The supply and use of organic material at the deep-sea floor

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ABSTRACT

Sediment traps and benthic respirometers have been used to measure the supply of particulate materials to, and the use of organic material by the North Atlantic deep-sea benthos. The area of the sea floor less than 2 kilometers deep is relatively small but accounts for 85% of the total oceanic benthic oxygen consumption, which reflects the primary productivity of the surface waters. *In situ* measurements of nutrient fluxes across the sediment-water interface differ markedly from the Redfield ratios. Sediment traps at three locations in the western North Atlantic yielded fluxes of 205 to 280 mg $m^{-2}day^{-1}$ of total particulate material, 33 to 150 mg $m^{-2}day^{-1}$ of carbonate, 14 to 30 mg $m^{-2}day^{-1}$ of organic carbon, and 0.3 to 1.2 mg $m^{-2}day^{-1}$ of nitrogen. Vertical fluxes of identifiable particulates included 2,000-11,000 $m^{-2}day^{-1}$ of foraminifera, 2,000-6,000 $m^{-2}day^{-1}$ of Radiolaria, 760-1200 $m^{-2}day^{-1}$ of pine pollen, 6-560 $m^{-2}day^{-1}$ of metal spheres and 30,000-700,000 $m^{-2}day^{-1}$ of diatoms. Comparison of the sediment trap fluxes with the benthic oxygen consumptions indicates that the vertical flux of particulate organic carbon is adequate to fuel the deep (3500 m) benthos, but that an additional input is required at shallower (600m, 1300m) depths. The transport of organic matter by vertically migrating organisms is suggested as the dominant additional input at the shallower depths.

1. Introduction

The physical environment of the oceans of the world below 1000 m is remarkably uniform compared to the variety of conditions that exist in oceanic surface waters and in neritic and estuarine environments. The organisms that live in the deep sea, however, are not spatially uniform in either density or species composition. Deep-sea communities also have a high diversity even though there can be a few niches defined by physical divisions of the environment. A map of the density of deep-sea macrofaunal organisms (Belyaev *et al.*, 1973) bears a strong resemblance to a map of the primary productivity of the world oceans (Koblentz-Mishke *et al.*, 1970). Sokolova (1976) also found that the relative abundance of deposit feeders and suspension feeders in the deep sea was related to the primary productivity of the surface waters. Thus, it is likely that the supply of food materials to the deep-sea is of

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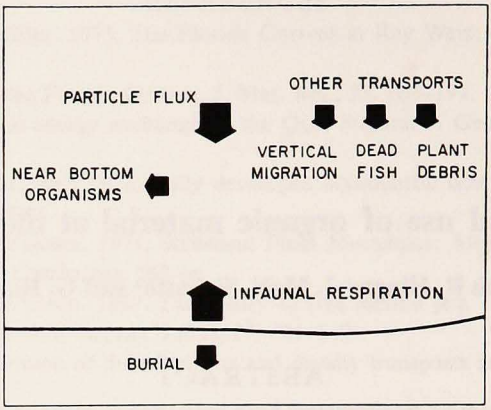


Figure 1. Conceptual pathways for the supply and fate of organic carbon at the deep sea floor.

prime importance in sustaining the distribution, density, and structure of deep-sea communities.

The supply of food for deep-sea organisms traditionally has been viewed as a rain of detritus slowly settling to the benthos. This perception has been modified in recent years since McCave (1975) has emphasized that the flux of material is dominated by relatively rare large particles. Fecal pellets seem to be responsible for a large part of the particulate transport Wiebe *et al.*, 1976; Honjo and Roman 1978). Organic matter associated with these pellets supplies food to deep-sea organisms.

Other transports of organic matter to the deep-sea also have been suggested. Vertically migrating organisms may feed in surface waters then migrate to deeper waters where undigested organic matter is excreted or where the organisms themselves are eaten (Vinogradov 1962, Ketchum 1957). Both diel and ontogenetic vertical migrations could transport organic material to depth in this manner. Large macroscopic debris is another proposed transport mechanism. Wiebe *et al.* (1976) reported plant debris in the Tongue of the Ocean and Menzie *et al.* (1967) reported similar material on the deep-sea floor off North Carolina. The "monster" camera deployments (Isaccs and Schwartzlose, 1975) and baited traps (Shulenberger and Hessler, 1974) have identified populations of organisms in the deep-sea that are well suited to utilize the bodies of dead fish and mammals.

Figure 1 summarizes the supply and fate of organic matter at the deep-sea floor. Once the organic matter reaches the benthos it may be utilized by infaunal or near-bottom organisms or be buried in the sediment. Near-bottom organisms are operationally defined as organisms living on or near the sediment that are not enclosed in chambers placed on the sediment to measure the respiration of infaunal organisms. Lateral transport of sediment by bottom currents is not included in Figure 1. If one tries to supply significant amounts of organic carbon by resuspending and transport-

ing oceanic sediments, typically less than 1% organic carbon, the rates of sedimentation in the areas of deposition would need to be unrealistically high. Techniques to measure a number of the components in Figure 1 are available. The burial rate can be calculated from dated cores, the particulate flux can be measured in sediment traps, and carbon usage by infaunal organisms can be calculated from benthic oxygen consumption measured by benthic respirometers. When all these techniques are used at a single location it is also possible to infer the importance of the fluxes that cannot be measured directly. We have used sediment traps and benthic respirometers to study the fate of organic matter at a number of deep-sea locations.

In contrast to deep-sea studies which have dealt only with the infaunal macrofauna, these techniques used together allow the entire benthic community to be considered as a system. Thiel (1975) estimated that the production of micro-organisms and meiofauna are both as great as that of the macrofauna. Haedrich and Rowe (1977) found the megafaunal organisms have a biomass as great as the macrofauna. Clearly if we are to understand deep-sea communities, we must evaluate more than the infaunal macrofauna alone.

The implications of sediment trap and respirometer measurements extend beyond biological questions. Measurements of oxygen and carbon fluxes at the benthos aid in calculations of the oceanic budgets for these elements: a factor in the assessment of the oceanic response to the injection of fossil-fuel carbon. The amount of oxygen consumption measured in benthic chambers can be compared with consumptions predicted by models of oceanic oxygen distribution.

2. Materials and methods

Ten deployments were made at seven locations utilizing a respirometer or sediment trap. At three locations, both systems were deployed simultaneously (Table 1, Fig. 2). The length of each deployment was made as short as possible while still allowing for a measurable accumulation of material in the traps. Since no attempt was made to poison the sediment traps, a short deployment minimizes the decay of organic material in the sediment traps. Similarly, it is necessary that sufficient time be allowed for oxygen consumption within the benthic respirometer chambers, but not allowing all the oxygen to be depleted.

Respirometer. The benthic respirometer used in this study measures fluxes of dissolved materials across the sediment-water interface. Chambers placed on the interface enclose an area of the sediment and a volume of water above the sediment. After an appropriate period of time, water samples are removed from the chambers for analysis. If, for example, the concentration of a dissolved substance has decreased from the initial concentration, then the sediment has taken up the dissolved substance and the uptake rate can be calculated using the length of incubation, the area, and the volume of the chamber.

