circles, Honjo & Manganini (1993); upright triangles, Stienen & Zeitzschel (personal communication). There is some uncertainty about the primary production rate around day 131 due to the possibility of zinc contamination depressing some measurements (Martin *et al.* 1993; Lochte *et al.* 1993). The appropriate value is probably about 1000 mg m^{-2} d^{-1}. Also presented are flux data collected during the 1989 JGOFS NABE. It is not appropriate to compare flux at one depth with flux at another depth at the same time, the reason being that sharp temporal changes in flux are known to occur. Flux in the upper water column should be compared with flux at greater depth at some later time. In this instance we have taken flux data from drifting and fixed sediment traps and compared them assuming the material left the surface on day 131 (11 May) and sank at a rate of 150 m d^{-1}. Each flux value is a ten day average centred on the predicted time of the arrival of material at that depth.
(*b*) POC flux measured during the 1990 Lagrangian experiment. These were obtained using single drifting sediment traps deployed on 20, 24, 26 May for 80, 49 and 65 hours, respectively. Symbols: circles, 20 May; squares, 24 May; triangles, 26 May; dashed line, predicted flux. Also shown is the predicted flux based on the equation of Betzer *et al.* (1984) and the mean level of primary production at that time (1068 mg C m^{-2} d^{-1}). Productivity was derived from on-deck incubations and an algorithm derived by Dr. P. Boyd incorporating insolation and *in situ* beam attenuation.

changes from DOC to macroaggregates possibly via non-living colloidal (< 0.2 μm) and sub-micron (0.2–1.0 μm) particles (Koike *et al.* 1990). However, these particles have not been studied in the north eastern Atlantic. An important component during the 1989 JGOFS NABE was bacteria; their biomass was equivalent to phytoplankton biomass, it was substantially greater than the combined micro- and mesozooplankton biomass; they accounted for 20–30 % of the POC (Weeks *et al.* 1993*a*) and their production averaged 30 % of primary production (Ducklow *et al.* 1993). Bacteria have been implicated in aggregate formation particularly in areas rich in DOC or POC (Biddanda 1985). Indeed, the BOFS sediment trap studies during 1989–1990 (see figure 2) revealed that bacteria are transported into the deep-sea in large numbers (up to 32×10^9 cells m^{-2} d^{-1}) through their association with rapidly sinking particles (Turley & Mackie 1995). Two major particle flux events occurred during 1989, of which the second event, covering 12 % of the year, transported 74, 77, 29 and 49 % of the annual total bacterial, cyanobacterial, mass and POC fluxes, respectively (see figure 2). The composition of this material was different to that at other times of the year: it was gelatinous and sticky, contained high POC, mucopolysaccharide (Newton *et al.* 1995) and bacterial (Turley & Mackie 1995) concentrations. Several interpretations of these results are possible.

1. Bacteria were involved in aggregate formation.
2. The sticky nature and high mucopolysaccharide content of the material may indicate involvement of TEP.
3. The high loading of POC on the particles stimulated bacterial growth.
4. Mucus feeding webs produced by a localized bloom of organisms such as Appendicularia which concentrate small particles were involved in this flux event.

The latter is unlikely as Newton *et al.* (1994) found no zooplankton feeding structures in these samples.

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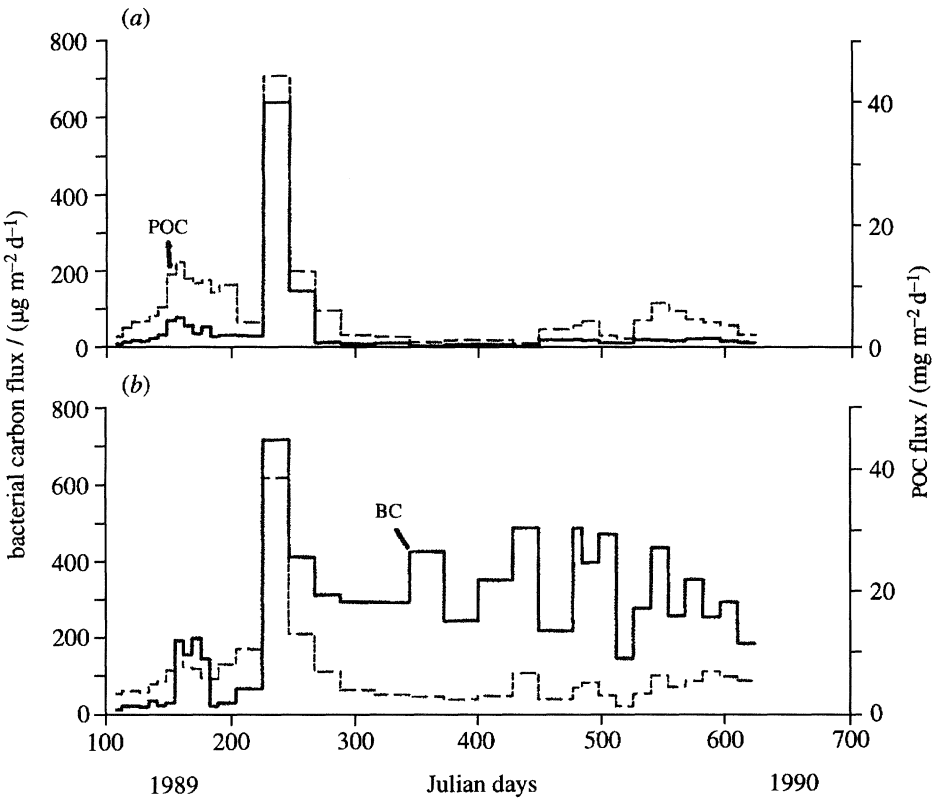

Figure 2. Flux of POC (from Newton *et al.* 1994) and bacterial carbon (BC) (from Turley and Mackie 1995) to (*a*) 3100 and (*b*) 4465 m water depth around 47° N 20° W during 1989 and 1990 measured by long term moored sediment traps.

