

## **Group Report**

### **Transformation of Seafloor-arriving Fluxes into the Sedimentary Record**

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P.A. Jumars, Rapporteur  
A.V. Altenbach  
G.J. De Lange  
S.R. Emerson  
B.T. Hargrave  
P.J. Müller

F.G. Prahl  
C.E. Reimers  
T. Steiger  
E. Suess

#### **INTRODUCTION**

Seafloor processes control the transfer of biogenous detritus into the sediment by burial or into the overlying water by nutrient reflux and resuspension. Either transfer is in part biologically mediated and can involve complex interactions among micro-, meio-, and macrofauna. Recent reports show that phytodetritus that reaches the seafloor hosts vigorous bacterial and protozoan activity (Lochte and Turley 1988; Gooday 1988), so initial breakdown may be surprisingly rapid and direct. This finding at first seems to contradict observations on microbes attached to sinking particles intercepted in the water column (Karl et al. 1988; Cho and Azam 1988). These latter authors showed that biomass as well as microbial activity on sinking particles diminishes with increasing water depth. How then is it possible that the microbial population attached to particles recovered from the seafloor is so unusually active? Could it be that only after the phytodetritus reaches the seafloor is it populated by specialized, barophilic heterotrophs that would metabolize the most labile material first (Deming and Colwell 1985; Suess 1988)? The most labile material arriving on the bottom comes in the form of rapidly sinking particles, whose residence time in the water column is short and exposes attached organisms to rapidly increasing pressure. Clearly, the mechanism of turnover of incoming flux at the seafloor is not merely an extension of that in the water column: the biological species that mediate that turnover are different from those in the water column; a suite of oxidants rarely used in organic matter degradation in the water column often comes into play at the seafloor; solute transport

is dominated by molecular diffusion and animal pumping from the sediment-water interface downward; and, unlike the case in the water column, virtually all benthic bacteria live attached to particles.

Our specific focus thus was to understand (well enough to identify and evaluate indicators of past surface-water productivities and bottom-arriving fluxes) transformation into the sedimentary record of the flux of matter arriving at the bottom. As addressed by Groups 1 and 2 (see Williams et al. and Bruland et al., both this volume), there is no simple proportionality between surface production and the bottom-arriving flux. New production arriving at the bottom below 1000 m water depth is significant in the carbon cycle because even the major fraction that is oxidized to CO<sub>2</sub> is kept out of contact with the atmosphere by circulation patterns for roughly 10<sup>3</sup> yr. We emphasize that there are differences in benthic processes between continental margins and "open-ocean," depositional environments. The former contain the bulk of buried organic carbon and are sites of injection from the benthos of remineralized and resuspended material into midwater circulation systems (Romankevich 1984; Jahnke and Jackson 1987). Open-ocean sediments appear stratigraphically and diagenetically less complicated, however, and may thus allow easier reconstruction of the paleoenvironment.

We selected a limited goal, avoiding in general environments of turbidite and slump deposition, contourites and reworked facies that produce records difficult or impossible to interpret in terms of paleoproductivity. Thus for the most part we do not treat deep-sea regions of episodic erosion, although they may be quite widespread (Hollister et al. 1984). We also made no attempt to include in our goal estimates of past contributions to seafloor food supplies from chemolithoautotrophy at hydrothermal or cold-seep sites, except insofar as this chemoautotrophic signal might be confused with the rain of material from the surface ocean. Chemolithotrophic production and its effect on the sedimentary record is just emerging as a field of research.

#### **A VIEW OF THE SEABED UNDER DIFFERING CARBON FLUX REGIMES**

The key in the generation of vertical geochemical structure is the ratio in fluxes of organic carbon versus oxygen into the seabed. The succession of dissolved oxidants is the focus of the classic approach to defining geochemical structure. It varies strongly with sedimentation rate. Oxygen flux is usually calculable from pore water gradients (Fig. 1) and is generally proportional to bottom-water O<sub>2</sub> concentration if organic carbon is supplied in excess. Even complete knowledge of organic carbon flux and bottom-water O<sub>2</sub> concentration, however, is insufficient to allow accurate prediction of the proportion of organic carbon that will survive diagenesis, for organic matter arriving at the seabed is a chemically heterogeneous mixture. This