Table 1.

Deployment	Depth	Lat.	Long.	Bottom temperature (°C)	Bottom oxygen (μmoles/kg)	Date	Study
76B	3450m	23°49.0N	85°36.1W	4.6	181	March 1976	respirometer
76C	70m	04°58.6N	05°05.8W	13.0	185	May 1976	respirometer
76D	4000m	00°03.5N	10°34.5W	2.4	246	May 1976	respirometer
76E	278m	04°55.7N	05°07.2W	11.1	44	May 1976	respirometer
77A	3515m	38°23.0N	69°45.0W	3		May-June 1977	trap
77C	3525m	38°23.0N	69°45.0W	3		May-June 1977	respirometer
77D	1345m	33°30.0N	76°15.0W	4.1	246	June 1977	respirometer and trap
77E	1345m	33°30.0N	76°15.0W	4.1	246	June 1977	respirometer
77F	675m	27°42.0N	78°54.0W	10.0	142	June 1977	respirometer and two traps
77G	645m	27°42.0N	78°54.0W	10.0	142	June 1977	two traps

The sampling respirometer consists of a frame, anchor, four enclosure chambers, and a sampling mechanism. The overall configuration of the respirometer is shown in Figure 3. The frame (1.8×1.2×0.7m) is 5cm square aluminum tubing bolted together for easy disassembly and shipping. Below the frame is the anchor, a ring of chain encased in concrete. A ring anchor was chosen to minimize sediment disturbance by water displaced as the respirometer approaches the sediment. A release, either acoustic or timed, holds the anchor to the frame until recovery. The respirometer was designed for use at the bottom of a mooring. A string of other instruments and flotation is attached to the top of the respirometer. Observations during deployment indicate that the moorings descend at approximately 1 meter per second.

The chambers are teflon coated aluminum, 23.75cm in diameter by 8cm high, with a 1mm wall thickness. Each chamber is an independent unit that suspends from two rods passing through the frame. The rods are free to move through the frame, allowing vertical movement of the chambers. The chambers are held up from the sediment by a dissolving link. For deep deployments an 8 hour link is used. This assures that the chambers are well flushed with bottom water and that any sediment stirred up by the anchor has dissipated before the chambers are placed. The dissolving link introduces an error of 1-2% in the length of the incubation. When the link releases, the chambers are allowed to drop and penetrate 4cm into the sediment. Further penetration is prevented by a 200cm^2 flange around each chamber. A check valve allows water to escape from the chamber during emplacement. A savonius

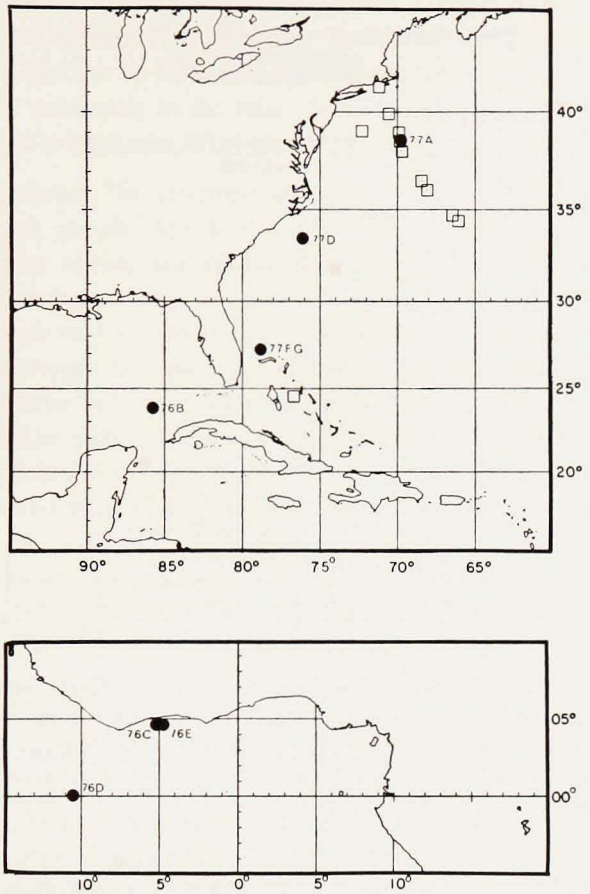


Figure 2. Station locations, solid circles are stations from this study. Open squares are locations of other benthic respiration measurements.

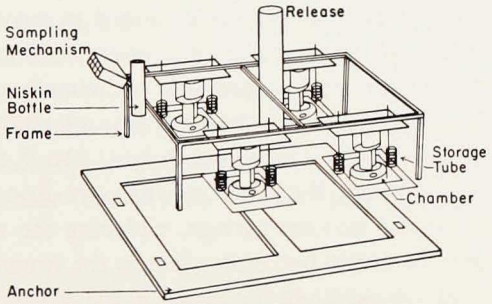


Figure 3. Benthic respirometer.

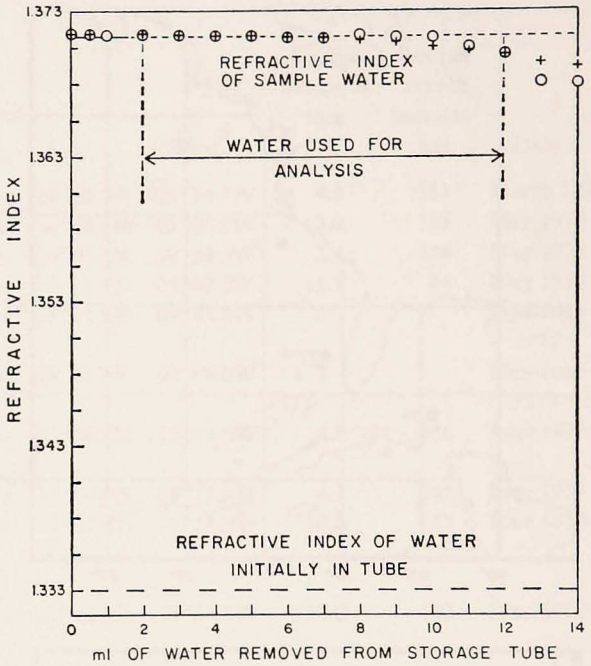


Figure 4. Degree of contamination of respirometer in two different sample storage tubes. Twelve of the twenty milliters of sample drawn into the sample storage tube have less than 2% mixing with the water initially in the storage tube. The last two milliters of sample drawn into the storage tube are not used for analysis, providing 22cm of separation between the sample and the sampling end of the tube.

rotor attached to the top of each chamber magnetically drives a teflon and polyvinylchloride stirring bar suspended within the chamber to prevent the formation of chemical gradients.

