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The role of bacteria in the turnover of organic carbon in deep-sea sediments

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ABSTRACT

The cycling of organic carbon in the deep sea was inferred from measurements of sediment trap and box core samples taken on the Biscay and Demerara abyssal plains of the North Atlantic. Of the input of organic carbon to the bottom, less than 10% was buried, i.e., not consumed biologically. Based on laboratory measurements of bacterial activity in the sediment samples, incubated under *in situ* temperature and pressure, it was possible to attribute at least 13 to 30% of the total inferred biological consumption of organic carbon to microbial utilization. The complementarity of results from these biochemical and microbiological measurements implies that the decompression of cold abyssal samples during retrieval efforts does not prevent meaningful experiments on the microbial inhabitants, once returned to *in situ* pressure.

1. Introduction

Deep open-ocean sediments far from continents or plate-boundary spreading centers are thought to receive most of the organic matter they contain from overlying shallow water (Rowe and Staresinic, 1979; Suess, 1980). This organic matter comes to the deep sea as a slow rain of particulate organic detritus or as somewhat larger particles such as fecal pellets, the discarded outer skeletal material of crustaceans, or carcasses. Although the flux occurs at extremely low rates, it must support all the life both on the bottom and just above it. Any residual material left after this utilization by organisms is buried in very low concentrations with the inorganic mineral components of the sediments as they accumulate at rates as slow as a gram cm^{-2} Ky^{-1}.

The flux of organic particulate matter into the deep sea has been measured by placing "sediment traps" at great depths in the ocean. Many different designs of such traps have been used in a variety of regions. While it is not yet possible to generalize about what are hopefully small variations that result from differences in trap design, it is possible to discern how the flux in general varies with depth (Rowe and Gardner, 1979; Hinga *et al.*, 1979), latitude, surface productivity (Honjo, 1978, 1980) and season (Deuser *et al.*, 1981).

In any given area the organic particulate flux decreases in magnitude with depth as

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its composition is altered by biological activity (Wakeham *et al.*, 1980; Lee and Cronin, 1982). The consumption of such detritus in the water column has been reviewed by Angel (1984) and modeled by Vinogradov and Tseitlin (1983). In principle, the process of heterotrophic consumption of organic matter in the deep water column has been approached earlier as a first-order rate process based on the vertical distribution of POC, e.g. its exponential decline with depth and the distribution of oxygen (Wyrtki, 1962; Craig, 1971). Likewise, on the bottom itself the utilization of oxygen by the biota has been measured by placing small chambers on the bottom and monitoring the loss of oxygen from within them for several days (Smith, 1978; Hinga *et al.*, 1979; Smith and Hinga, 1983; Smith and Baldwin, 1984) or by applying mathematical models to the distribution of oxygen in sediment pore waters (Murray and Grundmanis, 1980). The role of nitrate as a terminal electron acceptor has been estimated for some regions (Froelich *et al.*, 1979), and the effects of the CO_2 production of both aerobic and nitrate metabolism on pore water pH and $CaCO_3$ dissolution rates have been considered (Berner, 1980; Emerson and Bender, 1981).

Deep-sea sediments recovered from the sea floor contain bacteria that appear to carry out metabolic processes that are not very different from marine bacteria recovered from lesser depths (ZoBell, 1946). Results of some studies of deep-sea sediment and water samples have indicated that most of the bacteria present actually originated in shallower waters, since their response to increased hydrostatic pressure is similar to that of shallow water bacteria, i.e., pressures of 200 to 500 atm reduce their metabolic rates several orders of magnitude below that which occurs at atmospheric pressure (Jannasch and Wirsen, 1973, 1981; Wirsen and Jannasch, 1975; Jannasch and Taylor, 1984). However, other studies have revealed a predominance of microorganisms that display barotolerance or even metabolic rates that are greater at extreme pressures than at atmospheric pressure (Schwarz *et al.*, 1976; Deming and Colwell, 1981, 1982; Jannasch *et al.*, 1982). The latter, termed barophiles, have been isolated in pure culture from decomposing crustaceans (Yayanos *et al.*, 1979), from the guts of marine invertebrates (Deming and Colwell, 1981, 1982), from sediments and sinking particulates (Deming, Abstr. N67, Annual Meeting ASM, 1983; Deming and Colwell, 1985), and from the water column (Jannasch *et al.*, 1982). While it is obvious that bacteria exist in the deep sea, and that some proportion of them can metabolize and grow *in situ*, albeit slowly, on the very limiting supplies of organic energy we alluded to above (Williams and Carlucci, 1976; Sorokin, 1981; Jannasch and Wirsen, 1981), no generalizations can be made yet about the contribution of bacteria to the overall cycling of organic matter in deep-sea sediments. The principal barrier to making such generalizations is the absence of data on *in situ* microbial activities at sites where other pertinent biological and chemical parameters have been measured.

The purpose of the present paper is to examine what proportion of the total turnover of organic carbon on the sea floor can be attributed to bacterial metabolism, based on chemical and microbiological data we have obtained from two abyssal plains in the

Atlantic Ocean. These data are derived from sediment trap deployments to assess the vertical flux of particulate organic carbon (POC) from cores of surface sediments to assess carbon accumulation rates, bacterial densities by direct count, and bacterial metabolic rates by measuring the utilization of ^{14}C-glutamic acid at *in-situ* pressures and temperatures recreated aboard ship. Our goal is to determine the coherence between metabolic rates inferred from sediment traps and cores and those actually measured on the organisms themselves. We anticipate that our results will provide a degree of confidence in the validity of these two independent methods of looking at the cycling of organic carbon in the deep sea.

2. Methods

The work presented here has been a part of a general effort being made at the *Centre Oceanologique de Bretagne,* IFREMER, in Brest, France, to understand the structure and function of deep-sea benthic communities. Several regions of study have been sampled, including the two that we discuss in this paper, the Demerara Abyssal Plain in the north equatorial Atlantic off northeastern South America and the Bay of Biscay off the west coast of France. The strategy on these expeditions has been to select several typical deep locations in each region and then to sample these specific stations intensively. In the Bay of Biscay this has amounted to establishing stations that have been sampled repeatedly by COB biologists at various seasons over a number of years. For the purpose of our paper, we will present data from two locations on the Demerara Abyssal Plain (DAP) (Fig. 1a) and two in the Bay of Biscay (BoB) (Fig. 1b). Depths, respectively, were about 4.4 km (A) and 4.8 km (B) (DAP) and 4.1–4.2 (St. 2 and 3) and 4.7 km (BoB) (St. 4).

In each of these two areas (DAP and BoB), sediment traps were deployed for intervals of up to 9 days. The trap design used was a modification of that of Rowe and Gardner (1979, a cylinder with a diameter of 25 cm and a length of 75 cm). Our traps were mounted on vertical arrays consisting of an acoustic release and disposable anchor on the bottom and floatation spheres that were up to 200 m off bottom. The individual traps themselves were covered at their tops by a 1 cm × 3 cm honeycomb-like grid to reduce turbulent flow across their tops. An internal lid in each trap was closed at the end of a deployment on command from a timed release. Each trap terminated in a 30-cm funnel with a valve for emptying the traps after recovery. No preservative was used but the deployment times were kept short to minimize *in situ* degradation of the organic material captured. No correction has been made for degradation that might have occurred (Gardner *et al.*, 1983). The samples were handled and analyzed in a manner similar to that described by Rowe and Gardner (1979). Splitting was accomplished with a Folsom plankton splitter (McEwen *et al.*, 1954). Total gravimetric analyses were made with pre-weighed glass fiber filters. These were then combusted on a Perkin-Elmer elemental analyzer for C and N, after acid removal of carbonate.