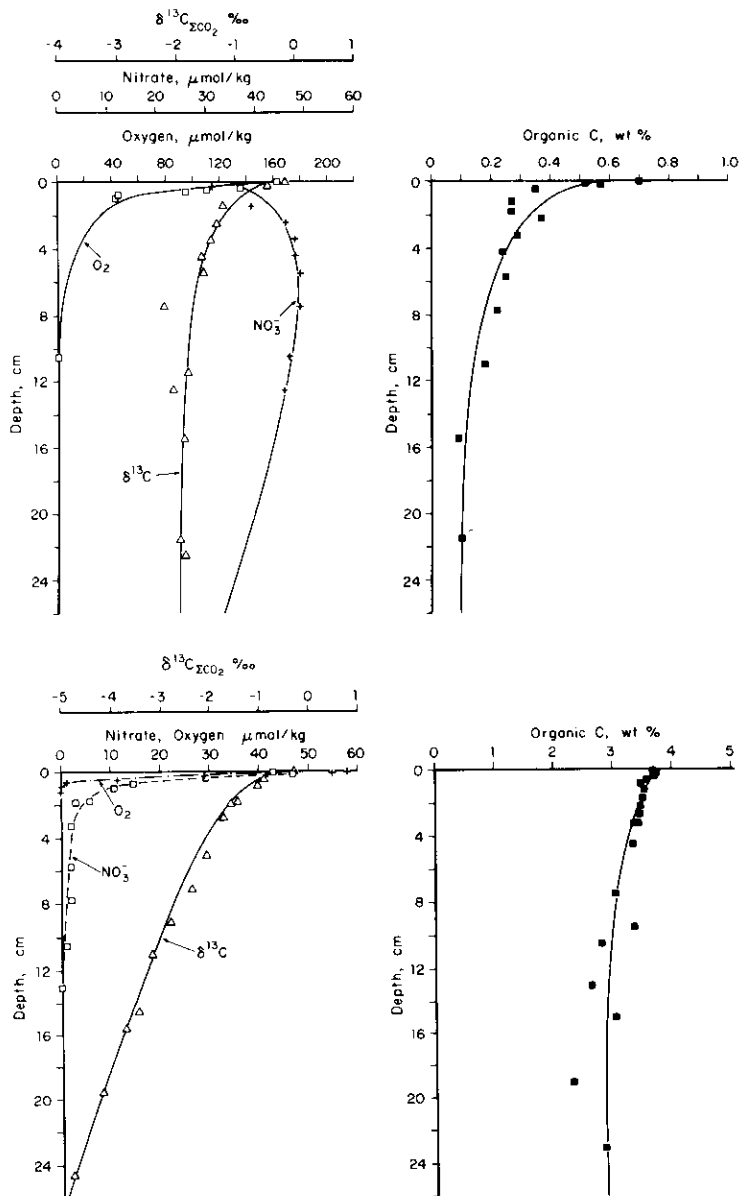


Fig. 1—Depth distributions of chemical properties at an open-ocean site (1°N, 139°W; MANOP site C; top panels) and a hemipelagic site (33°N, 118°W; San Clemente Basin; bottom panels), comparing pore-water O<sub>2</sub>, NO<sub>3</sub><sup>-</sup>, and  $\delta^{13}\text{C}$  and solid organic carbon contents. Data are compiled from Reimers et al. (1984), Reimers (1987), McCorkle (1987), and Shaw (1988). (Figure prepared by C. Reimers and S. Emerson).

heterogeneity is most often represented via multicomponent models that assume first-order behavior for each component (Reimers, this volume, Eq. 1).

There is a wide and no doubt very complex spectrum of reactivities among the organic carbon molecules arriving at the seabed. Although carrying the idea of a full spectrum is clearly more accurate, for the sake of convenience we will adopt a less accurate three-component, qualitative model (cf. Reimers, this volume). Seasonality of benthic flux measurements (Smith and Baldwin 1984) requires that a major fraction of the bottom-arriving flux of organic matter have a lifetime of several months or less and that it not be mixed extensively into the sediments by bioturbation. Recent  $^{14}\text{C}$  measurements of organic carbon in the bioturbated layer (Emerson et al. 1987) imply that a substantial component (30–40%) of this layer's organic matter has a degradation residence time of less than 1000 yr, with the remaining refractory portion degraded on time scales much longer than the bioturbated layer residence time ( $> 10^4$  yr). The most refractory material appears to be degraded more readily by aerobic than anaerobic processes (Reimers, this volume; Emerson and Hedges 1988). At present, a glaring lack exists in our knowledge of the chemical identities of these classes of organic matter. These patterns are consistent, however, with the existence of organic compound classes that yield too few kcal mol $^{-1}$  when oxidized with  $\text{SO}_4^{2-}$  to repay the capital and operating costs of the metabolic machinery that would be required to carry out the oxidation.