In the side wall of each chamber, 3cm above the sediment-water interface, are two polypropylene bulkhead tubing connectors. Fitted to the outside of each connector is 2m of 3.5mm inside diameter stainless steel tubing in a 5cm by 15cm coil. Each storage coil holds 14ml. The coils are arranged to prevent air bubbles from traveling up the coil when the respirometer is removed from the water. At the end of the coil away from the chamber is a valve that is manually closed upon recovery. A length of polyethylene tubing connects the valve on each coil to a reversing syringe. The plunger for each syringe is a 1.5kg lead weight. The 8 reversing syringes are extended into the syringe barrel. When the syringes are reversed the plungers fall drawing water out of the coil into the syringe, replacing the water in the coil with water from the chamber. A niskin bottle attached to the frame provides a reference sample. The syringes are reversed and the niskin bottle is tripped before the anchor is released. Immediately upon recovery, the valves are closed and the storage tubes

are removed from the respirometer and refrigerated. Oxygen analyses are performed within an hour of recovery. The sampling mechanism draws 20ml of water into each storage tube, but not all the water can be used for analysis since there is some mixing with water previously in the tube. Tests indicate that about 10ml of usable sample is recovered in each tube (Fig. 4).

Respirometer Analyses. The relatively small volume of sample limits the number of analyses of each sample. Standard autoanalyzer techniques were adequate for silicate, nitrate plus nitrite, and phosphate analyses. Ammonia analyses using a Solorzano (1969) technique required 3ml of sample. Total CO_2 was measured using a gas chromatograph on 1 ml samples. At one location (76E) the gas chromatograph was also used for oxygen determination. All other oxygen analyses were done using the 5ml micro-Winkler technique described below.

The micro-Winkler technique used throughout this research is based on the work of Fox and Wingfield (1938) and Puerto Rico Nuclear Science Center Report 162, appendix. The micro-Winkler technique is similar to a standard Winkler technique with adjustments in procedure and glassware to allow a small sample size without serious loss of accuracy or precision. The micro-Winkler gives results reproducable to 1.5 μmoles liter^{-1} and within 1% of standard Winkler analyses (Carritt and Carpenter, 1966). An accurate sample volume and isolation of the sample during the fixing steps was accomplished by using specially prepared 5ml glass syringes. Each syringe was fitted with a metal frame that limits the draw of the barrel, thus determining accurately the volume of the solution which may be drawn into the syringe. The draw of the barrel was adjustable by a screw on the frame to allow reagents to be drawn into the syringe after the sample was drawn. Each syringe and frame unit was calibrated gravimetrically with water.

A reaction syringe was prepared before each analysis by filling the dead volume of the syringe (mostly the tip of the syringe, approximately 0.12ml) with a manganous chloride solution (400 g liter^{-1}) taking care to exclude all bubbles. The sample was then drawn into the syringe, followed by 0.25ml (twice the dead volume of the syringe) of alkaline iodide solution (320 grams sodium hydroxide and 100 grams potassium iodide per liter), then shaken. After five minutes reaction time, 0.8ml of concentrated phosphoric acid was drawn into the syringe. When the precipitate had dissolved, the solution was ejected into the titration vessel followed by two 2ml rinses of distilled water. The solution was titrated with sodium thiosulfate (1.5 g liter^{-1}) standardized against 0.0250M potassium iodate using a 2ml micrometer buret fitted with polyethylene capillary tubing that allowed direct injection of the titrant into the titer. The oxygen concentration of each sample was calculated from the equation:

$$\frac{N(Vt-Vr)2.47\times10^5}{Vs} = \mu\text{moles } O_2/\text{liter}$$

Where N is the normality of the thiosulfate, Vt is the volume of the thiosulfate, Vr is a volume of thiosulfate to account for the oxygen in the reagents, and Vs is the volume of the sample. A correction of 158 μmoles liter^{-1} was made for oxygen in the manganous chloride and the alkaline iodide reagents.

Analytical errors in the oxygen chemistry and timing errors in the dissolving link and timers introduce errors of less than 5% of the oxygen fluxes. Because of the smaller relative changes that occur for the nutrient concentrations, the errors may be larger, up to 10%. The greatest error associated with respirometer measurements is in the chamber volume. Since the height of the chamber above the sea floor is only 4cm, irregularities on the sediment surface or incomplete penetration of the chamber may lead to volume errors ranging up to 25%.

Sediment Traps. The sediment traps are polyvinylchloride cylinders 20cm in diameter by 45cm high. A butterfly valve is recessed 12cm below the top of the trap. On the edge of the valve is an O-ring that seats against the machined interior wall of the trap when closed. The valve pivot rests in a slot, allowing the valve to center in both the open and closed position, and is spring loaded to close when released. A wire connected to an external timer holds the valve open. The wire is cut by the timer before the mooring is released. Sediment traps were on the same mooring as the respirometer with the flotation 50 meters above the top sediment trap. For stations 77A and 77D single sediment traps were placed 50 meters above the bottom, while at stations 77F and 77G traps were 50 and 100 meters above bottom.

After the traps were recovered, all the contained water (10.5 L) was quantitatively divided using a modified Otto plankton splitter. The subsamples were then filtered through precombusted and preweighed Gelman A/E glass fiber filters. An aliquot of distilled water was washed through the filter to remove residual sea water. The filters were frozen in individual containers, returned to the lab, and then dessicated to a constant weight. The entire area of each filter was viewed at 100× magnification and identifiable particles were counted using a microscope with a mechanical stage. After counting, subsamples were cut from each filter. Some of the samples from each filter were treated for 24 hours in the fumes from concentrated hydrochloric acid to remove carbonate. This treatment was sufficient to remove all carbonate from samples of much heavier foraminifera than were found in the sediment trap samples. Both fumed and unfumed samples were analyzed in a CHN analyzer for carbon and nitrogen. Approximately 80% of the total trapped material was used for carbon and nitrogen analysis to assure that the splitting procedure did not introduce errors. Unused portions of the filters were retained for observation with the scanning electron microscope.

Errors in the carbon analyses and in the light microscope counts, except for the diatoms, are less than 5%. The nitrogen analyses of the sediment trap samples may have error of up to 10%. The sediment traps are similar in design to those which

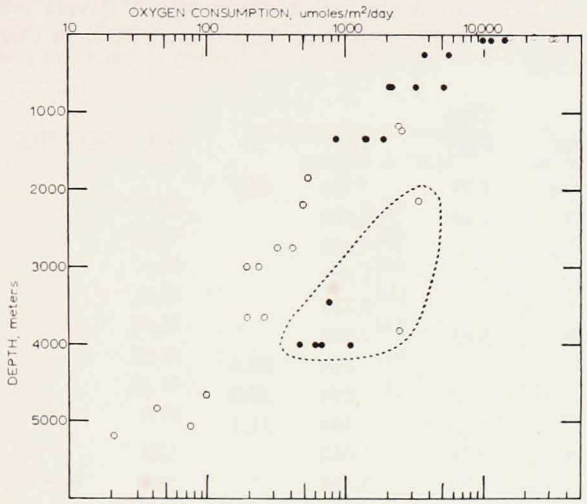


Figure 5. Oxygen consumption of the deep-sea benthos. Solid circles are from this study. Open circles are from Smith and Teal (1973), Smith (1974), Smith *et al.* (1976), Smith (1978), Smith *et al.* (1979) and Smith reported by Wiebe *et al.* (1976). The four stations with high oxygen consumptions are from an equatorial station (4,000 m) a station beneath the California corvent (3815 m) and two from tropical stations near land and which are not representative of normal pelagic conditions (3535 m, 2050 m).