3. PARTICLE COMPOSITION AND TRANSFORMATION DURING SINKING

(*a*) *Influence of plankton size and composition*

The composition of aggregates reflects, in part, the composition of the plankton community and in part the processes involved in aggregate formation (Alldredge & Silver 1988; Turley 1992). As discussed by Newton *et al.* (1994), 17 months of measurements at 3100 m in the mesotrophic north eastern Atlantic (see figure 2) revealed similar deep water annual flux patterns with spring and late summer/autumn peaks. However, the timing of the peaks and the integrated annual average flux — most notably for POC — was different in the two years. The reasons for these differences were not immediately obvious as the levels of primary production during the spring bloom and the two years appear to be very similar. A modelling study indicated that the size composition of the phytoplankton community is a critical factor affecting the efficiency of the biological pump (Boyd & Newton 1995).

The composition of the zooplankton and nekton may also effect the magnitude of the vertical particle flux. For example, in the same area during spring 1988, mass occurrence (up to 3500 m^{-2}) of salps, *Salpa fusiformis*, exerted a sufficiently high grazing pressure that although primary production was high there was little accumulation of phytoplankton biomass. They can graze a broad range of cell sizes, including picoplankton, and produce large, rapidly sinking faecal pellets. Salp faeces appeared within a short time on the deep-sea bed in large numbers (up to 2000 m^{-2}) providing a mechanism of rapid carbon transfer to the deep sea (Pfannkuche & Lochte 1993). In contrast to this, microzooplankton grazing is likely to reduce the efficiency of the biological pump. Microzooplankton were found to graze up to 50% of primary production during the 1989 NABE and 1990 Lagrangian Experiment (Weeks *et al.* 1993*a*; Burkill *et al.* 1993), but as their faecal pellets are small and sink less rapidly, most of this carbon is being respired within the UML. It is likely that while microzooplankton play the dominant role in controlling phytoplankton biomass, the mesozooplankton and nekton may have a stronger influence on export flux from the UML.

(*b*) *The influence of vertical migration*

Vertical migration by mesozooplankton and micronekton may transport material through the water column (Angel 1984). This may occur on a daily basis or seasonally and may be related to the ontogenetic development of the individuals. During their migration cycle, which may extend over the top 1000 m of the water column, these plankton feed, respire, defaecate, excrete, reproduce and die. The rates of these processes will depend on the distribution of their food and water temperature. Release of respired carbon and excreted dissolved inorganic nitrogen by migrants at depth may constitute a significant active flux of material (Longhurst *et al.* 1989, 1990). Flux of solid material due to retention of faecal material in the gut seems unlikely to be significant because gut retention times would be too short for a significant quantity to be defecated at depth (Lampitt *et al.* 1993*b*). However,

Morales *et al.* (1993) demonstrated significant differences between migrant and non-migrant mesozooplankton, with the migrants retaining their gut content for much longer than expected and, furthermore, reaching a peak in gut fullness at the surface just prior to their descent. Gut flux may yet prove to be a significant means by which material is actively transported down through the water column. Other mechanisms by which material may be transported to depth such as reproductive products and mortality have to date been poorly examined but are unlikely to be of great significance.

(*c*) *Variability of vertical flux*

In addition to biological remineralization, particles will be subject to dissolution of their inorganic components and release of organic and inorganic material which is already in solution but retained by solid structures such as cell walls. An assessment of the changes in the particle pool during sinking is best made by comparing sediment trap material from different depths. One would assume that the many deployments which have been carried out to date would yield unambiguous trends from which dissolution and remineralization rates could be deduced. One of the harder facts to reconcile is that in many instances this is not the case and there are apparent increases in flux at intermediate locations in the water column. This can in some cases be related to advective input as in the Panama basin (Honjo *et al.* 1982) but in other cases is less easy to interpret. These trends are however small in comparison to those occurring in the upper water column. As implied by the various equations describing biogenic particle flux variations with depth (Suess 1980; Betzer *et al.* 1984; Martin *et al.* 1987; Pace *et al.* 1987; Walsh *et al.* 1988), these changes, due to dissolution or remineralization, are most rapid in the near surface zone and it is here, unfortunately, that the greatest uncertainties exist mainly due to swimmer contamination of sediment trap samples (Michaels *et al.* 1990) and hydrodynamic effects (Gust *et al.* 1994).

Two sediment trap moorings separated by 100 km showed very similar levels of particle flux over spring–summer 1989 during the NABE, indicating that at least in deep oceanic environments, mesoscale variability is small at this time (see figure 1*a*) (Honjo & Manganini 1993; Newton *et al.* 1995). Similarly, contemporaneous deployments of deep drifting traps and bottom mounted traps separated by between 85–215 km showed good agreement (Martin *et al.* 1993). This is probably because the diverse particles entering a trap had been produced over a wide surface area of the ocean depending on the current regime at the time they were sinking through the water. This 'statistical funnel' (Deuser *et al.* 1990) would have had a surface manifestation of diameter about 100 km (based on a residual current of 5 cm s^{-1}, a sinking rate of 150 m d^{-1} and a mooring depth of 3100 m) in the vicinity of each mooring site (Newton *et al.* 1994). The second large flux peak in 1989 recorded by the U.K. traps was present at both 3100 m and 4465 m (see figure 2) and had unique characteristics (s.a.; Newton *et al.* 1994) and although not recorded 100 km away, is unlikely to be an artefact.

(*d*) *Transformation by microrganisms*

The aggregate microniche is an area of nutrient enriched microzones, containing high concentrations of both active photosynthetic and microheterotrophic cells. Macroaggregates, from the aggregate maximum just below the seasonal thermocline at 45–55 m during May 1990 (Lampitt *et al.* 1993*b*), contained several orders of magnitude higher concentrations of bacteria, cyanobacteria and flagellates than in the surrounding seawater (Turley & Mackie 1994). At this time when aggregates were most numerous (Lampitt *et al.* 1993*a*), attached bacteria constituted up to 25% of free-living bacterial carbon and 2% of the total bacterial production (Turley & Mackie 1994).

About 40 different species of heterotrophic flagellates have been isolated from aggregates from the north eastern Atlantic water column (Patterson *et al.* 1993). Most of these were small and bacterivorous and although the community extended to the ocean floor there was a decline in both species diversity and numbers of individuals. This decline may be due to a decrease in food availability with depth. For this reason, many of the flagellates below the UML are probably bound to the aggregates, grazing on attached bacteria rather than being suspension feeders. Bacterivorous flagellates are likely to reduce bacterial abundance on aggregates and, thereby, influence the rate of particle remineralization and solubilization (Lochte 1991). The decline in flagellate species diversity with depth may also be attributed to death of pressure sensitive species on sinking aggregates, although some flagellates can tolerate high pressures (Turley & Carstens 1991).