Another pair of related problems that would benefit from more precise knowledge of chemical structure and classification at the level of chemical compounds are those of the terrestrial contribution and of the contribution of marine material originally deposited elsewhere to the sedimentary record at a given site (e.g., Prahl and Muehlhausen, and Walsh, both this volume). Conventional wisdom formulated primarily from analysis of  $\delta^{13}\text{C}$  holds that sedimentary organic carbon in the open ocean is predominantly marine derived. Illumination of aeolian fluxes, geochemical evidence of horizontal midwater transport from continental margins to the open ocean (Martin et al. 1985) and uncertainty in  $\delta^{13}\text{C}$  values previously assigned to the marine endmember all have led to skepticism about earlier assessments. That 20% of sedimentary organic matter in the open ocean is terrestrially produced is now within reasonable model estimates based on biomarker analyses (Prahl, this volume, Fig. 1). If this terrestrial material has slow reaction kinetics due either to decomposition during its extensive horizontal transit, to its initially highly degraded chemical form on entry into the ocean, or to protective incorporation within detrital particles, it may make a major contribution to the sedimentary organic carbon preserved in the geological record. The problem of horizontal redistribution is a most thorny one. By working only at sites of apparently continuous sedimentary accretion, one

must be biased towards sites that are the ultimate resting places for material resuspended after initial deposition elsewhere. Perhaps this bias of focusing on regions from which present-day erosion is unlikely helps, together with more traditional explanations, to account for anomalies in  $^{14}\text{C}$  ages of core-top sediments.

Provided reliable calibration of terrestrial biomarkers can be achieved, geographic maps of terrestrial contributions to total sedimentary organic carbon could be constructed. This information would provide, albeit indirectly, an assessment of marine contributions to the organic carbon record preserved in sediment cores, thus facilitating the use of such records in paleoenvironmental reconstructions. Lipid biomarkers of terrestrial organic carbon occur as homologous series of compounds (Prahl and Muehlhausen, this volume, and references therein). Compositional characteristics of those series can vary with source region (Gagosian et al. 1987). Variations in the intensive properties of these series deposited with depth in marine sediments could provide indications of how source regions or mechanisms of delivery (aeolian transport versus riverine transport and turbidity current dispersal) of terrestrial organic carbon to a given oceanic location changed with long-term climatic variations.

A commonly used method to estimate the terrigenous organic matter fraction in marine sediments is Rock-Eval pyrolysis. This method, originally developed to screen the quality and maturity of hydrocarbon source rocks (Espitalie et al. 1977), has also become one of the standard methods for typing organic matter in paleoceanographic studies, e.g., in the ocean drilling program (Peters and Simoneit 1982). The hydrogen index obtained by Rock-Eval pyrolysis is the amount of pyrolyzable hydrocarbons normalized to total organic carbon ( $\text{mgHC/gC}_{\text{org}}$ ) and equivalent to the H/C ratio of the organic material. The proportions of marine and terrigenous organic matter in a sediment sample, in principle, can be partitioned by its hydrogen index because the material derived from marine plants is richer in hydrogen than the organic remains of terrestrial vegetation. A problem associated with the Rock-Eval technique, however, is that bulk sediment samples may yield spuriously low hydrogen index values due to the adsorption of hydrocarbons onto clay mineral surfaces ("mineral matrix effect," e.g., Espitalie et al. 1984). This effect is particularly important in sediments with low organic carbon contents ( $<1\% \text{C}_{\text{org}}$ ) which dominate the geological record. Hydrogen indices based on whole-rock samples therefore tend to overestimate the terrestrial component in marine sediments. Low hydrogen index values, in particular, should therefore be verified by some other means, e.g., by pyrolyzing organic matter concentrated via chemical extraction.