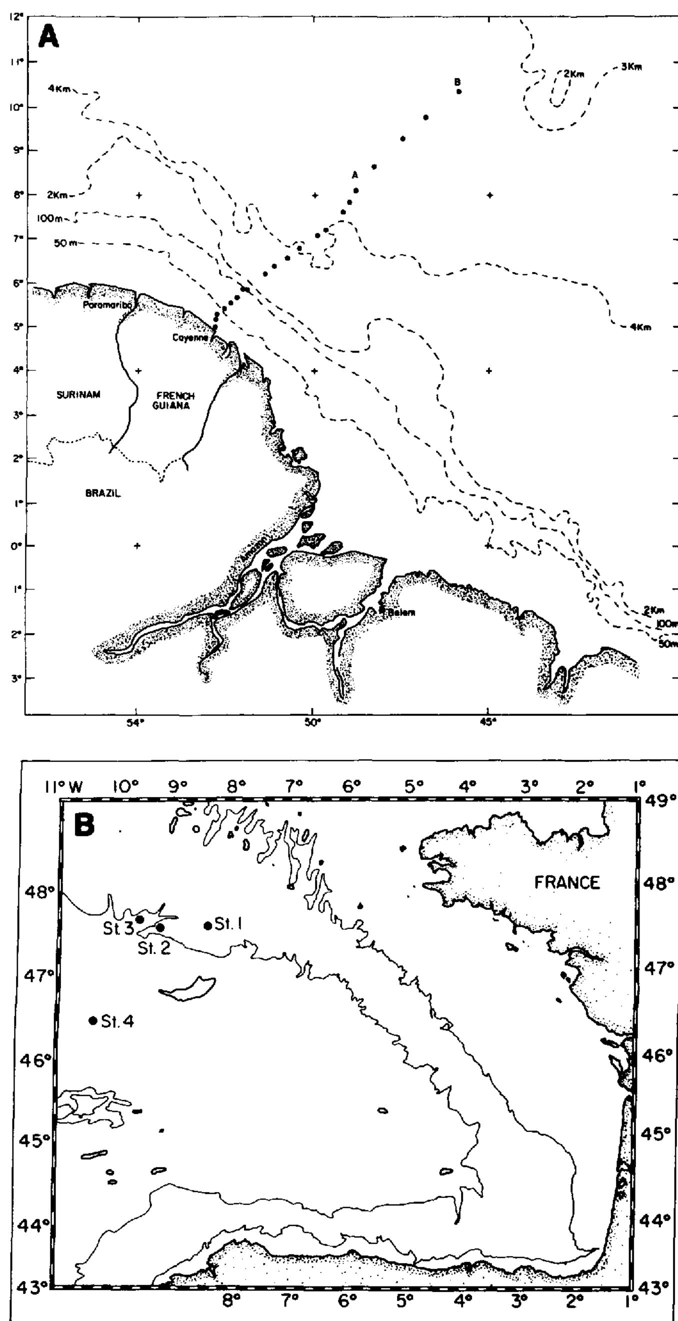

Figure 1. (a) Demerara Abyssal Plain with sampling locations, 4.5 km (A) and 4.8 km (B). (b) Bay of Biscay with sampling locations, stations 1–4 at 2.1, 4.1, 4.2 and 4.8 km depth, respectively.

Sediments and their contained biota were sampled using a US-NEL box (spade) corer. It covered 1/4 m^2 and penetrated between 30 to 45 cm into the bottom. The signal from an acoustic pinger mounted just above the box corer was monitored in order to control bottom contact precisely.

Immediately upon retrieval, our colleagues drained overlying sea water carefully from the surface by siphon. The temperature of the sediment at 5 cm depth was recorded. Subcores measuring 6 × 20 cm were taken at each station except at the Biscay stations at 4200 and 4715 m, where the undisturbed surface sediment in the boxcores was sampled directly and aseptically to a depth of 1 cm. All subcores and surface samples were removed immediately to the shipboard coldroom (3°C) for subsequent manipulations.

In the coldroom, sediment cores were extruded onto sterile foil and cut into sections with a sterile spatula at depth intervals of 2 to 4 cm. Subsamples for microbiological analyses were removed aseptically from the center of each section. Sediment suspensions were prepared by diluting the sediment 1:5 (wet wt: vol) with filtered (0.2 μm), autoclaved, artificial sea water (ASW). Measured portions of each suspension were collected on Whatman filter paper (5.5 GF-C) and dried at 60°C for 18 hr to determine dry weight in grams. Additional portions were fixed in a final concentration of 2% formaldehyde and stored at 3°C for later examination by epifluorescence microscopy after acridine orange staining. Total bacterial counts were determined for each sediment suspension and normalized to gram dry weight sediment, as described by Deming and Colwell (1982).

A duplicate subcore was also taken from each boxcore above and frozen for eventual analysis of calcium carbonate, organic carbon and total nitrogen. The $CaCO_3$, C, and N were measured using methods described above for sediment trap samples. Pore water, obtained with a Reeburgh squeezer or stainless steel press (Manheim, 1966), was analyzed using conventional colorimetric nutrient analyses adapted for an autoanalyzer (Whitledge *et al.*, 1981), after dilution with standard sea water in some cases.

Microbial utilization of glutamic acid. Time-course experiments, measuring total microbial utilization of ^{14}C-glutamic acid (incorporation plus respiration) in sediment suspensions from core depths of 1, 5, and 15 cm at stations in the Demerara Abyssal Plain, have been described in detail elsewhere (Deming and Colwell, 1985). The procedural points of relevance to our present purposes are that the sediment samples were (1) kept cold (3°C) at all times; (2) diluted 1:10 (wet wt:vol) with ASW; (3) supplemented with ^{14}C-glutamic acid (1.97 μCi/μg; Commissariat a l'Energie Atomique, France) to achieve a final, low concentration of 9.4 ng/ml; and (4) recompressed as soon as possible to *in-situ* pressures (420 or 480 atm) in stainless steel pressure vessels, one for each incubation interval. Duplicate samples were incubated at 3°C and atmospheric pressure (1 atm) in order to assess barosensitive vs. barophilic responses

and, therefore, to detect any potentially negative effects of a brief period of decompression on the resident population of indigenous, barophilic bacteria. In each experiment, fate of the radiolabeled substrate was monitored in duplicate subsamples at 12–36 hr intervals over a total incubation period of 5 days, providing a degree of detail and reproducibility difficult, if not impossible, to achieve through *in situ* experimentation. Substrate incorporation and respiration were differentiated by sample filtration and $^{14}CO_2$ capture, according to methods of Hobbie and Crawford (1969) modified by Paul and Morita (1971).

From the initial portions of the radioisotope uptake curves presented by Deming and Colwell (1985), we calculated rate of total substrate utilization, or uptake velocity (v), using linear regression analysis. Rates were then normalized to gram dry weight sediment for comparative purposes. We also calculated glutamic acid utilization rates from uptake curves determined for the two surface sediment samples from Biscay stations at depths of 4.2 and 4.7 km. Procedures were identical to those already described for Demerara samples (Deming and Colwell, 1985) except that radiolabeled substrate was added to achieve an even lower, final concentration of 2.0 ng/ml.