Bacteria are able to solubilize POC by extracellular hydrolytic enzymes (ectoenzymes) which may be bound to the cell membrane or free in the seawater (Smith *et al.* 1992). It has been proposed that macromolecules of sinking POC are hydrolysed by the ectoenzymes of attached bacteria, and that part of the produced DOC diffuses into the surrounding water and is utilized by free-living mesopelagic bacteria (Azam & Smith 1991). Factors controlling enzyme activity and production, for example temperature, pressure or concentration of specific organic molecules, which either may lead to catabolic enzyme repression or may induce enzyme production, will obviously affect the degree of particle solubilization and have significant biogeochemical consequences. For example, bacteria on an aggregate with a high concentration of directly utilizable dissolved organic carbon (UDOC) will rapidly take up the UDOC while repressing ectoenzyme activity and production to save metabolic energy (Chróst 1991). When UDOC concentration is low, production of ectoenzymes is induced leading to increased hydrolysis of POC, solubilization and a higher possibility of disaggregation.

The position of the aggregate in the water column will have some influence on the microbial processes on the aggregate. Rates of substrate uptake, enzyme

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Table 1. *Thymidine incorporation rates expressed on a per bacterial cell basis measured under in situ pressures and temperatures in samples from the north eastern Atlantic around 59° N 20° W taken during 17–20 June 1989*

(Bacteria attached to suspended particles were sampled *in situ* using a stand alone pump (SAP) capable of filtering large volumes (circa 1000 l) through a 293 mm diameter, 0.6 μm pore size Nuclepore filter. Free-living bacteria were sampled using 30 l NIO bottles during the same period as the SAP deployments. Free-living bacteria were also sampled using 10 l GoFlo bottles attached to a CTD during 14–15 June at the same station. Standard deviations are shown within parenthesis; n.d. denotes not detectable.)

depth	bacteria attached to suspended particles	free-living bacteria 30 l NIO bottles	ratio attached: free-living bacteria	free-living bacteria 10 l GoFlo bottles	
(m)	(mol × 10^{-21} cell^{-1} h^{-1})	(mol × 10^{-21} cell^{-1} h^{-1})		depths (m)	(mol × 10^{-21} cell^{-1} h^{-1})
50	0.18 (0.06)	4.18 (0.16)	0.04	40, 50	4.83 (0.32), 6.49 (0.61)
500	3.88 (0.61)	0.75 (0.67)	5.17	400, 600	3.35 (0.42), 0.74 (0.04)
2200	0.15 (0)	0.19 (0.13	0.79	2250	n.d.

Table 2. *The range of thymidine (Tdr) and leucine (Leu) incorporation rates expressed on a per cell basis for bacteria attached to macro-aggregates sampled in the north eastern Atlantic using a range of different sampling methods*

(Data for macroaggregates sampled by SCUBA divers in the Pacific are given for comparison.)

location	date	depth (m)	sampling method	method	incorporation rate (mol × 10^{-21} cell^{-1} h^{-1})	reference
NE Atlantic, 48° N 16.5° W open ocean	1–3 June 1990	200	drifting sediment trap, unpoisoned	Tdr	6–7	Turley (1993)
Pacific, 32–34° N, 119–121° W, Southern Californian coast	3–9 April, 25–30 September	15–20 m	SCUBA	Tdr	6–20	Alldredge & Gotschalk (1990)
NE Atlantic, 48° N 17° W, open ocean	20–29 May 1990	45	1000l marine snow sampler	Leu	12–206	Turley & Mackie (1994)
NE Atlantic 48° N 16.5° W, open ocean	1–3 June 1990	200	drifting sediment trap, unpoisoned	Leu	60–80	Turley (1993)

activity and production as well as bacterial growth are likely to be reduced by the colder temperatures below the seasonal thermocline. In deeper waters, high pressure also inhibits microbial synthesis of DNA and protein on aggregates (Turley 1993). Larger and faster sinking particles, therefore, have a greater possibility of escaping microbial solubilization in the upper water column, especially if they contain a good supply of UDOC. Slower sinking particles are likely to be degraded more extensively in the upper 1000–2000 m of the water column, contributing more to the carbon demand of mesopelagic bacteria. This view is supported by observations in the Atlantic in 1989, when particles rich in both POC and bacteria (see figure 2) were found during the high period of flux at 3100 m indicating relatively undegraded material on presumably fast sinking particles.

Thymidine incorporation rates (a measure of bacterial production) of bacteria attached to SAP-sampled particulate material from 500 m are more than 20 times higher than those of bacteria attached to material from 50 or 2200 m (see table 1). At 500 m, attached bacteria had about five times greater incorporation rates per cell than free-living ones, whereas at 40 m free-living bacterial incorporation rates are about 23 times higher than those of attached cells. At 2200 m there is little difference between the two populations, thymidine incorporation rates per cell of both being low. These findings support those of Ritchie and Shimmield (1991), studying ^{210}Po/^{210}Pb disequilibria, that break-up or remineralization/solubilization of large rapidly sinking particles is greatest at depths around 500 m and, furthermore, indicates that these processes are mediated by attached bacteria. The high thymidine incorporation rates of free-living bacteria at 50 m presumably reflect the greater availability of UDOC in the UML.

The thymidine incorporation rates of bacteria attached to SAP-sampled particles (see table 1) are substantially lower than those measured on macroaggregates from the north eastern Atlantic and Pacific (see table 2). Also leucine incorporation, a measure of bacterial protein synthesis and generally 10–20 times greater than thymidine incorporation rates, is also high on the macroaggregates (see table 2). The SAPs filtered 500–1200 l of seawater, retaining particles > 0.6 μm, and would include substantial quantities of suspended or slowly sinking particulate material as well as the rarer, rapidly sinking macroaggregates. The larger aggregates are likely to be generally 'younger' than the smaller particles, contain more assimilable organic carbon and, therefore, have a higher capacity to support bacterial growth.