Both inherent organic matter properties and the agents acting on it determine the fraction buried. Much organic matter consumption is thought to be bacterial but to be strongly modulated by the numerous kinds of

animals that graze bacteria. The water-column view has shifted from one of bacteria as the overwhelmingly dominant remineralizers of labile organics to one of the predators of bacteria as remineralizers and regenerators of DOM (Blackburn and Fenchel 1979), and there is no reason to expect the benthos to differ in this regard. Feeders on bacteria (e.g., foraminiferans, many meiofauna, and deposit feeders) increase mineralization by both digesting and respiring assimilated bacterial organic matter and also by making room for younger, more rapidly growing and respiring bacterial individuals on fresh surfaces. As organic material becomes more refractory, greater inefficiency in bacterial assimilation becomes evident (Benner et al. 1988), and bacteria relative to bacterivores assume a correspondingly greater direct role in respiration and mineralization (e.g., Cho and Azam 1988). Studies under simulated *in situ* conditions of organic carbon cycling in sediment-trap and box-core samples from the Biscay and Demerara abyssal plains showed that <10% of the flux was buried and 13–30% of biological consumption was due to bacteria (Rowe and Deming 1985).

This line of argument emphasizes the paucity of direct information on deep-sea organisms. There is little information on standing stocks and identities of species under the open ocean, and there are almost no direct measurements of activities or rates of population change (Rowe 1983). Surprises in animal abundance patterns continue to arise. There is now good reason to suspect that foraminiferans dominate many and perhaps most deep-sea biotas in biomass (Altenbach and Sarnthein, this volume; Fig. 2). A carbon budget partitioning benthic boundary layer respiration exists for but a single deep-sea site, Santa Catalina Basin (Smith et al. 1987). It lies at about 1300 m and has bottom-water oxygen concentrations of only about 15  $\mu\text{M}$ /liter because the basin's sill lies within the oxygen minimum zone of the eastern North Pacific. Measurements suggest that 38–68% of benthic carbon mineralization occurs *above* surface sediments (but within the bottom boundary layer), with 18–55% being due to free-living bacterioplankton. This study site, whose surface sediments contain 5–7% organic carbon, cannot be considered representative of abyssal plains far from land, or even of slope depths outside semi-enclosed basins. The fact that the overall budget does not balance, i.e., that vertical sedimentation into sediment traps can account for only 17–43% of benthic respiration emphasizes the need to evaluate the role of horizontal transport in the deep sea.

Although Smith et al. (1987) did not attempt to partition community respiration on the basis of animal size, some speculation on partitioning of roles at their and other deep-sea sites seems safe based on shallow water information. Larger organisms dominate the process of bioturbation (Jumars and Wheatcroft, this volume), but small organisms almost always dominate the process of POC degradation in terms of any overall rate measure (because metabolic rate scales as body volume or weight to some exponent