In addition to the direct calculation of uptake velocity (v) from these time-course experiments, a theoretical maximum uptake velocity (V_{max}) for glutamic acid was determined for surface sediment from the Biscay station at 4715 m, using the kinetic (multiple substrate concentration) approach of Wright and Hobbie (1965). Replicate samples of the sediment suspension were supplemented with increasing concentrations of radiolabeled glutamic acid (2.0, 5.0, 10, and 20 ng/ml) and incubated for a single time period of 12 hr at 3°C and 470 atm with duplicate at 1 atm. V_{max} was calculated as the reciprocal of the slope of the straight line generated by plotting added substrate concentration against substrate turnover time. Turnover time in this instance is defined as t/f, where t is incubation time and f is the fraction of available isotope utilized (incorporated and respired) during the incubation time. See Wright (1974) or Wright and Burnison (1979) for a complete discussion of the theoretical considerations involved in measuring microbial activity using this kinetic approach.

3. Results

a. Bacterial abundances. The abundance of bacteria in all surficial (1–5 cm) sediments (Table 1) varied from 2 to 8.3×10^8/gm-dry-sediment, with the highest being found at the 4.4 km Demerara station (Fig. 2). There, and at the other stations as well, the numbers of bacteria dropped about one order of magnitude over the top 10 cm of sediment. In selected cases where bacterial counts were obtained in triplicate, the average error in counting was ±16%.

The total numbers of microbes in a sediment core can be calculated from graphical integration of the AODC data (Table 1, Fig. 2). These totals would be 2.10×10^9 (4.5 km on the Demerara), 1.16×10^9 (4.8 km on the Demerara) and 0.99×10^9 cells/cm^2 (at 4.1 km on the Bay of Biscay). The mean would be 1.4×10^9 cells/cm^2.

Table 1. Depth profiles of bacterial concentrations and rates of total microbial utilization of glutamic acid in deep-sea sediment cores.

Location[a] and depth (m)	Core depth (cm)	Bacteria/g[b]	Ng glutamic acid/g/d[c]
Demerara, Station A, 4470	surface	4.65×10^8	10.2
	3	8.29×10^8	
	5	4.58×10^8	21.0
	8	1.05×10^8	
	11	1.48×10^7	
	15	1.66×10^7	0.945
Demerara, Station B, 4850	surface	3.08×10^8	10.0
	3	3.10×10^8	
	5	2.39×10^8	9.95
	8	9.12×10^7	
	11	7.35×10^7	
	15	2.20×10^7	2.57
Biscay, Station 2, 4100	surface	2.02×10^8	
	2	2.04×10^8	
	4	2.82×10^8	
	7	1.12×10^8	
	10	5.75×10^7	
	14	1.82×10^7	
	16	1.23×10^7	
	20	6.17×10^6	
	26	8.71×10^6	
Biscay, Station 3, 4200	surface	4.26×10^8	10.0
Biscay, Station 4, 4715	surface	3.34×10^8	19.2 (108)[d]

[a]See Fig. 1.

[b]Determined by epifluorescence microscopy; average error ±16%.

[c]Rate of total microbial utilization of glutamic acid (incorporation plus respiration) under *in situ* temperature and pressure, calculated directly from uptake curves (Deming and Colwell, 1985) using linear regression analysis. Average correlation coefficient was 0.957. Rate is per gram dry sediment.

[d]Parenthetic value is V_{max}, determined by the kinetic approach of Wright and Hobbie (1965).

This represents an underestimate of the total numbers because in no sediment core did we reach an abiotic condition with depth. Such an integration includes those organisms that are active in the remineralization processes on the DAP, through the depths in the sediments over which total organic carbon is decreasing in concentration, but it also includes any "inactive" organisms that may be present in the upper 15 cm. However, the lack of an organic carbon gradient of any significance below 15 cm implies that remineralization at greater depth has ceased. This is also supported by the metabolic rate measures discussed below.

An estimate of total bacterial biomass in terms of carbon per square meter is useful

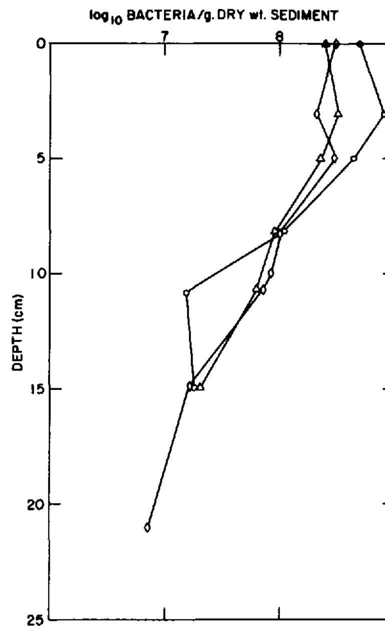

Figure 2. Bacterial counts in sediments, Demerara Abyssal Plain, 4.8 km (Δ), 4.4 km (○); Bay of Biscay, 4.1 km (◇).

for comparison with carbon fluxes and other living stock sizes. The total microbial organic carbon can be estimated from the conversion factor of Williams and Carlucci (1976), where a single deep-sea bacterium, based on its size and shape, contains 10^{-14} g organic carbon. With an average porosity of 0.8, determined from weight loss on drying, and with a specific gravity for dry sediment of 2.6, we converted the above counts to total microbial carbon as follows:

Microbial organic carbon/m^2 = 2.6 g cm^{-3} × (1 − porosity) × 10^4 cm^2/m^2 × integrated numbers of bacteria/g over depth range sampled in sediment × 10^{-14} gC/cell, or,

	Depth (km)	Bacterial Biomass (mg C/m^2)
Demerara	4.5	210
Demerara	4.8	116
Bay of Biscay	4.1	99
Mean	4.5 km	142 mg C/m^2

Total microbial biomass was greater at both of the Demerara stations than in the Bay of Biscay, even though the depth of integration in the latter was to 26 rather than 15 cm.

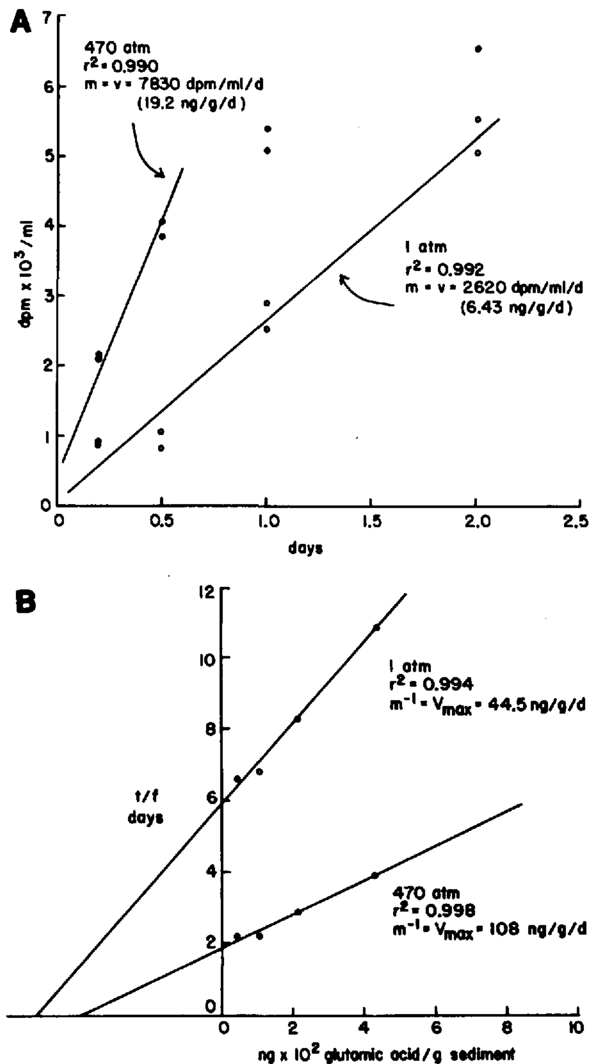

Figure 3. (a) Total microbial utilization of ^{14}C-glutamic acid (incorporation plus respiration) in a surface sediment suspension from Biscay station 4715 m. Duplicate subsamples were supplemented with 2 ng ^{14}C-glutamic acid/ml and incubated at 3°C under an *in situ* pressure of 470 atm (●) and at atmospheric pressure (○). (b) Total microbial utilization of ^{14}C-glutamic acid (incorporation plus respiration) determined for the same sample under pressures of 470 atm (●) and 1 atm (○), using the kinetic approach of Wright and Hobbie (1965). See text for procedural details and definition of terms.