(*e*) *Transformation by zooplankton and micronekton*

Diving observations (e.g. Alldredge 1976, 1986; Hamner *et al.* 1975) and experimental evidence (e.g. Lampitt *et al.* 1993*b*) indicate that zooplankton and

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micronekton feed upon marine snow. Sometimes only parts of the particle may be ingested leaving the rest to disintegrate (Lampitt *et al.* 1990). Such behaviour may be a major factor in particle disruption (Karl *et al.* 1988).

Marine snow contains high concentrations of particles (e.g. picoplankton) normally too small to be directly grazed by some filter feeding zooplankton. Ingestion of aggregates therefore represents a food chain short cut by which these small cells are available to the mesozooplankton (Lampitt *et al.* 1993*b*). Zooplankton are themselves important producers of aggregates in the form of faecal pellets, through repackaging the remains of their prey or directly grazing aggregates containing a range of different organisms. Around 70% of ingested bacteria can survive gut passage and can exhibit high amino-peptidase activity in faecal pellets and have been implicated in their solubilization (Lawrence *et al.* 1993). Indeed, the concentration of bacteria associated with faecal pellets in the north eastern Atlantic was generally higher and less variable ($29–38 \times 10^8$ ml^{-1} faecal pellet) than the concentration on the amorphous aggregates ($2–25 \times 10^8$ ml^{-1} aggregate) and may be due to growth within the faecal pellet (Turley & Mackie 1994).

4. TRANSFORMATION ON THE SEA BED

(*a*) *Deposition of detrital matter on the sea floor*

At the sea floor, the deposition of POC is strongly influenced by the small-scale bottom topography. Small mounds and depressions on the sea floor may act as traps for fine organic particles (Lampitt 1985; Thiel *et al.* 1988, 1989; Hecker 1990) or accumulation may be enhanced by sessile animals (Graf *et al.* 1995). Freshly sedimented phytodetritus has a distinct green-brown colour and may form a flocculent, easily resuspended layer on the sediment (Lampitt 1985).

In the wake of the spring bloom, phytodetrital matter has been observed on the sea floor in different regions of the north eastern Atlantic (Porcupine Sea Bight: Billett *et al.* 1983; Lampitt 1985; Rice *et al.* 1986; BIOTRANS station: Thiel *et al.* 1988, 1989; Greenland-Norwegian Sea: Graf *et al.* 1995). Because long term benthic investigations of fixed deep-sea stations are plagued with a multitude of logistic difficulties, evidence for seasonal variations in the benthos have so far been mainly drawn from compilations of several years of investigations. In this way, temporal changes in phytodetrital input and sediment biomass and activity parameters were found in the sediment at 4500 m depth at 47° N 20° W. Variations between spring and summer from these data are summarized in table 3. Concentration of phytodetrital matter (indicated by chlorophyll) increased more strongly than activity of small sediment organisms (indicated by ATP) or respiration and biomasses (total adenylates and bacterial numbers). Such an estimate has to remain a rough approximation, but it gives some appreciation of the scale of seasonal variation in deep-sea sediments of this region. Thus, epipelagic production and its sedimentation are reflected in the benthic response although strongly dampened.

Spring phytoplankton development at 47° N 20° W was reflected in deep sediment traps (see figure 2, Newton *et al.* 1994) and in benthic pigment concentrations after 4–6 weeks (see figure 3). Due to differential settling the sedimentation pulse of the spring phytoplankton bloom spreads out over a longer period of time. This has to be taken into account when estimating the flux of material to the sea floor. Using integrated productivity data for 1989 (Bender *et al.* 1992) and 1990 (Savidge *et al.* 1992) and POC fluxes from 3100 m sediment traps for both years (events 1989A and 1990B in Newton *et al.* 1994) extrapolated to the sea floor at 4500 m depth using the equation of Martin *et al.* (1987), a flux of 2–4% of the spring primary production to the sea floor can be estimated. Estimates based on *in situ* respiration measurements gave comparable results of 1.1% of primary production being consumed at the sea floor (Pfannkuche 1993).

In areas with different bioturbation rates the mode of deposition changes. On the Voring Plateau (1500 m), high abundance of macrofauna caused intense bioturbation which transported sedimented phytodetrital matter rapidly into burrows in 9 cm sediment depth (Graf 1989; Romero-Wetzel & Gerlach 1991). Enzymatic activities and bacterial abundances were higher in burrows than in the surrounding

Table 3. *Overview of data obtained at the BIOTRANS site (47° W 20° N, 4500 m depth) during spring (March–April) and summer (July–August) of different years and the estimated factor of increase from spring to summer*

(The data represent average values for the upper 2 cm of sediment except for bacterial numbers (averaged over the top 10 cm) and respiration (*in situ* measurement in enclosed chambers).)

variable	spring	summer	factor of increase	source
chlorophyll *a*/(g cm^{-3})	0.03[a]	0.20–0.52[d]	6–17 fold	Pfannkuche (1993)
total adenylates/(ng cm^{-3})	20.7[a]	81.9–114.6[d]	4–5 fold	Pfannkuche (1993)
bacterial numbers/($\times 10^{13}$ cells m^{-2})	16[b]	19–36[e]	1.2–2.2 fold	Lochte (1992)
ATP/(ng cm^{-3})	1.0[a]	7.4–12.6[d]	7–12 fold	Pfannkuche (1993)
respiration/(μmol O_2 m^{-2} h^{-1})	18.0[c]	37.4[d]	2 fold	Pfannkuche (1993)

[a] March 1985.
[b] April 1988 (mean).
[c] April 1988 (mean).
[d] July 1986 and August 1989.
[e] July 1988 and July/August 1986.