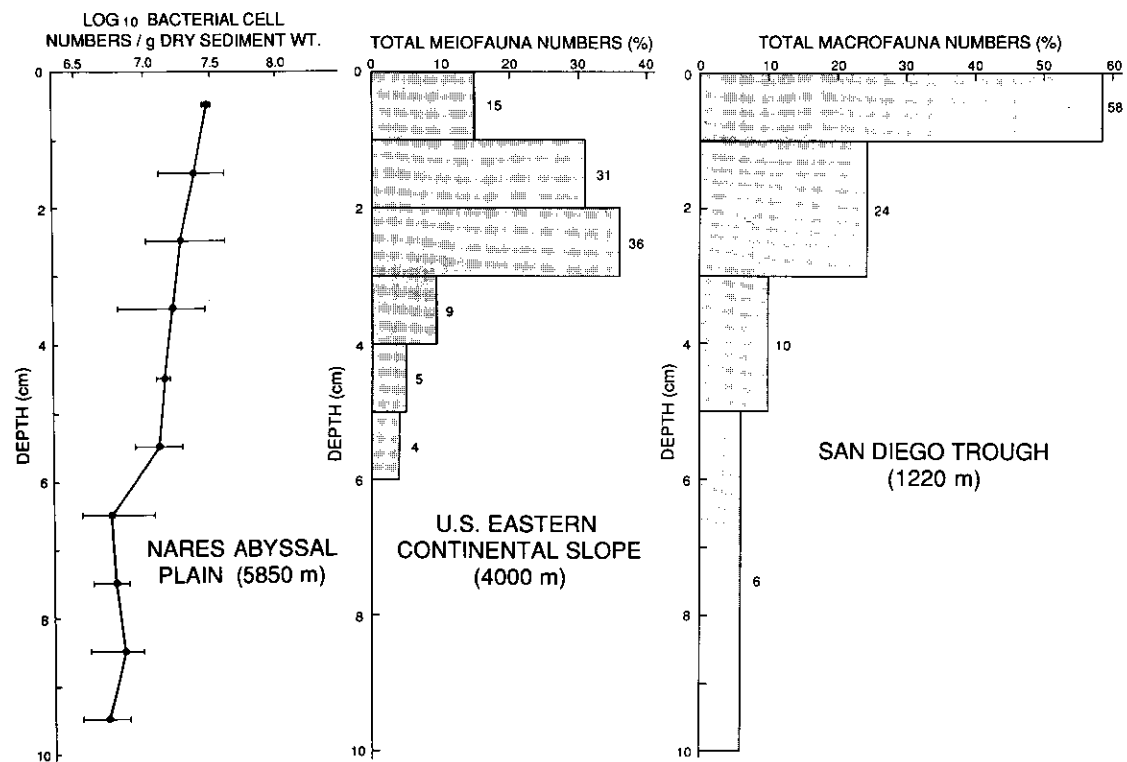


Fig. 2—Depth distributions of biotic components at several deep-sea sites. Bacterial data are from J. Deming (unpublished); the bars represent ranges for three replicates at each depth. Data for meiofauna come from Coull et al. (1977) and data for macrofauna from Jumars (1978). (Figure prepared by B. Hargrave).

between 2/3 and 3/4). It is important to remember, however, that this overall rate would fall (at least for all but the most labile and initially poorly colonized organics) if the bacteria (and their immediate predators in turn) were not being eaten. This consideration underscores the fallacy—demonstrated long ago in studies of forest litter decomposition (e.g., Bockock 1964)—of concluding from work with an isolated animal component or an isolated bacterial component that degradation rates in the deep sea are slow. Removal of the influence of metazoans may be one of the reasons for enhanced efficiency of preservation of organic matter in anaerobic environments (Kristensen and Blackburn 1987).

Interaction between sediment- and water-moving animals and organic matter-digesting bacteria helps to explain the seeming paradox that a greater fraction of organic matter is buried where particulate bioturbation is deeper and more intense (Aller and Cochran 1976; Emerson et al. 1985). The same phenomenon can be seen in radioisotopes whose decay constants roughly match those of the organic matter in question. The effects of this mixing downward by animals are compounded in organic matter, however, by shifting material of intermediate reactivity to anaerobic strata where its decay rate may drop dramatically. An understanding of what chemical species and what proportions of them succeed in running the interfacial gantlet is thus unlikely to be achieved by contemplation of mean vertical snapshots such as those of Fig. 1. Spatial and temporal variability on the scales of organisms is the rule. Aggregations of a few bacteria can make the space among them anoxic. Tube and burrow environments differ radically from the horizontal mean condition (Reimers, this volume).

A nearly completely unexplored environment is that of animal guts. Every particle in oxic deposits passes through them more than once judging by analogy with shallow water. We know deep-sea animal guts are sites of elevated microbial abundance and probably elevated activity. Some of the fastest growing bacterial species isolated from deep-sea sedimentary environments have come from animal guts (Deming and Colwell 1982). Animal guts may have either high or low pH and may be aerobic or anaerobic, but we know of no direct measurements on a single deep-sea species. We suspect that degradation within animal guts or in fecal pellets supporting high bacterial growth rates may be a major cause for the lack of entry of the labile component into even the first centimeter of the sedimentary record. Furlong and Carpenter (1988) found, for example, that < 1% of the pheopigment flux out of the water column of a coastal fjord accumulated in the upper 2 cm of sediment. A corollary is that early degradation is likely to be poorly modeled by incubation experiments with particles that are not continuously transiting among these heterogeneous gut and external microenvironments. Particularly steep redox gradients in the horizontal are likely to result at high organic fluxes; in order to fulfill its

respiratory function, animal ventilation of burrows will have to be most intense when animals are large and oxygen demand of the surrounding sediments is great.