Gardner (written comm., 1978) found to have trapping efficiencies of 100 ± 25% for silt-sized material settling under oceanic conditions. The flux of organic material is concentrated in larger, faster-moving particles which should be trapped with efficiencies comparable to those for finer particles.

3. Results

Benthic Oxygen Consumption. Figure 5 shows the oxygen consumption values for the six locations presented in Table 2, as well as other reported benthic oxygen consumption values (Smith and Teal, 1973; Smith *et al.*, 1976; Smith 1974: Smith, reported by Wiebe *et al.*, 1976; Smith, 1978, and Smith *et al.*, 1979). Consumption rates decrease by nearly three orders of magnitude from the shallow sea floor to 5,000m depths. The decrease at the deep stations reflects both the greater distance for particulate material to travel through the water column and the lower primary productivity of pelagic waters. The four stations with anomalously high consumptions (circled in Figure 5) are from one equatorial station, from a station beneath the Californian Current where the primary productivity of the surface waters is high, and from two tropical stations near land, which are not representative of normal pelagic conditions. The temperate-region values in Figure 5 can be used to estimate the depth distribution of benthic oxygen consumption (Table 3). The shallow depth

Table 2. Respirometer data, all numbers are μmoles $m^{-2}day^{-1}$. Oxygen values are uptake, all other values are releases. Values on the same line are from the same chamber. * = analysis run, no detectable flux.

Deployment	Depth	Time Days	O_2	Si	NH_3	NO_2+NO_3	PO_4	CO_2
76B	3450m	7.79	740	26.7			1.23	
76C	70	0.49	>14,000					
			>14,000					
			11,521					
			9,735					
76D	4000	6.05	1,067		*			1,190
			464	28.4				991
			674	30.0				
			594	31.1				
76E	278	0.19	5,052		547			18,900
			3,368	*	294	947	187	
				*		802	166	
77C	3535	13.75		185				
77D	1345	3.92	1,876	*				
			1,478	*				
77E	1345	4.0	1,469	*				
			851					
77F	675	0.8	2,184					
			2,099					
			3,260					
			5,091					

intervals cover a relatively small fraction of the North Atlantic, but are responsible for a large fraction of the benthic oxygen consumption. The benthos below 2km accounts for only about 10% of the total oxygen consumption even though it occupies more than 80% of the area. This view is somewhat oversimplified, since Figure 5 suggests that benthic consumption in equatorial and some tropical areas may be an order of magnitude greater than in temperate areas. Clearly, a global picture of oceanic benthic oxygen consumption will require measurements from a range of depths in all the major oceanic regimes.

A rough calculation of the relative importance of oxygen consumption in the water column and by the benthos is possible using the benthic data and deep water oxygen consumption estimate from a model. Table 4 is a compilation of the benthic and water column consumption estimates. Benthic consumptions were selected from Figure 5 and the water column consumptions were calculated using the oxygen consumption *vs* depth relation from Fiadeiro and Craig's (1978) three-dimensional circulation model. The water column oxygen consumption is found to be 5 times greater than the benthic consumption. The water column consumption is underesti-

Table 3. Benthic oxygen consumption by depth interval. Benthic oxygen consumptions were selected as the midpoint of each depth interval from a straight line drawn through the temperate region points in Figure 5. Areas for each depth interval are from Menard and Smith (1966).

Depth km	Area %	Oxygen consumption μmoles $m^{-2}day^{-1}$	% of Total benthic oxygen consumption
0-0.2	7.02	5000	61
0.2-1	5.17	2500	22
1-2	4.30	1000	7.2
2-3	8.59	300	4.4
3-4	19.33	100	3.3
4-5	32.45	50	2.2
5-6	22.33	10	0.4
6-9	0.86	—	—

mated to some unknown extent in these calculations since no allowance is made for increased consumption that likely occurs in the shallower regions. In any case, it seems that more of the oxygen consumption below 1000m in the Atlantic occurs in the water column that at the sea floor, although both components are significant. For the depth interval between 1 and 2km, the benthic oxygen consumption is greater than the water column consumption (Table 5).

Silicate flux. The flux of dissolved silica was measured at three deep stations (Table 2). The flux at the northern temperate station (185 μmoles m^{-2} day^{-1}) is higher than the fluxes found in the Gulf of Mexico (26.7 μmoles m^{-2} day^{-1}) and equatorial stations (28.4-31.1 μmoles m^{-2} day^{-1}). The higher flux at the northern station

Table 4. Comparison of water column and benthic oxygen consumption. Benthic oxygen consumptions are the same as in Table 3. Water column consumption over a square meter of benthos up to 1 km depth was calculated using the oxygen consumption *vs* depth relation from Fiadeiro and Craig (1978) $J=J_1e^{-B(d-1)}$, where J_1=0.483 μmoles $kg^{-1}year^{-1}$, B=1.2km^{-1}, and d=depth in km.

Depth km	Benthic consumption μmoles $m^{-2}day^{-1}$	Cumulative water consumption μmoles $m^{-2}day^{-1}$	Area $10^{12}m^2$	Benthic consumption $10^{15}\mu$moles day^{-1}	Water consumption $10^{15}\mu$moles day^{-1}
1-2	1000	363	3.7	3.7	1.3
2-3	300	582	7.4	2.2	4.3
3-4	100	647	16.7	1.7	10.8
4-5	50	666	28	1.1	18.6
5-6	10	672	19	0.2	12.8
Totals:				8.9	47.6

Table 5. Pore water chemistry, gravity core EN008-GC1, same location as stations 77A and 77C.

Depth interval cm	Silicate μmoles L^{-1}	Phosphate μmoles L^{-1}	Nitrate plus nitrite μmoles L^{-1}
bottom water	23		
0-1	145	3.0	32.5
1-2	192	3.6	34.0
2-3	240	4.4	27.5
3-4	281	5.4	11.4
4-5	303	7.6	4.0
5-6	310	8.1	4.0
6-7	313	8.1	5.5
7-8	313	8.1	3.5
8-9	318		
9-10	325		

presumably reflects the greater opal content of the sediment. At two shallow locations, the short deployment times did not allow a measurable change in the silica content of the chambers to develop. This suggests that the flux of silica at the shallow temperate, 1345m and tropical, 278m, stations is not much greater than at the deep stations (less than 100 and 200 μmoles m^{-2} day^{-1} respectively).