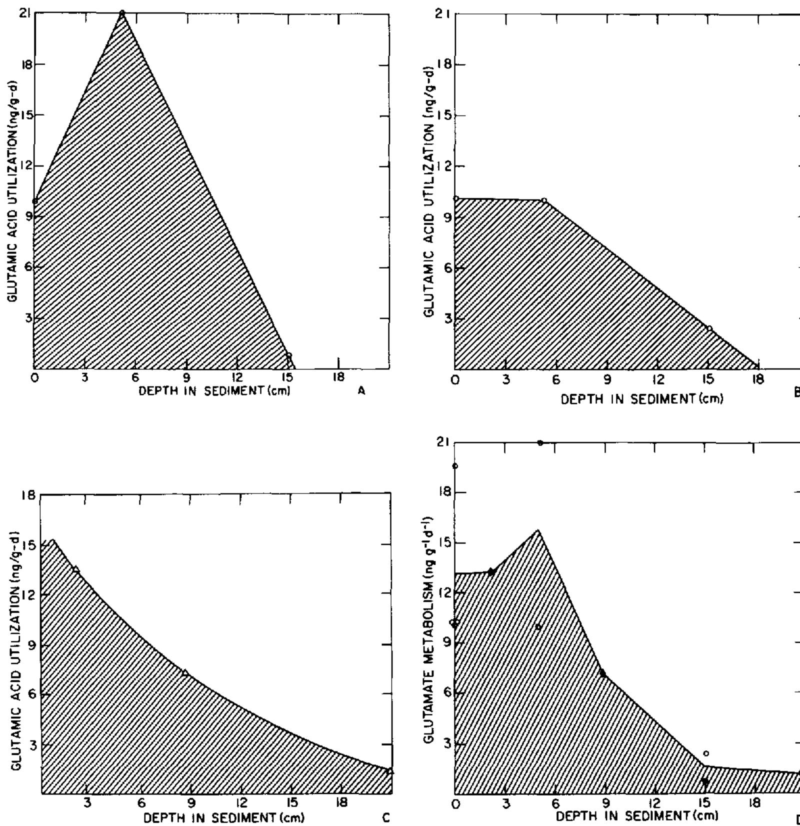

Figure 4. Profiles of data in Table 1 used for integration of rates of glutamic acid incorporation, (a) Demerara, 4.4 km (b) 4.8 km (c) Bay of Biscay, 4.2 km (d) Average for all areas.

b. Microbial utilization of glutamic acid. Rates of total microbial utilization of glutamic acid in sediment suspensions, determined under *in situ* temperature and pressure, ranged from 0.94 to 21 ng/g-d (Fig. 3a). Conversion of substrate to CO_2 (respiration) accounted for 87 to 97% of the total substrate utilization, the rate of which was always faster under *in situ* pressure than at atmospheric pressure (Deming and Colwell, 1985). Use of the kinetic approach on a surface sample from 4715 m in the Bay of Biscay resulted in a theoretical *in situ* V_{max} of 108 ng glutamic acid/g-d (Fig. 3b), 5.6 times faster than the direct calculation of uptake velocity from the complementary time-course experiment under deep-sea temperature and pressure (Fig. 3a).

In general, both bacterial concentrations and rates of glutamic acid utilization decreased with depth in a sediment core. The subsurface increase in both parameters at the 4.5 km Demerara station may be related to an anomalous, watery break observed in the sediment core at a depth of 3–5 cm.

For the two locations on the Demerara Abyssal Plain where metabolic rates were measured at both surface and subsurface depths in the core (DAP, 4.4 and 4.8 km), total integrated rates, again taking porosity into consideration and expanding to a square meter, were 1.0 mg glutamic acid/m^2-d at the shallower station, and 0.6 mg glutamic acid/m^2-d at the deeper station. The principal difference between these two values was attributable to the high rate of 21 ng/g-d measured at 5 cm in the core from the shallower station (Fig. 4a).

From the above utilization rates one can also calculate average utilization per unit of bacteria in the sediments. (We use $\log_{10}$ bacteria for convenience, but total bacterial numbers could be used as well.) This rate would be expected to decrease with depth in the sediment because the water column is the primary source of both the terminal electron acceptors (O_2, NO_3, NO_2, etc.) and organic substrates. For the interval 0 to 5 cm, the average was 1.63 ng/$\log_{10}$ unit of bacteria-h, whereas at a depth of 15 cm the average was 0.24 ng/$\log_{10}$ unit of bacteria-h. Given these depth-dependent rates of metabolism per unit of bacteria and interpolating between surface and 15-cm depths to obtain intermediate values, one can use profiles of bacterial number alone to calculate overall (integrated) metabolism at those locales, such as the Bay of Biscay, where metabolism at depth was not measured. The total integrated uptake using this approach there was 132 ng/g-d or 0.68 mg glutamate m^{-2} d^{-1} (Fig. 4c). This value was intermediate between the Demerara stations, even though the bacterial counts were determined for greater depths in the sediment at the Biscay station. The BoB rates at depth were derived from the DAP rates per unit biomass at slightly lesser depth and such a conversion may not be very accurate.

c. Organic matter in the sediments. Percent organic carbon in the sediments decreased within the top 20 cm at all locations sampled (Figs. 5 and 6). Below that depth, organic C appeared to increase slightly to 30 cm, the maximum depth of the cores. The general trend appeared to be a greater concentration of organic C on the Demerara compared to the Bay of Biscay, a pattern observed also in the microbial biomass. In the Bay of Biscay at 4.2 km the organic C decreased from about 0.6% at the surface of the mud down to about 0.35% at 20 cm, whereas on the Demerara at the same levels in the sediment the concentration decreased from about 0.8% to about 0.4%. Total organic carbon in the sediments was calculated by integrating the profiles in Figure 5 (again taking into account porosity). These summations were 546 and 448 g C/m^2 in the top 15 cm at the 4.4 and 4.8 km Demerara stations, compared to 300 g C/m^2 in the same depth interval at the single Biscay station, or about 60% of the average Demerara value.

Percent total nitrogen followed a pattern similar to that of organic carbon (Fig. 6). Although it was decidedly higher on the Demerara, compared to the Bay of Biscay, both sets of data demonstrated declines in N with depth to 10 cm, a stabilization between 10 and 20 cm, and then a slight increase as depth increased to 30 cm.