Upward pore-water flow due to pressure differentials in geological formations—created by tectonics or sediment loading—adds further to the diversity of benthic interfacial environments. Pore fluids venting along active continental margins and seepage along passive margins provide nutrients and dissolved gases to the benthos and might, in places, mask those benthic signals usually controlled by supply from the sea surface. Particularly severe interference with the paleoproductivity reconstructions using  $\delta^{13}\text{C}$  contents of benthic foraminiferan tests is expected from the injection of  $^{13}\text{C}$ -depleted  $\Sigma\text{CO}_2$ . This depletion is generated by methane-based chemoautotrophic benthic communities (Kulm et al. 1986; Childress et al. 1986) and mimics, even at slow venting rates, enormous fluxes of phytodetritus to the seafloor. At present it is unclear how much of the ocean floor sediments are affected by upward expulsion of pore fluids, but any stable carbon isotope signal of benthic Foraminifera that indicates abnormally  $^{13}\text{C}$ -depleted metabolic  $\Sigma\text{CO}_2$  in the benthic environment should be examined for evidence of venting before it is interpreted in terms of apparent oxygen utilization of normal oceanic bottom waters. The degree of  $^{13}\text{C}$  depletion in pore waters from the Oregon subduction zone is between  $-5\text{‰}$  PDB at the sediment-water interface and  $-34\text{‰}$  PDB at about 100 cm depth below (Suess and Whiticar 1988), a substantial change over normal profiles (Fig. 1). Benthic forams are present at these vent environments but have not been examined in as much detail as the macrofauna. If this problem proves severe, there may be help in the form of biomarkers. Chemoautotrophic bacteria are rich in otherwise exotic structural compounds (Langworthy 1985; Taylor 1984). In conjunction with depleted  $\delta^{13}\text{C}$ , they might be used to diagnose vent environments.

#### SEABED RESPONSE TO TEMPORAL VARIATION IN FLUXES

Among the most far-reaching conclusions of recent modeling is the rapid utilization, on time scales of  $< 1$  yr, of rapidly deposited pulses of organic matter (Reimers, this volume). Equally supportive is the observed speed of population response to such pulses (Gooday 1988; Lochte and Turley 1988). Data are too sparse, however, to know whether such inputs and responses are seasonally predictable or more episodic both within and between years. Among the many implications of such rapidity in benthic response is that *in situ* experiments of relatively short duration might be very informative.

Perhaps the most informative experimental manipulations, however, have been carried out by nature herself on time scales normally inaccessible to experimenters. Sediments initially deposited under high fluxes of organic

matter have been redeposited by turbidity currents to regions of presentl, low organic carbon rain rates. Organic matter of distally deposited and ungraded silty clays, now buried under a thin and well oxidized pelagic sediment cover of the Madeira abyssal plain, is presently being remineralized with oxygen from bottom water (Colley et al. 1984; Wilson et al. 1985; de Lange et al. 1987). Total organic content of the turbidite is much lower above than below the oxygen front, illustrating the slow kinetics of anaerobic processes when operating on organic material of intermediate reactivity. Furthermore, to achieve such penetration, oxygen must diffuse past less reactive organic matter in sediments now overlying the turbidite to consume the more oxidizable material below. Similar "burn down" phenomena may operate at a given locality, without redeposition by turbidity currents, following a decrease in organic carbon flux or increase in bottom water oxygen concentration. Such changes occurred after the last glacial period and may be continuing today (Wilson et al. 1986). This phenomenon dramatically illustrates the importance of oxygen to organic matter degradation in deep-ocean marine sediments.

A similar "carbon burn-down" phenomenon may have affected Mediterranean sapropels, organic carbon-rich sediments originally deposited under anoxic conditions, whose upper portions are now peculiarly depleted in organic carbon (Emeis et al. 1988; de Lange et al., submitted). Reestablishment of oxic bottom waters may have mineralized this reactive organic matter and produced a redox front similar to that seen in the Madeira abyssal plain. Conversely, increased organic sedimentation effectively caps off organic matter that would otherwise decompose.

A major under-explored arena in diagenesis comprises regions in which erosion, physical reworking, and redeposition occur sporadically (e.g., Nowell and Hollister 1985). Such regions are difficult operating environments for equipment as well as steady-state chemical models, and neither flux chambers nor pore water gradients in solute concentration may indicate the quantitatively important fluxes during sediment transport episodes. We know that floras and faunas of such regions differ from those where sediment transport is infrequent (Jumars and Wheatcroft, this volume), but we do not know whether mean remineralization rates and net long-term burial rates of organic carbon are radically out of line with those found at comparable depths in the presence of steady accretion. Similarly, we do not know what fraction of the organic carbon being buried below animal reworking depths is contained in major turbidity flows and slumps.