A silica budget for the oceans prepared by Heath (1974) included a calculation of the amount of biogenic silica redissolved both in the water column and in the sediment. Recalculating this on an areal basis gives 480 μmoles $m^{-2}day^{-1}$ of silica redissolution. Since Heath's (1974) figure includes dissolution both in the water column and at the sea floor it should exceed the direct measurements of silica redissolution from the sea floor, as we observe. Fanning and Pilson (1974) made direct measurements of the flux of silica from 5 refrigerated cores. The fluxes they measured (from 40 to 500 μmoles $m^{-2}day^{-1}$) overlap the *in-situ* measurements. The lowest fluxes from Fanning and Pilson (1974) for typical oceanic sediments underlying areas of low productivity are about 30% higher than the *in-situ* fluxes for the deep Gulf of Mexico and equatorial stations.

Pore water data from gravity cores were used to calculate a flux for comparison with *in-situ* data. At station 77A a 76cm gravity core, taken without a core catcher to assure an undisturbed sediment-water interface, was immediately refrigerated. After 48 hours the top 10cm was sliced into 1cm slices and hydraulically squeezed to extract pore waters. The pore waters were analyzed for silica, phosphate, and nitrate plus nitrite (Table 5). The silica flux calculated from the silica gradient in the top centimeter, using an interstital diffusion coefficient of 3.3×10^{-6} cm^2 sec^{-1} (Fanning and Pilson, 1974), is 690 μmoles m^{-2} day^{-1}, or 3.7 times higher than the measured *in-situ* flux at the same station. A gravity core from the equatorial station

(76D) treated similarly (Froelich *et al.*, in press; P. Froelich, written comm. 1978) gives a silica flux of 233 μmoles m^{-2} day^{-1} or 7.8 times greater than the measured flux. Two cores from the Gulf of Mexico 60 and 130km from station 76B have calculated fluxes of 134 and 249 μmoles m^{-2} day^{-1} respectively (K. Fanning, oral comm. 1977) or 5.0 and 9.3 times greater than the measured *in-situ* flux. The discrepancy between the fluxes calculated from pore water data and the measured fluxes suggests that the simplistic assumption of a linear silica gradient across the top 1 centimeter of the sediment is unrealistic.

Other flux data. Measurements of flux of ammonia (2 stations), nitrate plus nitrite (1 station), phosphate (2 stations), and total carbon dioxide (2 stations) are summarized in Table 2. Little can be concluded from this scant data other than that relative release rates do not fit the Redfield ratio. The flux of oxygen is high relative to phosphate at a deep station (76B). At another station (76D) the release of total carbon dioxide is about twice as great as the consumption of oxygen. If a respiratory quotient of 0.9 is assumed for the organic matter being consumed at the sea floor, then about half of the total carbon dioxide flux results from the dissolution of calcium carbonate and is the amount of carbonate dissolution expected from the organic carbon dioxide production. At the shallow station (76E) the oxygen consumption is low relative to total carbon dioxide, phosphate, and nitrogen regeneration. This may result from the organic matter in the sediment consuming oxidants other than oxygen.

4. Sediment trap studies

Samples from each location are distinct in appearance. The northernmost sample, 77A, consists of a mass of diatom debris dominated by girdles from broken frustules (Fig. 6A, B). Station 77D, off Cape Hatteras, recovered many more foraminifera and Radiolaria and lacked the large and broken diatoms. The short deployments at 77F and 77G resulted in much less material in the samples. Nevertheless, diatoms are rare. Sponge spicules, intact fecal pellets and dinoflagelates were found in this sample (Fig. 6C, D). The filtering, freezing and dessication procedure used to preserve samples for carbon and nitrogen analysis apparently caused disintegration of many fecal pellets making reliable counts impossible. A few tests of pteropods and tintinnids were found in each sample. Observations of samples by scanning electron microscopy revealed coccoliths and silicoflagelates that were not visible with light microscopy (Fig. 6E, F). A few zooplankton also were found in each sample (Fig. 6B).

Diatoms. Diatom counts were difficult and are correct only to an order of magnitude (Table 6). The abundant debris in sample 77A and the lack of shapes distinctive to diatoms made better counts impossible.

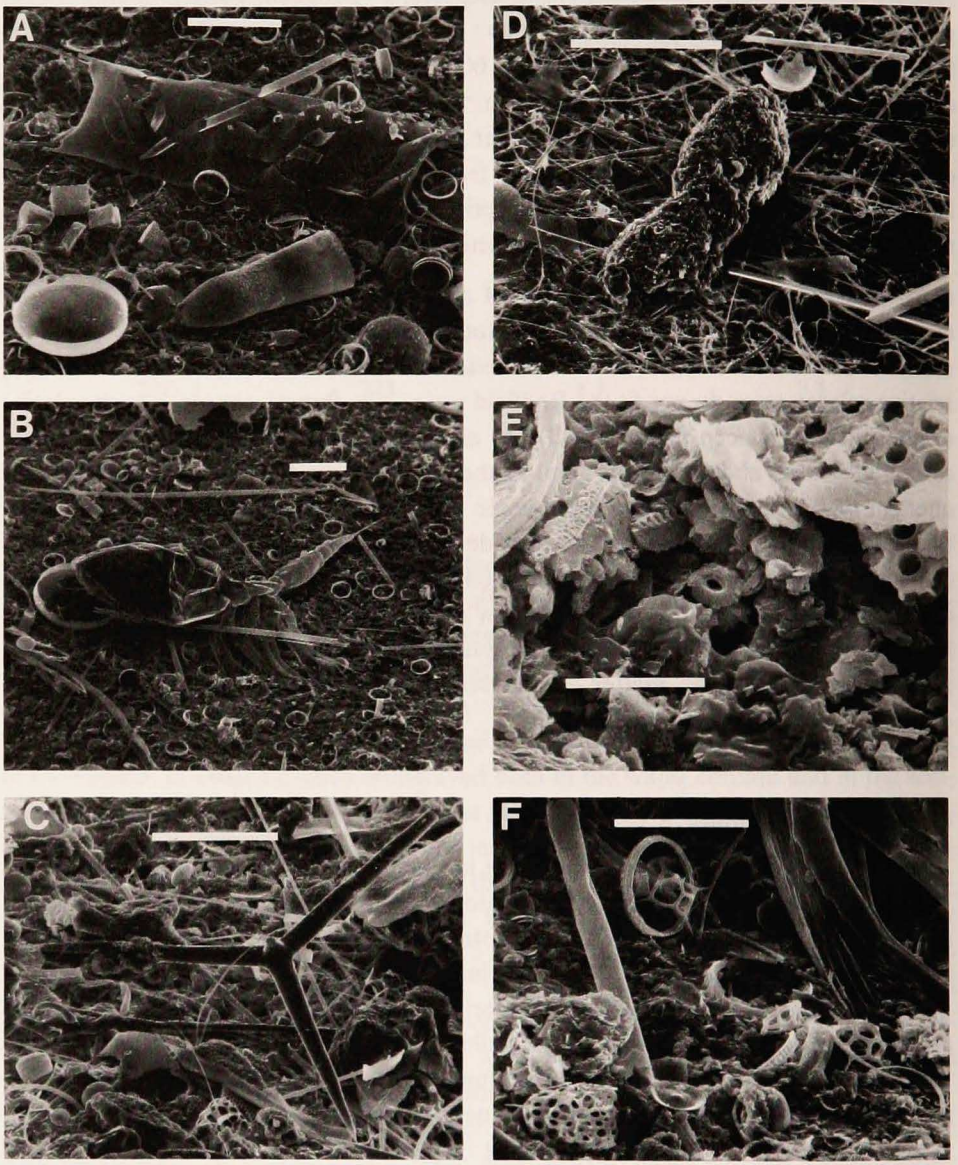


Figure 6. Representative particles from sediment trap samples.