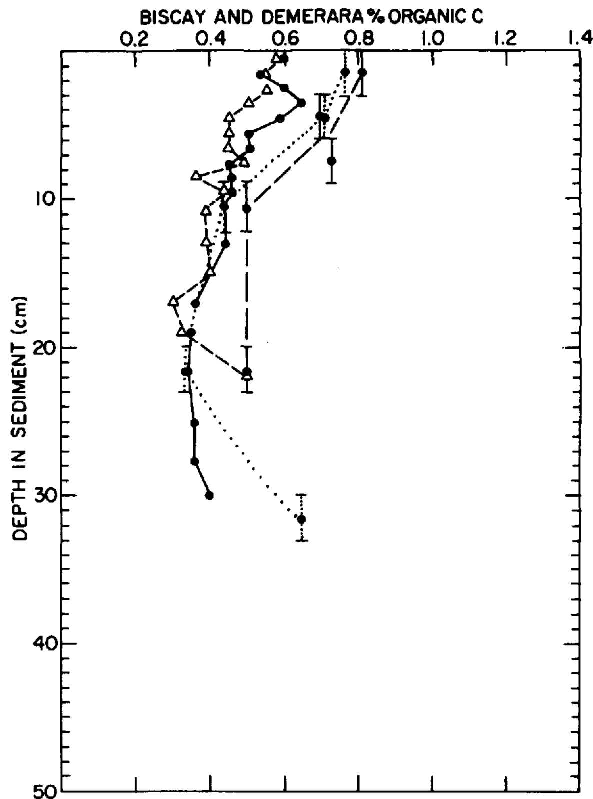

Figure 5. Organic carbon in sediments, Bay of Biscay (St. 1, 2.1 km, Δ, St. 3, 4.2 km, ●) and Demerara Abyssal Plain (St. A, 4.4 km, ---; St. B, 4.8 km, ...).

In the Bay of Biscay, the rate of decrease of organic carbon (based on the slopes of the lines in Fig. 5) was on the order of 0.15 mg C/gm-dry-wt sediment-cm, over a 10 cm depth interval, whereas the general Demerara pattern was a more marked decrease of about 0.3 mg C/gm-dry-wt sediment-cm over a 10 cm depth interval. Total nitrogen displayed a similar pattern (Fig. 6). The rate of catabolism per unit depth, therefore, would be expected to be greater in Demerara than in Biscay sediments.

d. Particulate fluxes. The fluxes of particulate matter to the sediment (Table 2) were measured in terms of total particulate material (TPM), calcium carbonate, particulate organic carbon (POC), and total fixed nitrogen. The measured flux of TPM ranged from 372 mg/m^2-d at a trap 200 m off-bottom (m.o.b.) at the 4.4 km Demerara station to a low of only 66.3 mg/m^2-d at the similarly positioned trap at 4.8 km in the Bay of Biscay. The Demerara average for the two stations (287 mg/m^2-d) was more than three times the Bay of Biscay average (92.4 mg/m^2-d). The POC and total nitrogen

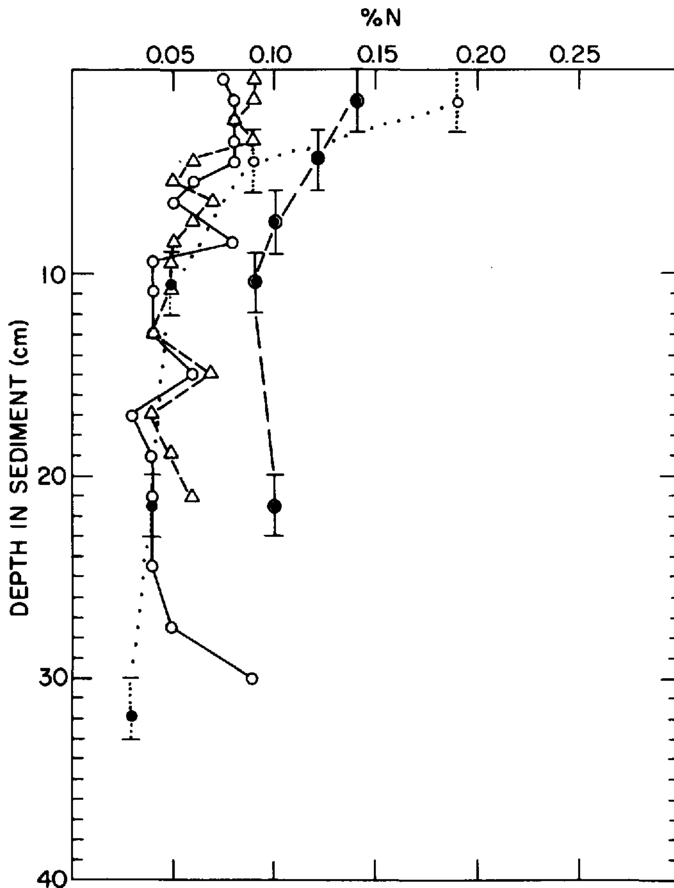

Figure 6. Total fixed nitrogen in sediments, Bay of Biscay (St. 1, 2.1 km, Δ; St. 3, 4.2 km o) and Demerara Abyssal Plain (St. A, 4.4 km, ---; St. B, 4.8 km, ...).

followed the same pattern as the TPM, with the highest (15.9 mg C/m^2-d) and the lowest (4.9 mg C/m^2-d) being at the same locations as the TPM extremes, although the lowest flux in POC was in the trap 15 m.o.b. in the Bay of Biscay rather than in the trap positioned highest off the bottom (200 m), as might be expected. The percent POC of the TPM ranged from 3.1% in the trap 70 m.o.b. at the 4.8 km Demerara station to 9.5% in the trap 200 m.o.b. in the Bay of Biscay. The overall average was 4.5% POC. The C/N ratio ranged from 12.2 in the trap 200 m.o.b. at the 4.4-km Demerara station to a low of 7.7 in the trap 200 m.o.b. at the Biscay station. The lowest C/N ratio was found in the trap with the lowest TPM flux but the highest % POC. The Bay of Biscay, although having lower fluxes in all measurements, had higher % POC and lower C/N ratio on average than the Demerara traps.

Table 2. Flux of particulate matter measured in sediment traps (mg/m^2-d).

Trap location and collecting interval	Total	$CaCO_3$	Organic C	N
Demerara Abyssal Plain (September, 1980)				
Station A, 4450 m,				
9-d deployment, 7 m.o.b.* (8°08.4'N × 40°00.93'W)	227	186	13.7	1.3
10-d deployment, 200 m.o.b. (8°09.13'N × 49°01.66'W)	372	245	15.9	1.37
mean	300	215	14.8	1.3
Station B (10°25.09'N × 46°44.7'W), 4850 m				
9-d deployment, 145 m.o.b.	241	112	9.8	1.1
9-d deployment, 70 m.o.b.	299	85	9.4	0.82
9-d deployment, 20 m.o.b.	282	103	9.4	0.82
mean	274	100	9.5	0.91
Bay of Biscay (October, 1981)				
Station 4 (46°31'N × 10°27'W), 4800 m				
8-d deployment, 200 m.o.b.	66.3	—	6.3	0.82
8-d deployment, 100 m.o.b.	88.8	—	6.8	0.82
8-d deployment, 15 m.o.b.	122	—	4.9	0.55
mean	92.4	—	6.0	0.70
overall mean (mg/m^2-d) of all 3 stations	222	157	10.1	0.97
annual mean (g/m^2-y) of all 3 stations	81.1	57.3	3.7	0.35

*meters off bottom

e. Organic carbon accumulation. Accumulation rates of organic carbon and nitrogen at the three locales can be calculated on the basis of published dating of deposited sediments. Here, we estimate the rate of incorporation of organic carbon at our study sites, using rates of sediment accumulation published by Mauviel *et al.* (1982) and our measurements of sediment density and concentrations of organic carbon below the depth of biological mixing (Table 3). These indirect estimates of burial rates for organic matter are only slightly higher than similar estimates, presented by Khripounoff and Rowe (1985) for two of our locations, as a result a few higher organic carbon values measured at depth in our cores.