### **ESTIMATION OF PAST PRODUCTION AND FLUXES**

Based on the preceding background, which details recent insights into early diagenesis and seafloor processes, we again emphasize that most buried

signals record bottom-arriving flux and not surface-ocean paleoproduction. There are no biogenic particles or organic chemicals known to be completely immune to degradation, whose accumulation rate in the sediments could be taken as a direct measure of their production rate at the sea surface. The problem of estimating paleoproduction is conceptually divided into quantifying the relationship between (a) total production and export flux (new production), (b) export flux and bottom-arriving flux, (c) bottom-arriving flux and shallow burial flux, and (d) shallow burial flux and deep burial flux. We examined primarily the third relationship, with some consideration of the fourth, whereas one would have to combine the recommendations of Groups 1 and 2 (see Williams et al. and Bruland et al., both this volume) with ours in order to evaluate the prospects for recording surface production in bulk sedimentary variables.

The first attempt to estimate surface ocean production short-circuited these subdivisions and predicted surface production directly from the deeply buried sedimentary record (Müller and Suess 1979). In so doing the immense complexities of all the intervening transformations were reduced to one empirical function. Recently, Sarnthein et al. (1988) have improved this approach by greatly expanding the data base for calibration and by incorporating relationships between surface production and export flux and between export flux and water depth, the latter to take into account degradation in the water column. Both approaches contain as a variable the bulk sedimentation rate, ostensibly to account for seafloor processes. In essence the loss of organic matter by benthic degradation is higher when the sedimentation rate is slower, but this control of carbon preservation is not without controversy. Emerson (1985) and Emerson et al. (1985) stress instead the rate of bioturbation as another of the controlling factors. In stressing bioturbation they introduce another subdivision in the carbon burial pathway, i.e., the relationship between shallow burial and deep burial (the depth below which little additional decrease in sedimentary organic carbon is observed). According to this view, the loss at the interface (as envisioned by Müller and Suess 1979; Reimers and Suess 1983; and Sarnthein et al. 1988), is a two-step process whereby higher bioturbation rate increases carbon preservation. The mechanism can perhaps best be envisioned as a feedback in which more intense bioturbation more rapidly buries more reactive material and the degradation of that material in turn limits further penetration of oxygen into the sediments. The issue is far from being resolved, but we suspect that explicit models exploring more than two types of reactive organic matter, different magnitudes of carbon residence times within the bioturbated layer, fast and slow sedimentation rate regimes, and high and low bottom-arriving fluxes of organic matter may succeed in pinpointing the mechanism(s) behind the empirical observation that a greater fraction of organic carbon is preserved under greater absolute flux rates.

At present the sole means, independent of sedimentary organic matter, to estimate surface production on the basis of sedimentary evidence derives from the relation between qualitative structure of the planktonic death assemblage and surface-ocean productivity (Mix, this volume). Interestingly, the approach gives results divergent from those based on bulk organic carbon preservation. Nevertheless, so long as they are relatively insensitive to taphonomic (preservational) artifacts, species compositions of buried planktonic microfossils can provide useful estimates of surface production.

For hindcasting of bottom-arriving fluxes, several direct and indirect means are promising enough to warrant further investigation. Interpretations of any of them are still aided by correlative measurements of TOC, total carbonate, and biogenic opal in the same stratum. Especially exciting is the recent finding of species of benthic forams that respond opportunistically to pulsed inputs of organic matter (Gooday 1988). Not only may analysis of benthic foram community structure allow hindcasting of the magnitude of flux (Altenbach and Sarnthein, this volume), but the presence or abundance of these "event opportunists" might also provide an indication of the short-term variation in the flux.

Among the refractory materials whose abundances may yield estimates of paleofluxes, the long-chained alkenones of coccolithophorids discussed by Prahl and Muehlhausen (this volume) are particularly promising biomarkers. They are relatively well characterized chemically and appear to be highly refractory. Their decomposition kinetics require additional study, however, in order to test their adequacy as paleoflux estimators. If the kinetics are genuinely first order and the same is true of the major constituents of TOC, then it is not clear that these alkenones provide a better estimate of bottom-arriving organic flux due to coccolithophorids than TOC itself provides of the bulk arriving organic flux. To be superior would require that the alkenone degradation rate is both slower and more constant than the rate for TOC decomposition at the site. Nevertheless, biomarkers such as those produced by coccolithophorids exist as a series of molecules both structurally and functionally different from each other. Hence, the series potentially displays differential reactivities under variable environmental conditions (Prahl et al. 1988). Such differences can be exploited by studying stratigraphic changes in composition of the chemical series. Examinations of this sort could resolve to what extent preservational factors for the biomarkers vary with time and location. Parallel information cannot be obtained from the single measurement of a bulk property such as TOC.