6A, trap 77A, diatoms; Biddulphia, Coscinodiscus, Thalassiosira, and Rizosolenia, and a tintinned (Bar is 100 μm).

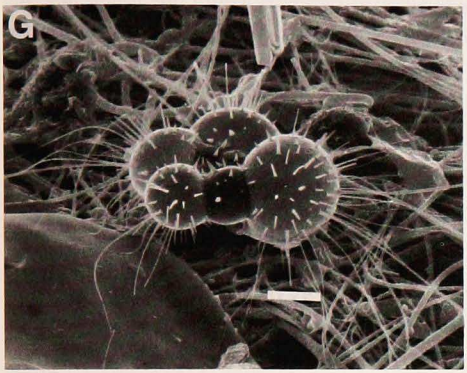
6B, trap 77A, copepod carcass (Bar is 100 μm).

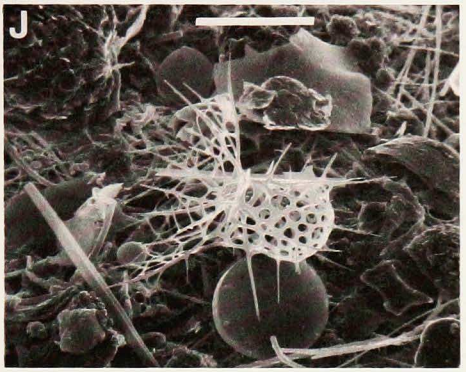
6C, trap 77F, spongue spicule (Bar is 50 μm).

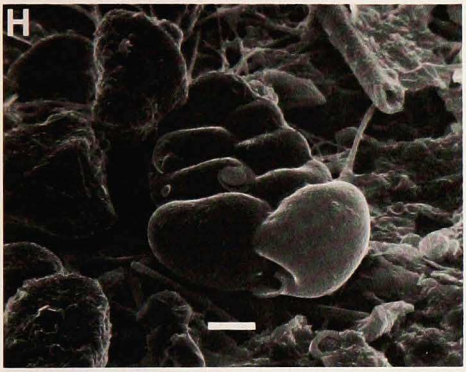
6D, trap 77F, fecal pellet (Bar is 100 μm).

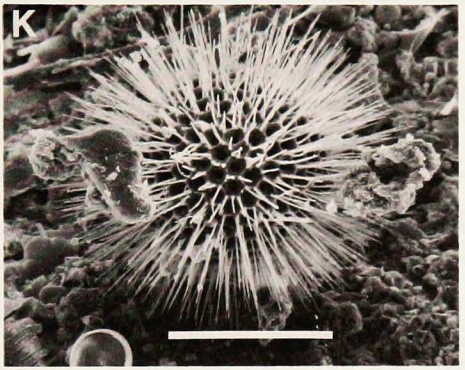
6E, trap 77A, coccolith (in center) (Bar is 10 μm).

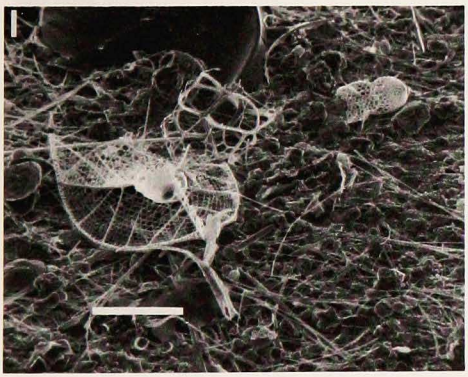
6F, trap 77A, silicoflagelates; Distephanus and Dictyocha (enlargement of area in 6B) (Bar is 50 μm).

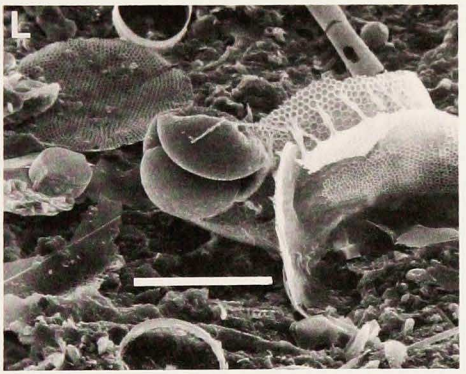












6G, trap 77F, spinose foraminifera (Bar is 10 μm).
6H, trap 77F, biserial foraminifera (Bar is 10 μm).
6I, trap 77F, radiolarians; Callimitra, Lithomelissa, and Lirospyris (Bar is 100 μm).
6J, trap 77F, diatoms; Thalassionemia and Asterolanpra marylandica, radiolarian; Archnocorys (Bar is 50 μm).
6K, trap 77D, radiolarian (?) (Bar is 100 μm).
6L, trap 77A, diatoms; Rhaphonesis and Stephanopyxis, and pine pollen (Bar is 50 μm).

Table 6. Summary of sediment trap data. No significant differences could be found for the four traps used at location 77F and 77G. The values listed under 77FG are the averages for the four traps. (++ an accurate flux of pine pollen could not be calculated at this station because of the high pine pollen background in the water).

Station	77A 3520m	77D 1345m	77F-G 660m
		Numbers m^{-2} day^{-1}	
Foraminifera	1820	11400	3810
Radiolarians	1920	5920	3940
Diatoms	7×10^5	2×10^5	0.3×10^5
Pine pollen	1210	759	++
Metal spheres	6	14	563
		mg m^{-2} day^{-1}	
Total	205	280	220
Carbonate	33.5	137	154
Organic carbon	15.4	29.8	14.4
Nitrogen	0.47	1.24	0.31

Foraminifera and Radiolaria. The foraminifera and Radiolaria were not identified to the species level, but a few qualitative observations were made. The majority of the foraminifera are thin-walled and almost transparent under the light microscope. These thin-walled foraminifera are much more susceptible to dissolution and breakage than the heavy individuals preserved in the sediment record. Approximately 10% of the foraminifera and Radiolaria were spinose (Fig. 6G, K). One doubts that such spinose forms could have passed through a digestive tract without extensive visible damage to the spines. These forms must either live deep in the water column or settle from the surface waters without being incorporated into fecal pellets. At the two shallower locations a few examples of biserial foraminifera were found in the sediment trap samples (Fig. 6H). Since biserial foraminifera are thought to be exclusively benthic their presence in sediment traps 50 and 100 meters above the sediment was unexpected. At station 77D they may form part of the debris carried by the Gulf Stream. Another possibility is that benthic feeders ingest benthic forams then move off the bottom before excreting the foraminiferal tests. The second explanation is more plausible at stations 77F and 77G where there is not nearby shallow water or strong offshore current.