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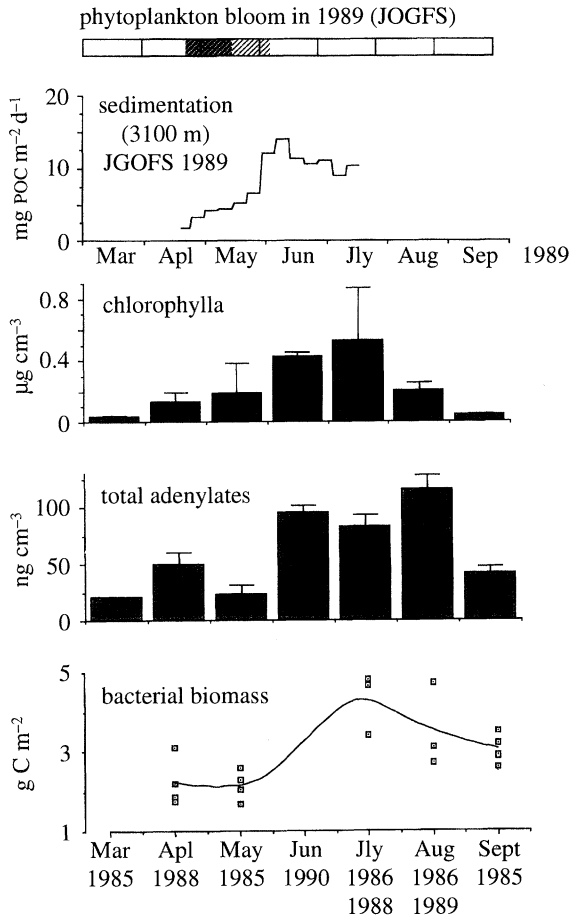

Figure 3. Compilation of data from 47° N 20° W to indicate the timing of the surface water phytoplankton bloom (from 1989 JGOFS NABE) and peaks in POC flux (spring flux event 1989A; Newton *et al.* 1994), sediment concentrations of chlorophyll, total adenylates (Pfannkuche 1993) and bacterial biomass (Lochte 1992). Deep sea sediment data are compiled from several years.

sediment (Köster *et al.* 1991). In such strongly bioturbated sediments the diffusive exchange of oxygen is increased due to the much larger surface area (Gundersen & Jørgensen 1990) and bio-irrigation furthermore effectively enhances solute transport. The mid-oceanic station at 47° N 20° W, in contrast, has a much lower proportion of macrobenthos, 80% of which is found in the top 5 cm. The lower bioturbation rates result in reduced transport, which slows down degradation processes and restricts biological activity to the upper few cm of sediment. Since bioturbation activity seems to be related to the amount of sedimenting organic matter (Smith 1992), seasonally and regionally varying POC fluxes may regulate this process.

(*b*) *Biological transformations at the deep-sea floor*

POC reaches the sea floor in an already advanced state of degradation depending on its residence time in the water column (s.a.). Incubation experiments with detrital organic material showed that deep-sea bacteria degraded organic components during the first five days at much faster rates than during the later period (Lochte & Turley 1988; Turley & Lochte 1990; Lochte 1992). The rapidly degradable fractions support bacterial growth at conversion efficiencies from 40% decreasing to 20%. Subsequent degradation rates are considerably slower and a much smaller proportion of carbon is converted to biomass; obviously energy and maintenance metabolism predominate. Therefore, benthic biomass production by bacteria and other detritivorous organisms strongly depends on the newly deposited material; it is enhanced when POC settles fast and degradation in the water column remains small. This pattern of declining biological decay rates finds its equivalent in geochemical models (e.g. Berner 1980; Rabouille & Gaillard 1991). The experimentally determined biological degradation rates, however, only cover the initial decay periods of the models.

Inputs of organic matter were found to induce production of certain extracellular hydrolytic enzymes, a prerequisite for bacterial breakdown of macromolecules (Meyer-Reil & Köster 1992; Boetius & Lochte 1994). Increases of ATP content as a fast response to food supply were also observed in benthic foraminifera (Linke 1992) or in whole sediment cores (Graf 1989). Such metabolic responses have time scales in the deep-sea of less than a week. In contrast, biomass production may become detectable in natural mixed populations only after longer periods of time. A growth response to seasonal sedimentation was mainly found for small benthic organisms (bacteria, foraminifera, nematodes) (Gooday & Turley 1990; Lochte 1992; Pfannkuche 1993). Comparison of sediment community oxygen consumption with bacterial growth and respiration at 47° N 20° W indicates that 60–80% of the annual rise in respiration is due to microorganisms inhabiting phytodetritus (Pfannkuche 1993). Degradation of organic matter in the deep-sea is mainly accomplished by bacteria because of their very high abundance even in deep sediment layers, their rapid response in cell metabolism and growth and their enormous metabolic versatility which enables them to break down material unavailable to higher organisms (Deming & Baross 1993). Therefore, the bacterial contribution to the transformation of organic material in deep-sea sediments increases as the POC becomes more recalcitrant, i.e. towards central oceanic basins underlying oligotrophic regions and in deeper sediment horizons. While in the sediment surface layer a mixed assemblage of organisms feed on the more recently deposited organic matter, more and more specialized bacteria are required to transform the largely humified organic material in deeper sediment layers. The important role of the larger benthos in this system may lie primarily in their ability to deposit, transport and mix organic rich particles and solutes in the sediment.

Biologically mediated particle flux in the North Atlantic is of special interest because of the strong seasonal development of the phytoplankton spring bloom with its associated decrease in upper ocean CO_2 concentration (Watson *et al.* 1992), its northward progression, the seasonal succession of phytoplankton and zooplankton species and the frequent occurrence of large scale hydrographic features often containing different species to the ambient water (Savidge *et al.*

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1992; Weeks *et al.* 1993*a*,*b*). The majority of particle flux is in the form of macroaggregates which are exposed to biological, physical and chemical forces which modify them significantly during sinking. Seasonal and interannual variations in vertical flux can be detected in deep water sediment traps and on the deep-sea bed and often reflect upper ocean productivity. Further intensive transformation occurs at the sediment/water interface and upper sediment layers. The rates of return or residence times of carbon in the ocean are determined by the depth of remineralization and decomposition processes. Residual biogenic material which is not recycled in the deeper water column or on the sea bed provides a sedimentary record of previous changes in ocean productivity and can be linked to other data on climate change such as ice core data on previous CO_2 concentrations.

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REFERENCES

Alldredge, A.L. 1976 Discarded appendicularian houses as sources of food, surface habitats and particulate organic matter in planktonic environments. *Limnol. Oceanogr.* **21**, 14–23.

Alldredge, A.L. 1986 Aggregate dynamics: biological processes which form, alter and destroy aggregates in the ocean. *Aggregate dynamics in the sea* (ed. A.L. Alldredge & E.O. Hartwig), p. 109. Workshop report, ONR, ASILOMAR Conference Centre, Pacific Grove, California, 22–24 September 1986.