As the flux of particulate material to the bottom has been measured directly from sediment traps in our study, we can also estimate accumulation directly, as practiced previously (Rowe and Gardner, 1979; Honjo, 1978, 1980; Brewer *et al.*, 1980). Some of the compounds in the TPM caught by the traps, however, will not contribute to accumulation because of chemical or biological remineralization prior to burial. In the case of $CaCO_3$ and organic matter, this remineralization loss can be estimated from the difference between their concentrations in the trapped TPM and those at depth in the

Table 3. Indirect estimate of organic carbon accumulation rate below the sediment mixed layer.

Location	Sediment accumulation rate (cm/Ky)	Sediment density (g dry/ cm^3 wet)	Percent organic carbon below bioturbation layer (dry wt)	Organic carbon accumulation rate (mg C/m^2-d)
Demerara Station A	1.8*	0.8**	0.50	0.2 (= 72 mg C/m^2-y) (= 7.2×10^{-3} g C/cm^2-Ky)
Demerara Station B	0.3*	0.8**	0.35	0.02 (= 8.4 mg C/m^2-y) (= 8.4×10^{-4} g C/cm^2-Ky)
Bay of Biscay Station 4	2.0*	0.8	0.35	0.15 (= 56 mg C/m^2-y) (= 5.6×10^{-3} g C/cm^2-Ky)

*Mauviel *et al.*, 1982.
**Khripounoff and Rowe, 1985.

sediment. By subtracting the lost fraction from the deposited material we adjusted for chemical dissolution or metabolism after arrival on the sea floor (Table 4).

These more direct estimates of the accumulation of organic carbon (Table 4) were calculated from the available data (Tables 2 and 4), using the following equation:

Accumulation = {total input to traps − [(fraction of $CaCO_3$ in traps − fraction of $CaCO_3$ at depth in sediment) × total input to traps] − [(fraction of organic C in traps − fraction of organic C at depth in sediment) total input to traps]} × fraction of organic C at depth.

All estimates of the accumulation rate of organic matter, based on indirect methods (Table 3), are lower than estimates based on direct analyses of trap and core samples (Table 4). There is the possibility that the latter rates overestimate actual accumulation if constituents other than $CaCO_3$ and organic carbon are also being remineralized. One such constituent likely to be dissolving into the pore water is silicate from diatoms, radiolarians, etc., which are known to be principal components of the TPM flux. We have no measurements of the particulate siliceous matter, either in the traps or in the sediments, and so cannot use the above method to estimate silicate remineralization. However, we did measure $Si(OH)_4$ in the pore waters at the 4.1 km Biscay and the 4.8 km Demerara stations and can use the silicate gradient in the top few cm to estimate the flux of Si out of the sediment.

Table 4. Concentrations of organic carbon and calcium carbonate in cores and direct estimates* of organic carbon accumulation rate.

Location and Depth (km)	Sediment depth (cm)	% Organic carbon	% $CaCO_3$	Organic carbon accumulation rate* (mg C/m^2-d)
Demerara	surface	0.80	15	2.09
Station A (4.4)	20	0.50	35**	0.80
Demerara	3	0.78	42	2.1
Station B (4.8)	20	0.35	29	0.87
Bay of Biscay	surface	0.60	54	0.63
Station 3 (4.2)	20	0.35	41	0.33

*Calculated according to equation in text, p. 939.

**Increase at depth suggests change in sediment provenance and accumulation rate; see text.

The $Si(OH)_4$ concentration at 4.1 km (BoB) decreased on average from 300 $\mu M/\ell$ at 9 cm to 80 $\mu M/\ell$ at 1 cm. Using an effective diffusion coefficient (D) derived by Schink *et al.* (1975) of 3.3×10^{-6} cm^2/s, and a gradient of .22 $\mu M/cm^3$-8 cm,

$$\text{Flux} = D(d\text{Si})/dz = 78\ \mu M/m^2\text{-d}$$

and $Si(OH)_4$ will therefore have a Si mass flux of 5 mg/m^2-d. This is 4 to 6% of the trap-caught TPM and therefore further remineralization of the "residue," although occurring, does not appreciably affect estimates of organic carbon burial (accumulation) rates. At 4.8 km on the DAP a similar calculation leads to an estimate that is about an order of magnitude less (0.5 mg/m^2 d), because the dissolved pore water $Si(OH)_4$ gradient was much less (50 $\mu M/\ell$-5 cm). Therefore, it does not seem likely that preburial remineralization of additional (unmeasured) trap constituents can account for our more direct sediment trap estimates of organic carbon accumulation being higher than those based on published parameters in the deposited sediments.

f. Inferred subsurface organic matter utilization. Knowledge of the organic matter profile and TPM accumulation (see above sections) allows the calculation of the post-depositional metabolic utilization of substrates in the absence of any direct measurements of biological activity. At the locations we studied, this can be expressed as follows:

$$\int_{0\,\text{cm}}^{20\,\text{cm}} R\,dz = \text{flux}_{0\text{cm}} - \text{flux}_{20\text{cm}}$$

where the total heterotrophic utilization of organic matter between 0 and 20 cm, R, is equal to the vertical downward flux at 0 cm minus the vertical downward flux at 20 cm. The fluxes of organic matter derived above (Tables 3 and 4) can be used in this

equation to generate the following inferred rates of organic carbon utilization:

Demerara Station A (4.4 km)
$2.09_{0cm} - 0.80_{20cm} = 1.29$ mg C/m^2-d

Demerara Station B (4.8 km)
$2.1_{0cm} - 0.87_{20cm} = 1.23$ mg C/m^2-d

Bay of Biscay (4.1 km)
$0.63_{0cm} - 0.33_{20cm} = 0.30$ mg C/m^2-d

4. Discussion

Earlier work in the NW Atlantic attempted to use the vertical flux of POC, burial rates (accumulation) and bottom oxygen demand to partition quantitatively the fate of POC (Rowe and Gardner, 1979; Hinga *et al.,* 1979; and Rowe, 1981). This was accomplished by putting all the terms in the budget into organic carbon units from known stoichiometric or physiological relationships. Sediment accumulation was taken from nearby estimates in the literature or was calculated from the sedimentation rate of inorganic mineral matter into sediment traps, less the losses that would result from $CaCO_3$ dissolution and organic matter degradation. In one case (Rowe and Gardner, 1979), the loss due to biodegradation was estimated from sediment oxygen demand, measured by Smith (1978) in a separate study of the same area over which the traps were deployed (Rowe and Gardner, 1979; Honjo, 1978, 1980), whereas Hinga *et al.* (1979) measured both O_2 demand and trapped TPM at the same stations. To derive these estimates, 1 ml O_2 demand was assumed to be equivalent to 0.45 mg carbon remineralized to the dissolved inorganic form, CO_2, based on the relationship between the amount of oxygen required to oxidize organic matter and the presumption, albeit oversimplified, that the oxidized matter is separated into more or less equal portions of fat, carbohydrate, and protein.