Many of the radiolarians also are extremely delicate in appearance (Fig. 6I, J). Such forms are not likely to be preserved in the sediment. Radiolarians at all three locations were approximately equally divided between Supmellaria and Nassallaria. No Acantharians were observed in any sample.

Pine Pollen. Pine pollen has a two bladder structure (characteristic of the family Abietaceae) easily identified in the sediment trap samples (Fig. 6L). The pine pollen

observed in the samples has a distinctive yellow-green color under light microscopy. A large number of pollen grains were found in all trap samples. At the southernmost location (77F and 77G) 60 pine pollen grains per liter were collected in the water sample. As a result a reliable flux could not be calculated, even though there is clearly an input at this location. In some of the samples the pollen grains were clumped with other debris presumed to be fecal pellets destroyed during the freezing and dessication of the samples. This implies that the pollen grains were ingested by zooplankton and transported to depths much more rapidly than they would have been as single grains. Pines bloom in the spring. The northern station (77A) was deployed in May, so it appears that the pine pollen moved 350km offshore and through 3500m of water in approximately one month. Because the time of release of pollen depends on latitude and weather and the source of pine pollen in the traps cannot be identified, this estimate is crude, but it does illustrate the rapidity with which debris can reach the deep ocean. Other species of pollen were rarely observed in the trap samples. Pine pollen probably was dominant since the traps were deployed in the spring (many other plants pollinate in the fall) and pine pollen has evolved for long-distance transport. The pollen appearing in traps 77A and 77D likely originated on the east coast of North America. A probable source for the pollen found at stations 77F and 77G is the Bahamas. Traverse and Ginsburgh (1966) found up to 20 pine pollen grains per liter in Bahamian waters.

A sample of pure pollen from Austrian Pine (Pinus Sylvestrus, sub. sp. Algra) was weighed and counted to determine the average weight of a pollen grain. The pollen was selected because of its similarity in size and shape to the pine pollen observed in the trap samples. These pollen grains weighed 15 $\pm$ 5 ng each. Thus approximately 4% of the flux of organic material at station 77A is pine pollen. At station 77D, pine pollen accounts for about 1% of the flux of organic material. Thus, pine pollen is a small and probably seasonal input of organic matter to the deep sea at these locations. Groot and Groot (1966) calculated a supply of pollen to the western North Atlantic of similar magnitude to that measured in trap 77A. They then calculated that if all the pollen was incorporated into the sediment one should find about 10^6 pollen grains per gram of sediment. Groot and Groot (1966) and others, however, report finding only about 20-40 grains per gram in oceanic sediments, implying that pollen decays or is used as a food source by deep-sea organisms. Since marine fungi from deep sea sediments can be cultured on pine pollen (Höhnk, 1961; Gaertner, 1968), such fungi are possibly involved in the utilization of pollen in the deep sea.

Metal spheres. Metal spheres averaging 65μm in diameter (range, 10 to 160μm) were found in the trap samples from all three locations. Most of the spheres are black with smooth reflective or dull surfaces or are silver with a smooth reflective surface. Black spheres were found in low and reasonably equal numbers at all three

locations. Such spheres have been described previously as having an industrial source (Doyle *et al.*, 1976). The silver spheres were found in abundance 150km east of central Florida (77F and 77G). Most of the silver spheres were destroyed during the carbon analysis. A few of the remainder were examined by electron microprobe. The spheres were found to be hollow with 2 to 10μm walls. M. Kominz (written comm., 1978) reports that the spheres are predominantly iron with a surface enrichment of aluminum, silicon and magnesium. The absence of manganese and copper indicates that these spheres have a different origin from those reported by Doyle *et al.* (1976). The absence of nickel and cobalt and their abundance excludes an extraterrestrial origin. A speculative source is re-entry or fuel products from the rocket launchings at Cape Canaveral, Florida.

5. Discussion

Comparative Studies. Benthic respirometers and sediment traps are relatively new tools in the study of the deep oceans, but they already have provided important information for describing the deep-sea environment. Benthic respiration measurements from the Northwest Atlantic (Smith, 1978) show a decrease in oxygen consumption with increasing depth and with distance from land. Data from other regions (Table 2, Smith *et al.* 1979; Smith reported by Wiebe *et al.* 1976), however, indicate that the total amount of food available to the deep sea benthos is probably closely related to the productivity of the surface waters (Fig. 5). Using sediment traps in the low productivity Sargasso Sea, Honjo (1978) measured a flux of organic carbon about an order of magnitude lower than we found under the more productive waters at station 77A. The trap in the Sargasso Sea had a diatom flux nearly two orders of magnitude lower than that at station 77A but had an order of magnitude higher fluxes of foraminifera and radiolaria. The difference in the type of food materials available to the benthos at these two sites may cause differences in environments and benthic populations greater than those expected if the only variable is the total quantity of available food. Pine pollen is a food source that cannot be evenly distributed in the oceans and is not related to the primary productivity of the surface waters. If pollen utilizing organisms depend largely on this material, their distribution will be independent of the total flux of food material. The available measurements of nutrient fluxes (Table 2, Smith *et al.*, 1978, 1979) also demonstrate that the processes regenerating nutrients are neither uniform in the deep oceans nor are they a simple function of the benthic respiration. Further use of sediment traps and benthic respirometers should provide information that will help explain the abundance, composition, and diversity of deep-sea populations.

Although the supply of food to the deep-sea is of great importance it is not the exclusive controller of deep-sea biology. For example, Vinogradova (1959) found that the range of individual deep-sea species correlated with geological barriers in