Alldredge, A.L. & Gotschalk, C.C. 1990 The relative contribution of marine snow of different origins to biological processes in coastal waters. *Cont. Sh. Res.* **10**, 41–58.

Alldredge, A.L., Granata, T.C., Gotschalk, C.C. & Dickey, T.D. 1990 The physical strength of marine snow and its implications for particle disaggregation in the ocean. *Limnol. Oceanogr.* **35**, 1415–1428.

Alldredge, A.L. & Silver, M.W. 1988 Characteristics, dynamics and significance of marine snow. *Prog. Oceanogr.* **20**, 41–82.

Angel, M.V. 1984 Detrital organic fluxes through pelagic ecosystems. In *Flows of energy and materials in aquatic ecosystems*: *theory and practice* (ed. M.J.R. Fasham), p.475. New York: Plenum Press.

Azam, F. & Smith, D.C. 1991 Bacterial influence on the variability in the ocean's biogeochemical state: a mechanistic view. In *Particle analysis in oceanography* (ed. S. Demers), p. 213. NATO ASI Series, vol. G 27, Berlin, Heidelberg: Springer-Verlag.

Bender, M., Ducklow, H.W., Kiddon, J., Marra, J. & Martin, J. 1992 The carbon balance during the 1989 spring bloom in North Atlantic Ocean. *Deep Sea Res.* **39**, 1707–1725.

Berner, R.A. 1980 A rate model for organic matter decomposition during bacterial sulfate reduction in marine sediments. *Colloques int. Cent.* **293**, 35–44.

Betzer, P.R., Showers, W.J., Laws, E.A., Winn, C.D., DiTullio, G.R. & Kroopnick, M. 1984 Primary production and particle flux on a transect of the equator at 153° W in the Pacific Ocean. *Deep Sea Res.* **31**, 1–11.

Biddanda, B.A. 1985 Microbial synthesis of macroparticulate matter. *Mar. Ecol. Prog. Ser.* **20**, 241–251.

Billett, D.S.M., Lampitt, R.S., Rice, A.L. & Mantoura, R.F.C. 1983 Seasonal sedimentation of phytoplankton to the deep-sea benthos. *Nature, Lond.* **302**, 520–522.

Boetius, A. & Lochte, K. 1994 Regulation of microbial enzymatic degradation of organic matter in deep–sea sediments. *Mar. Ecol. Prog. Ser.* **104,** 299–307.

Boyd, P. & Newton, P. 1995 Evidence of the potential influence of planktonic community structure on the interannual variability of particulate organic carbon flux. *Deep Sea Res.* (In the press.)

Buesseler, K.O., Bacon, M.P., Cochran, J.K. & Livingston, H.D. 1992 Carbon and nitrogen export during the JGOFS North Atlantic Bloom Experiment estimated from ^{234}Th:^{238}U disequilibria. *Deep Sea Res.* **39**, 1115–1137.

Buesseler, K.O., Michaels, A.F., Siegel, D.A. & Knap, A.H. 1994 A three dimensional time-dependent approach to calibrating sediment trap fluxes. *Global Biogeochem. Cycles* **8,** 179–193.

Burkill, P.H., Edwards, E.S., John, A.W.G. & Sleigh, M.A. 1993 Microzooplankton and their herbivorous activity in the northeastern Atlantic Ocean. *Deep Sea Res.* **40**, 479–494.

Chróst, R.J. 1991 Environmental control of the synthesis and activity of ectoenzymes. In *Microbial enzymes in aquatic environments*. *Brock/Springer series in contemporary bioscience* (ed. R.J. Chróst), p. 6. New York, Berlin, Heidelberg: Springer-Verlag.

Deming, J.W. & Baross, J.A. 1993 The early diagenesis of organic matter: bacterial activity. *Org. Geochem.* (ed. M.H. Engel & S.A. Macko), p. 119. New York: Plenum Press.

Deuser, W.G., Muller-Karger, F.E., Evans, R.H., Brown, O.B., Esaias, W.E. & Feldman, G.C. 1990 Surface-ocean color and deep-ocean carbon flux: how close to a connection? *Deep Sea Res.* **37**, 1331–1343.

Ducklow, H.W. & Harris, R.P. 1993 Introduction to the JGOFS North Atlantic Bloom Experiment. *Deep Sea Res.* II **40**, 1–8.

Ducklow, H.W., Kirchman, D.L., Quinby, H.L., Carlson, C.A. & Dam, H.G. 1993 Stocks and dynamics of bacterioplankton carbon during the spring bloom in the eastern North Atlantic Ocean. *Deep Sea Res.* II **40,** 245–263.

Gardner, W.D., Walsh, I.D. & Richardson, M.J. 1993 Biophysical forcing of particle production and distribution during a spring bloom in the North Atlantic. *Deep Sea Res.* II **40**, 171–195.

Gooday, A.J. & Turley, C.M. 1990 Responses by benthic organisms to inputs of organic material to the ocean floor: a review. *Phil. Trans. R. Soc. Lond.* A **331**, 119–138.

Graf, G. 1989 Benthic-pelagic coupling in a deep-sea benthic community. *Nature, Lond.* **341**, 437–439.

Gundersen, J.K. & Jorgensen, B.B. 1990 Microstructure of diffusive boundary layers and the oxygen uptake of the sea floor. *Nature, Lond.* **345**, 604–607.

Gust, G., Michaels, A.F., Johnson, R., Deuser, W.G. & Bowles, W. 1994 Mooring line motions and sediment trap hydromechanics: *in situ* intercomparison of three common deployment designs. *Deep Sea Res.* I **41,** 831–857.

Hamner, W.M., Madlin, L.P., Alldredge, A.L., Gilmer, R.W. & Hamner, P.P. 1975 Underwater observations of gelatinous zooplankton: sampling problems, feeding biology, and behaviour. *Limnol. Oceanogr.* **20**, 907–519.

Hecker, B. 1990 Photographic evidence for the rapid flux of particles to the sea floor and their transport down the continental slope. *Deep Sea Res.* II **37**, 1773–1782.