Using the above approach, we partition the fate of organic matter in a similar manner (Figs. 7 and 8), but we also have attempted to go somewhat further with estimates of biological degradation rates. A flow diagram has been drawn for each study area (Fig. 7), each with a term for input, burial, and two sources of biological loss, one for the activities of surface-living heterotrophs and one for those living below the surface. These loss terms can be divided into losses due to remineralization (CO_2 production and NH_4 excretion) and ill-defined losses due to predation or an ontogenetic migration. For the purpose of these budgets, we make the assumption that the system is in steady state, or that the total carbon mass in the system is not increasing or decreasing over time. We attribute subsurface losses primarily to remineralization but assume a 10% loss to predation from above. This is probably oversimplified, but some fraction of the organic matter utilized by the microbial heterotrophs results in microbial production that is held in steady state by predation by deposit feeders

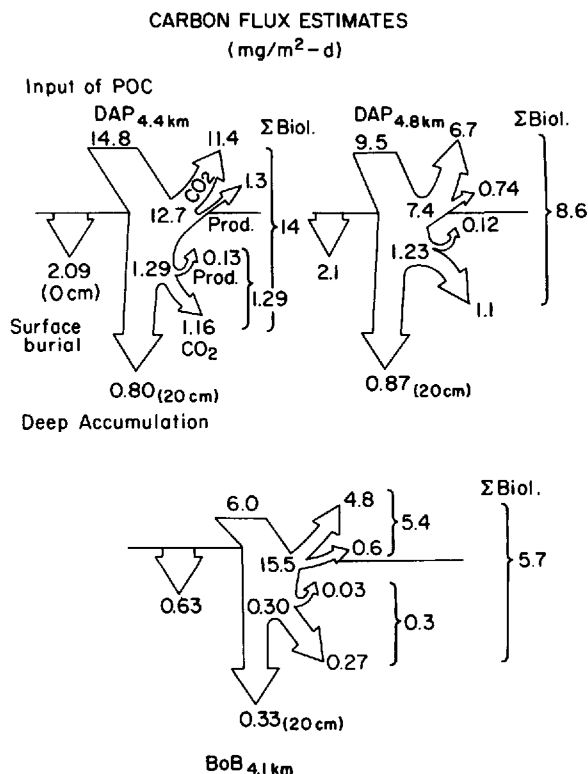

Figure 7. Diagram of inputs and fates of organic carbon inferred from trap and core samples at the locations indicated.

(Menzies, 1962; Sibuet and Lawrence, 1981; Deming and Colwell, 1982). We assume this production to be on the order of 10%, a value similar to that measured in each of the ^{14}C glutamic acid experiments described above. The surface-living organisms have also been divided along these lines, with the assumption that about 90% of the organic matter consumed goes to respiration and the rest to growth, gonad production, or predation. The assumption of steady state implies that any such growth would have to be exported in some form in order to maintain the steady state.

The two approaches used to estimate organic carbon accumulation on the bottom provide very different rates (Tables 3 and 4). Providing an obvious explanation for the differences is difficult. The indirect core-dating method is more accurate if dissolution of particulates is far greater than we have assumed. However, if sedimentation rates have increased gradually over the past 10 or so thousand years, then the trap estimates would acceptably represent only the present conditions. A comparison of the two kinds of accumulation estimates relative to the input is interesting. The mean of the dated core estimates was 0.12 mg C/m^2-d, whereas the mean estimated from the trap and core data was 0.66 mg C/m^2-d. These amount on average to 1.2% and 6.5% of the

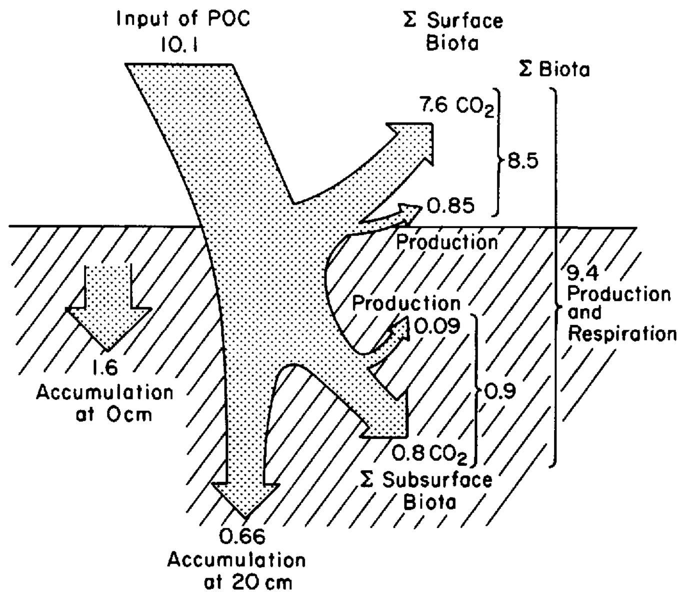

Figure 8. Average fluxes at 3 locations in Figure 7.

average input (10.1 mg C/m^2-d). In both cases, the carbon accumulation is a small fraction of the input. For the sake of further discussions of biological activity, we have chosen to utilize the larger, more direct estimates rather than those based on previously published core-dating. This is a conservative choice because "inferred biological utilization" is based on differences between input and accumulation: using the larger of the two accumulation values leads to a more cautious estimate of biological activity.

Others have used traps to measure the vertical flux of POC and TPM at sites several hundred kilometers to the northwest on the Demerara Abyssal Plain in water about 400 m deeper (Honjo, 1980; Lee and Cronin, 1982; and DeBaar *et al.*, 1983). There the organic matter and total flux to the bottom was on the order of 5 to 6 times less than what we measured. The validity of the lower fluxes is supported, according to Honjo (1980), by the fact that the total oxygen demand of sediment elsewhere in the ocean at that depth, as measured by benthic chambers *in situ* (Smith and Hinga, 1983), is about the same in terms of organic carbon. There are reasons, however, why the traps we set in the equatorial Atlantic should have collected sinking particles at rates somewhat higher than the other collections. Our traps were in shallower water in an area closer to the depositional influences of the Amazon River. Our traps were in the water for a far shorter time (days instead of months), thus minimizing by comparison any degradation that may have occurred in them (Gardner *et al.*, 1983). Moreover, because they are 3-to-1 cylinders and not funnel-shaped, our traps are less likely to lose material artificially over the course of the deployment (Gardner, 1980). There are also reasons

why *in situ* benthic chambers should be expected to underestimate the total oxygen demand implied by the vertical flux of POC and TPM, the most obvious one being that such chambers do not measure the demands of foraging megafauna (holothurians, amphipods, etc.).

Our measurements of biological activity in sediments, i.e., bacterial utilization of glutamic acid, must also be considered with appropriate caution. In order to measure the rates of microbial substrate utilization in sediments, samples had to be exposed to a short period (4–8 hr) of decompression during boxcore retrieval and sample preparation (but no marked increase in temperature), diluted, and supplemented with isotope. It is difficult to predict whether any one of these disturbances should lead to an overestimate or underestimate of *in situ* activity. Indigenous, deep-sea bacteria are believed to expire over an extended incubation period at atmospheric pressure, if the temperature is significantly warmer than that encountered at abyssal depths (Yayanos *et al.*, 1982; Yayanos and Dietz, 1983; Deming and Colwell, 1985). However, temperature was guarded closely and the decompression period was brief. All of the substrate utilization rates were barophilic (more rapid under *in situ* pressure than at atmospheric pressure), indicating that most of the indigenous sediment bacteria responsible for glutamic acid utilization *in situ* survived the brief period of decompression (Deming, 1985; Deming and Colwell, 1985).