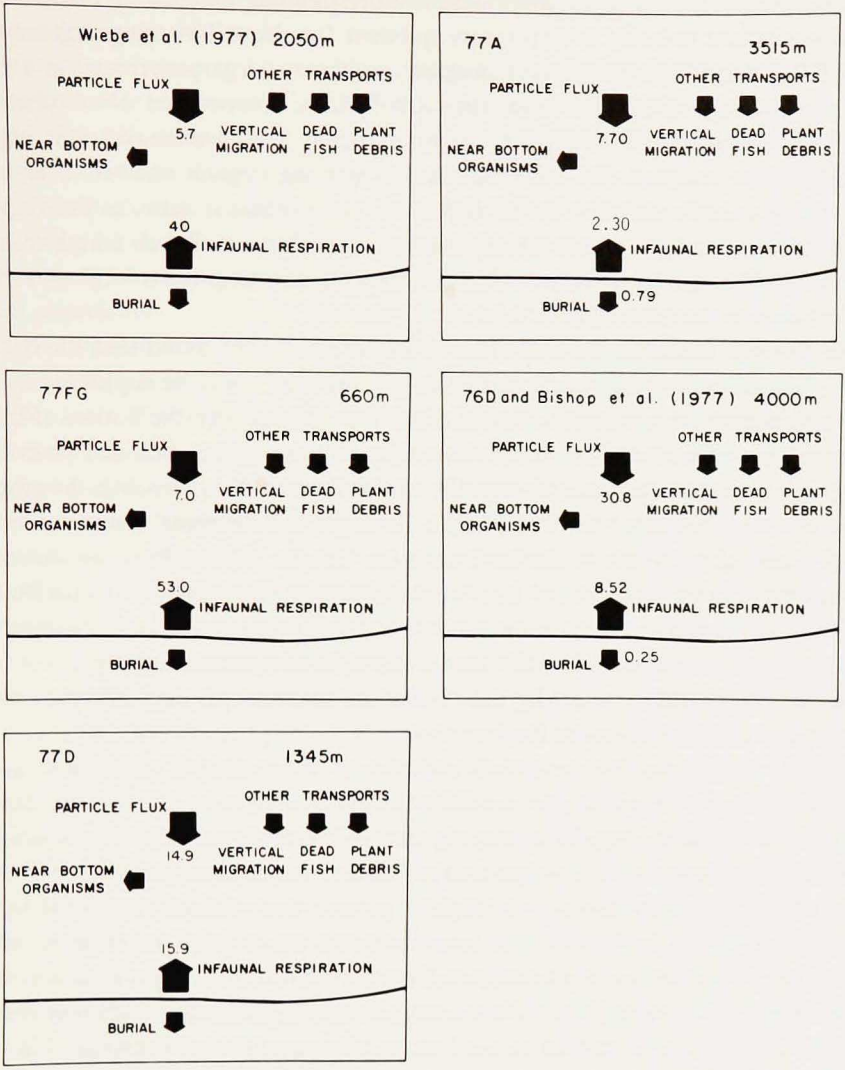


Figure 7. Summary of sources and sinks of organic carbon at the benthos at 5 locations in the North Atlantic.

the oceans; sediment type and the availability of hard substrates also will influence the biology of benthic organisms.

Benthic organic carbon budgets. The flux of organic matter measured in the sediment traps may be combined with the oxygen consumptions measured with the respirometer to throw light on the dynamics of the deep-sea benthos. Wiebe *et al.*

(1976) converted oxygen consumption to a corresponding amount of carbon by a method equivalent to using a respiratory quotient for the sedimenting organic carbon of 0.9. Such a high respiratory quotient requires a large percentage of carbohydrate in the organic matter. Since the carbohydrate composition of zooplankton is low (Raymount *et al.*, 1969), this in turn implies that protein-deficient phytoplankton debris accounts for most of the sedimenting organic matter. The large proportion of diatom debris with its high carbon to nitrogen ratio in the trapped material (Table 6) supports this assumption and the selection of such a high respiratory quotient. We also have converted benthic oxygen consumption to organic carbon assuming a respiratory quotient of 0.9.

In the Tongue of the Ocean at 2150m Wiebe *et al.* (1976) found that the oxygen consumption of the benthos was seven times greater than could be supported by the flux of organic carbon measured in a sediment trap 116m above the bottom (Fig. 7). They noted macroscopic plant material on the sediment in the area and postulated that this plant material is carried laterally along the sea floor beneath the trap to supply the extra carbon to the benthos. If, however, macroscopic plant material is to supply most of the needs of the benthos in the Tongue of the Ocean an unreasonably large supply of plant material must be derived from the nearby Bahama Islands. A deficiency of 34mg $m^{-2}day^{-1}$ for the 1.5×10^4 km^2 area of the Tongue of the Ocean requires an input of 5.1×10^3 tons wet weight of plant material per day from the islands. This amounts to 6.8 kg day^{-1} of plant material passing over each meter of the edge of the Tongue of the Ocean.

Results from stations 77F and 77G in 650m of water (Fig. 7) also close to the Bahamas give results remarkably similar to those of Wiebe *et al.* (1976). Station 77D in 1375m of water (Fig. 7) on the edge of the Blake Plateau also has insufficient carbon in the sediment trap to support the benthic respiration. At this station the benthic oxygen consumption is only slightly greater than can be supported by the organic carbon found in the sediment trap but when one considers that some of the organic carbon in the trap is probably utilized by near-bottom organisms and some is incorporated into the sediment the shortage becomes clear. Two different mechanisms can supply organic carbon to the benthos that would not be captured in sediment traps. Large parcels of organic matter, such as large fish and marine mammal carcasses, can transport material to the benthos with a vanishingly small probability of being caught in a sediment trap. At locations 77F and 77G, at least 200 one kilogram fish or 1 porpoise per square kilometer per day are required to supply the organic carbon deficiency. These figures approach the estimated total production of fish-sized organisms (Ryther, 1969). Alternatively, vertically migrating organisms may carry food past the sediment traps. This could involve either a true vertical migration or an onshore-offshore migration along the benthic boundary layer. In this case organic carbon would be carried as food ingested in shallower water then excreted in deeper water, or as the bodies of the vertically migrating organisms. This

mechanism is particularly attractive since it involves the relatively large supplies of carbon at lower trophic levels.

A similar analysis may be done for a deep temperate location by using the sediment trap data from station 77A (3500m) and a benthic oxygen consumption value selected from the temperature region in Figure 5. Since sediment trap 77A lies on the same transect as most of the oxygen consumption values and is within 75km of one of the measurements, the comparison is justified. At this site the organic material in the sediment trap is more than sufficient to support the benthic respiration. The excess organic flux must be incorporated into the sediment or be utilized by near-bottom organisms. Calculating the rate of organic carbon accumulation in the sediments then determines how much organic carbon is being utilized by near-bottom organisms. The organic carbon content of the sediment at this location is 0.5% (Sanders *et al.*, 1965), while a core 25km from this site (Ericson *et al.*, 1961; core A164-6, 3675m) has a sedimentation rate for the last 11,000 years of 6.8cm per year. Assuming 0.85 grams dry weight per cubic centimeter of wet sediment, organic carbon is accumulating at 0.79mg m^{-2} day^{-1}. The near bottom organisms thus utilize 4.61mg carbon m^{-2} day^{-1} or twice as much as the infauna (Fig. 7). We emphasize that the sediment accumulation rate of organic carbon is quite sensitive to the preceding assumptions and measurements. A proper determination of the importance of near-bottom organisms requires that adequate organic carbon accumulation determinations be made at each location where this type of analysis is attempted.

Bishop *et al.* (1977) used particle size distributions to estimate the flux of particles through a depth of 400m in the equatorial Atlantic 400km north of station 76D. Their calculated flux of organic matter at 400m is only 4 times greater than the organic matter needed to support the benthic oxygen consumption at 4,000m (Fig. 7e). Since the particles passing 400m must support organisms throughout most of the water column as well as the near-bottom fauna, their calculated particlate flux seems too low to account for the total flux of organic carbon. Burial of organic carbon is not important at this location (P. Froelich, written comm., 1978). Again it seems likely that vertically migrating organisms transport significant amounts of organic matter through the upper layers of the ocean.

Although the data are limited they support two conclusions: (1) vertically migrating organisms appear to be responsible for transporting significant quantities of organic material through the upper layers of the ocean; and (2) near-bottom organisms consume much of the organic carbon that reaches the deep-sea.

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