Honjo, S. & Manganini, S.J. 1993 Annual biogenic particle fluxes to the interior of the North Atlantic Ocean: studied at 34° N 21° W and 48° N 21° W *Deep Sea Res.* **40**, 587–607.

Honjo, S., Spencer, D.W. & Farrington, J.W. 1982 Deep

PHILOSOPHICAL TRANSACTIONS OF THE ROYAL SOCIETY B BIOLOGICAL SCIENCES

advective transport of lithogenic particles in the Panama Basin. *Science, Wash.* **216**, 516–518.
Karl, D.M., Knauer, G.A. & Martin, J.H. 1988 Downward flux of particulate organic matter in the ocean: a particle decomposition paradox. *Nature, Lond.* **332**, 438–441.
Koike, I., Shigemitsu, H., Kazuki, T. & Kogure, K. 1990 Role of sub-micrometre particles in the ocean. *Nature, Lond.* **345**, 242–244.
Köster, M., Jensen, P. & Meyer-Reil, L.–A. 1991 Hydrolytic activities of organisms and biogenic structures in deep-sea sediments. In *Microbial enzymes in aquatic environments* (ed. R.J. Chróst), p. 298. New York: Springer-Verlag.
Lampitt, R.S. 1985 Evidence for the seasonal deposition of detritus to the deep-sea floor and its subsequent resuspension. *Deep Sea Res.* **32**, 885–897.
Lampitt, R.S., Hillier, W.R. & Challenor, P.G. 1993*a* Seasonal and diel variation in the open ocean concentration of marine snow aggregates. *Nature, Lond.* **362**, 737–739.
Lampitt, R.S., Noji, T. & von Bodungen, B. 1990 What happens to zooplankton faecal pellets? Implications for material flux. *Mar. Biol.* **104**, 15–23.
Lampitt, R.S., Wishner, K.F., Turley, C.M. & Angel, M.V. 1993*b* Marine snow studies in the Northeast Atlantic: distribution, composition and role as a food source for migrating plankton. *Mar. Biol.* **116**, 689–702.
Lawrence, S.G., Ahmad, A. & Azam, F. 1993 Fate of particle-bound bacteria ingested by *Calanus pacificus*. *Mar. Ecol. Prog. Ser.* **97**, 299–307.
Linke, P. 1992 Metabolic adaptation of deep-sea benthic foraminifera to seasonally varying food input. *Mar. Ecol. Prog. Ser.* **81**, 51–63.
Lochte, K. 1991 Protozoa as makers and breakers of marine aggregates. In *Protozoa and their role in marine processes. NATO ASI Series, Vol. G*25 (ed. P.C. Reid, C.M. Turley & P.H. Burkill), p. 327. Berlin, Heidelberg: Springer-Verlag.
Lochte, K. 1992 Bacterial standing stock and consumption of organic carbon in the benthic boundary layer of the abyssal North Atlantic. In *Deep-sea food chains and the global carbon cycle. NATO ASI Series C, mathematical and physical sciences*, vol. 360 (ed. G.T. Rowe and V. Pariente), p.1. Dordrecht/Boston/London: Kluwer Academic Publishers.
Lochte, K., Ducklow, H.W., Fasham, M.J.R. & Stienen, C. 1993 Plankton succession and carbon cycling at 47° N 20° W during the JGOFS North Atlantic Bloom Experiment. *Deep Sea Res.* II **40**, 91–114.
Lochte, K. & Turley, C.M. 1988 Bacteria and cyanobacteria associated with phytodetritus in the deep sea. *Nature, Lond.* **333**, 67–69.
Longhurst, A.R., Bedo, A.W., Harrison, W.G., Head, E.J.H., Horne, E.P., Irwin, B. & Morales, C. 1989 NFLUX: a test of vertical nitrogen flux by diel migrant biota. *Deep Sea Res.* **36**, 1705–1719.
Longhurst, A.R., Bedo, A.W., Harrison, W.G., Head, E.J.H. & Sameoto, D.D. 1990 Vertical flux of respiratory carbon by oceanic diel migrant biota. *Deep Sea Res.* **37**, 685–694.
Martin, J.H., Fitzwater, S.E., Gordon, R.M. & Tanner, S.J. 1993 Iron, primary production and carbon nitrogen flux studies during the JGOFS North Atlantic Bloom Experiment. *Deep Sea Res.* **40**, 115–134.
Martin, J.H., Knauer, G.A., Karl, D.M. & Broenkow, W.W. 1987 VERTEX: carbon cycling in the northeast Pacific. *Deep Sea Res.* **34**, 267–285.
McCave, I.N. 1984 Size spectra and aggregation of suspended particles in the deep ocean. *Deep Sea Res.* **31**, 329–352.
Meyer-Reil, L.-A. & Koster, M. 1992 Microbial life in pelagic sediments: the impact of environmental parameters on enzymatic degradation of organic material. *Mar. Ecol. Prog. Ser.* **81**, 65–72.
Michaels, A.F., Silver, M.W., Gowing, M.M. & Knauer, G.A. 1990 Cryptic zooplankton 'swimmers' in upper ocean sediment traps. *Deep Sea Res.* **37**, 1285–1296.
Morales, C.E., Harris, R.P., Head, R.N. & Tranter, P.R.G. 1993 Copepod grazing in the oceanic north-east Atlantic during a six week drifting station: the contribution of size classes and vertical migrants. *J. Plankton Res.* **15**, 185–211.
Newton, P.P., Lampitt, R.S., Jickells, T.D., King, P. & Boutle, C. 1994 Temporal and spatial variability of biogenic particle fluxes during the JGOFS northeast Atlantic process studies at 47° N, 20° W. *Deep Sea Res.* I **41**, 1617–1642.
Osborn, T.R. 1974 Vertical profiling of velocity microstructure. *J. phys. Oceanogr.* **4**, 109–115.
Pace, M.L., Knauer, G.A., Karl, D.M. & Martin, J.H. 1987 Primary production, new production and vertical flux in the eastern Pacific Ocean. *Nature, Lond.* **325**, 803–804.
Paerl, H.W. 1973 Detritus in Lake Tahoe: structural modification by attached microflora. *Science, Wash.* **180**, 496–498.
Passow, U. & Wassmann, P. 1994 On the trophic fate of *Phaeocystis pouchetii* (Hariot): the formation of marine snow by *P. poucheti*. *Mar. Ecol. Prog. Ser.* **104**, 153–161.
Patterson, D.J., Nygaard, K., Steinberg, G. & Turley, C.M. 1993 Heterotrophic flagellates and other protists associated with oceanic detritus throughout the water column in the mid North Atlantic. *J. mar. biol. Ass. U.K.* **73**, 67–95.
Pfannkuche, O. 1993 Benthic response to the sedimentation of particulate organic matter at the BIOTRANS station, 47° N 20° W. *Deep Sea Res.* II **40**, 135–149.
Pfannkuche, O. & Lochte, K. 1993 Open ocean pelago-benthic coupling: cyanobacteria as tracers of sedimenting salp faeces. *Deep Sea Res.* I **40**, 727–737.
Rabouille, C. & Gaillard, J.-F. 1991 A coupled model representing the deep-sea organic carbon mineralization and oxygen consumption in surficial sediments. *J. geophys. Res.* **96,** 2761–2776.
Rice, A.L., Billet, D.S.M., Fry, J., John, A.W.G., Lampitt, R.S., Mantoura, R.F.C. & Morris, R.J. 1986 Seasonal deposition of phytodetritus to the deep-sea floor. *Proc. R. Soc. Edinb.* B **88**, 265–279.
Riebesell, U. 1992 The formation of large marine snow and its sustained residence in surface waters. *Limnol. Oceanogr.* **37**, 63–76.
Ritchie, G. & Shimmield, G.B. 1991 The use of $^{210}Po/^{210}Pb$ disequilibria in the study of the fate of marine particulate matter. In *Radionuclides in the study of marine processes* (ed. P.J. Kershaw & D.S. Woodhead), pp. 142–153. Oxford: Elsevier Applied Science.
Romero-Wetzel, M.B. & Gerlach, S.A. 1991 Abundance, biomass, size-distribution and bioturbation potential of deep-sea macrozoobenthos on the Voring Plateau (1200–1500 m, Norwegian Sea). *Meeresforsch.* **33**, 247–265.
Savidge, G., Turner, D.R., Burkill, P.H., Watson, A.J., Angel, M.V., Pingree, R.D., Leach, H. & Richards, K.J. 1992 The BOFS 1990 Spring Bloom Experiment: temporal evolution and spatial variability of the hydrographic field. *Prog. Oceanogr.* **29**, 235–281.
Smayda, T.J. 1970 The suspension and sinking of phytoplankton in the sea. *Oceanogr. mar. Biol.* **8**, 353–414.
Smith, C.R. 1992 Factors controlling bioturbation in deep-sea sediment and their relation to models of carbon diagenesis. In *Deep-sea food chains and the global carbon cycle.*