In shallow water environments, substrate enrichment is known to stimulate rates of microbial metabolism. Whether the same holds true in the cold, pressurized, low nutrient environment of deep-sea sediments is not at all clear (Nealson, 1982), although substrate enrichment does not appear to stimulate the actual growth, as opposed to metabolism, of sediment bacteria to any significant degree (Deming, 1985). In our study, only minimal concentrations of substrate, increasing that available naturally by less than 10%, were added to sediment suspensions. For example, the final concentration of ^{14}C-glutamic acid added to a surface sediment sample from Biscay station at 4715 m was 2 ng/ml, while the dissolved free glutamic acid present naturally in the filtrate (<0.2 μm) of the same (unsupplemented) sediment suspension was determined to be 20.6 ng/ml (S. Henrichs, pers. comm.). Based on the substrate enrichment factor alone, rates calculated directly from the uptake curves of Deming and Colwell (1985) and Figure 3A should not represent a significant stimulation or overestimation of *in situ* activity. Although sample dilution can be expected to alter the physical and chemical microenvironments of bacteria in sediment, the artificial resuspension of sediment for experimental purposes may not be very different from natural resuspensions due to currents and bioturbation.

The only rates of microbial substrate utilization that have been measured *in situ* in sediments of comparable depth were based on injections of ^{14}C-acetate and ranged from 2.1 to 91.2 ng acetate/g/d (extrapolated from data presented by Jannasch and Wirsen, 1981, assuming 1 cc^3 wet sediment to be equivalent to 0.5 g dry sediment). Our rates (0.945 to 21.0 ng glutamic acid/g/d), though based on a different substrate, are conservative by comparison. Furthermore, at 4715 m (Biscay station), where both v

and V_{max} were measured, the rate calculated from the time-course incubation experiment was considerably lower than that projected theoretically for sediments with an unlimited supply of organic substrate. Thus, for the broader purposes of this paper, we will assume that the rates listed in Table 1 (excluding V_{max} at the deepest Biscay station) represent conservative estimates of *in situ* activity.

A principal question in this study is how rates of biological activity inferred from the trap and core data (Fig. 7) match rates of bacterial activity, measured in the repressurized sediments and integrated over depth. To make this comparison, we converted the measured utilization of glutamic acid to dissolved free amino acid carbon, based on the average carbon content (41%) of the principal dissolved free amino acids (DFAA's). Resulting rates on the Demerara were 0.41 and 0.25 mg C/m^2-d at 4.4 and 4.8 km, respectively, and 0.34 mg C/m^2-d at 4.1 km in the Bay of Biscay. Averaging all of the rates gives 0.33 mg C/m^2-d or 120 mg C/m^2-y. At 5.7 and 4.7 nM/g wet sediment, glutamic acid represented 23 and 21% of the total dissolved free amino acids (Susan Henrichs, pers. comm.) in the Bay of Biscay at the 4.2 km and 4.1 km stations. Therefore, assuming no competitive effects among the various amino acids, we used a factor of 5 to convert the above rates to what we assume to be more accurate representations of the total microbial utilization of all DFAA's.

These final, extrapolated rates are 2.05, 1.25, and 1.7 mg C/m^2-d, at the 4.4-km and 4.8-km Demerara stations and the Biscay station, respectively (assuming that the Demerara DFAA concentrations are in about the same proportion as those in the Bay of Biscay). Therefore, of the total organic carbon input, DFAA utilization by sediment bacteria accounts for *ca.* 28% in the Bay of Biscay and *ca.* 13% on the Demerara Plain. Likewise, of the total biological utilization inferred in Figure 7, microbial DFAA utilization represents about 30% in the Bay of Biscay and 15% on the Demerara Plain. Of course, organic substrates other than DFAA's must also be available for microbial utilization, leading us to conclude that the overall contribution of bacteria to total inferred biological utilization of organic carbon at these study sites is greater than 13–30%. The remainder we speculate to be utilized by metazoans and foraging megafauna. Such a division of resources between bacteria and the larger organisms of the community is not an unreasonable portioning of energy.

This general agreement between inferred and measured rates suggests that in shipboard batch incubations, repressurized bacteria will utilize organic matter at rates that are of the same order of magnitude as those that would be expected to occur on the deep-sea floor. The estimate of a potential utilization rate under nonsubstrate-limiting conditions (V_{max}) suggests that additions to the DFAA pool, whatever the source, would be readily utilized.

Our microbial data can also be viewed in terms of the rate of cycling of carbon through the bacterial biomass. The data in Table 1 can be used to make such estimates if one assumes, as we have above, that glutamic acid utilization is *ca.* 1/5 of the total DFAA utilization, that DFAA's are the primary source of energy for the bacteria in question, and that the DFAA's are 41% carbon. By dividing stock size (in terms of

carbon) by utilization rate (in terms of carbon) for the top 5 cm in the Demerara Abyssal Plain and the surface for the Bay of Biscay, one is provided with a range of carbon cycling or turnover times of 86 d at 4.7 km in the Bay of Biscay to 208 d for the 4.2-km Biscay station. The Demerara stations were intermediate between these at 139 and 182 d at 4.5 and 4.7 km depth. The bacterial turnover time of organic matter at the one location where it was estimated relative to a maximum uptake rate was only 17 d. All these rates (v and V_{max}) are very low compared to rates measured in shallow water (where direct *in-situ* studies are more practical), but V_{max} calculated from our repressurized experimental samples suggests that rates of bacterial carbon cycling in abyssal sediments could be much higher if new substrates were made available.

We have had the opportunity to compare the input and fate of organic matter by direct and indirect approaches at three locations of approximately the same depth in the deep sea. Some parameters, such as %C in the sediments (Figs. 5–6), suggest that the Demerara Abyssal Plain should be characterized by a greater flux of energy and higher biomass than the Bay of Biscay. This is supported by most of the biological data. The total standing stock of bacteria is higher at both Demerara locations than in the Bay of Biscay (Fig. 2). Metazoan biomass in all size classes is higher at the 4.4 km station than at the 4.8 km station on the Demerara Plain (Sibuet *et al.*, 1984), but no similar suite of biomass data is available from Biscay stations. The average rate of utilization by the bacteria at the two Demerara stations is higher than in the area studied off France; the burial rate at both Demerara stations is more than twice their single counterpart in the Bay of Biscay.

Another appropriate way to view our total data set is in terms of the means of the locales and their overall variances (Fig. 8). In this case the mean POC flux at 4–5 km depth would be 10.1 mg C/m^2 d, the burial would be 0.66 mg C/m^2 d, and the total biological utilization would be on the order of 9.4 mg C/m^2 d, or *ca.* 3.4 g C/m^2 y. This value is well within the range of sediment community oxygen demand estimates for similar depths (Smith and Hinga, 1983).

Of the total input of organic carbon, 6.5% was buried below the sediment mixed layer. Of the other 93% utilized, 90% of that was consumed by organisms on or above the sediment water interface versus only 10% below it. Of the 93% utilized by the biota, our uptake rate measurements, in agreement with the general partitioning of energy in most ecosystems, suggest that at least 90% of the carbon consumed is converted to CO_2. The small amount of secondary production that is occurring, if the system is in steady state, must be exported by mechanisms such as predation by organisms from above, loss of planktonic eggs or juveniles or ontogenetic migrations.

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