PHILOSOPHICAL TRANSACTIONS OF THE ROYAL SOCIETY B BIOLOGICAL SCIENCES

NATO ASI, *Series C*, vol. 360 (ed. G.T. Rowe & V. Pariente), p. 375. Netherlands: Kluwer Academic Publishers.

Smith, D.C., Simon, M., Alldredge, A.L. & Azam, F. 1992 Intense hydrolytic enzyme activity on marine aggregates and implications for rapid particle dissolution. *Nature*, *Lond.* **359**, 139–142.

Suess, E. 1980 Particulate organic carbon flux in the oceans – surface productivity and oxygen utilization. *Nature*, *Lond.* **288**, 260–263.

Thiel, H., Pfannkuche, O., Schriever, G., Lochte, K., Gooday, A.J., Hemleben, C., Mantoura, R.F.C., Turley, C.M., Patching, J.W. & Riemann, F. 1988/89 Phytodetritus on the deep-sea floor in a central oceanic region of the Northeast Atlantic. *Biol. Oceanogr.* **6**, 203–239.

Turley, C.M. 1992 Formation, vertical flux and remineralisation of aggregates in the ocean: a short review. *Archiv. Hydrobiol. Ergebn Limnol.* **37**, 155–163.

Turley, C.M. 1993 The effect of pressure on leucine and thymidine incorporation by free-living bacteria and by bacteria attached to sinking oceanic particles. *Deep Sea Res.* **40**, 2193–2206.

Turley, C.M. & Carstens, M. 1991 Pressure tolerance of oceanic flagellates: implications for remineralisation of organic matter. *Deep Sea Res.* **38**, 403–413.

Turley, C.M. & Lochte, K. 1990 Microbial response to the input of fresh detritus to the deep-sea bed. *Palaeogeogr. Palaeoclimatol. Palaeoecol.* (*Global and Planetary Change Section*), **89**, 3–23.

Turley, C.M. & Mackie, P.J. 1994 The biogeochemical significance of attached and free-living bacteria and the flux of particles in the deep north eastern Atlantic Ocean. *Mar. Ecol. Prog. Ser.* **115**, 191–203.

Turley, C.M. & Mackie, P.J. 1995 Bacterial and cyanobacterial flux to the deep north eastern Atlantic on sedimenting particles. *Deep Sea Res.* I.

Walsh, I., Dymond, J. & Collier, R. 1988 Rates of recycling of biogenic components of settling particles in the ocean derived from sediment trap experiments. *Deep Sea Res.* **35**, 43–58.

Watson, A. 1992 Conveying that sinking feeling. *Nature*, *Lond.* **356**, 561–562.

Weeks, A., Conte, M.H., Harris, R.P., Bedo, A., Bellan, I., Burkill, P.H., Edwards, E.S., Harbour, D.S., Kennedy, H., Llewellyn, C., Mantoura, R.F.C., Morales, C.E., Pomroy, A.J. & Turley, C.M. 1993*a* The physical and chemical environment and changes in community structure associated with bloom evolution: the Joint Global Ocean Flux Study North Atlantic Bloom Experiment. *Deep Sea Res.* II **40**, 347–368.

Weeks, A.R., Fasham, M.J.R., Aiken, J., Harbour, D.S., Reid, J.F. & Bellan, I. 1993*b* The spatial and temporal development of the spring bloom during the JGOFS North Atlantic Bloom Experiment, 1989. *J. mar. biol. Ass. U.K.* **73**, 253–282.

PHILOSOPHICAL TRANSACTIONS OF THE ROYAL SOCIETY B BIOLOGICAL SCIENCES