A very promising indirect method is to measure a fossil signature of the gradients in bottom-water oxygen concentration as derived from the metabolic  $\Sigma\text{CO}_2$  input (Fig. 1). Required is a pair of preserved, calcium carbonate-containing species that record, at two distinct and known levels within (or one level within and one above) the sediment, at least one of

the parameters whose gradients correlate with magnitude of the organic carbon flux. The most useful combination of species and geochemical parameters found to date appears to be *Cibicidoides wuellerstorfi* and *Uvigerina peregrina*, with  $\delta^{13}\text{C}$  measurements of the tests (Zahn et al. 1986; Altenbach and Sarnthein, this volume). *C. wuellerstorfi* is not found living within a diffusive sublayer; it lives attached to worm tubes and other objects protruding above the bed, usually at heights of several mm above the bed. Thus it is clearly above any concentration gradient and is bathed in water containing bottom-water characteristics of  $\Sigma\text{CO}_2$  and  $\delta^{13}\text{C}$ . The sole exception would be those rare individuals poised in a secondary circulation (e.g., in the lee of a tube or nodule, Nowell and Jumars 1984) that entrains water from the diffusive sublayer. *U. peregrina* lives infaunally and is bathed in pore waters enriched in the lighter isotope via organic matter degradation. This example clearly demonstrates the need for, and value of, ecological information at the level of species, individuals, and microenvironments. In principle, Cd/Ca ratio in the same foram tests should afford the same opportunity as  $^{13}\text{C}$ , but the method remains to be explored.

## RECOMMENDATIONS FOR FUTURE RESEARCH

### Source and Chemical Identification of Organic Carbon Fractions

A fundamental block to further understanding of transformation of bottom-arriving organic carbon fluxes into the sedimentary record is the lack of knowledge concerning the identities of chemical compounds in those fluxes and the specific reactions in which they engage. One of the most troublesome unknowns in hindcasting bottom-arriving fluxes is the lack of a sufficiently precise means of estimating the terrigenous contribution to the total organic carbon preserved. The bulk of the terrigenous contribution remains chemically unidentified beyond crude operational catch-alls such as "humic acids." Acute problems with this imprecise identification are that the category includes a broad spectrum of reactivities and that numerous chemical transformations of a substance can occur without removing it from the category. Casual use of the analysis and the term lull one into believing that one knows more about a sample's chemistry than is true. Until estimates of the terrigenous contribution converge, we recommend a two-pronged attack combining a search for additional biomarkers with finer chemical subdivision of the bulk terrigenous component.

Now that it has become clear that a two-component, first-order degradation model is inadequate to treat the deep-sea sedimentary record and we have been forced to a three-component model for even a qualitative understanding, it seems appropriate to ask whether the best approach is to continue to treat degradation as a first-order, multi-component process or whether more

complex kinetics should be explored. Most degradation is biochemical, and even the simplest degradation of one substrate by one enzyme is poorly treated as simply first order. Resolution of the best kinetic approach again seems unlikely, however, until the substances whose kinetics are being studied are better identified. The problem also is acute in benthic biological oceanography, where the specific identities of organic substrates digested and assimilated in nature by benthic organisms, in particular by heterotrophic bacteria and deposit feeders, are unknown.

Use should be made of the turbidite burn-down effect as a natural "experiment" on very long time scales. Chemical analyses should be done on both sides of the oxidation front to examine the sensitivity of specific biomarkers to long-term differences in redox conditions. The ideal indicator of terrigenous source, paleotemperature or paleoflux (although for the turbidite no such flux determination would be attempted), should not change in its intensive or extensive properties across the front. Those chemical species that do fall in concentration on the oxic side of the front are less resistant to oxic degradation than to anaerobic degradation on time scales otherwise beyond experimental reach.

#### **Calibration of Paleoflux Estimators**

All the paleoflux estimators require calibrations, which should take the form of field programs that measure fluxes arriving at the seabed and compare model-estimated and directly measured fluxes of organic matter. At present, two methods appear to provide the most reliable organic carbon flux measurements. The first involves sediment trapping above the bottom boundary layer. Within the bottom boundary layer material can be resuspended or at least be held turbulently in resuspension to heights of 50–100 m. The second method is to (a) estimate burial rates and add them to chamber measurements of total benthic respiration of those organisms living on and in the seabed and (b) to estimate respiration of organisms not caught in such chambers (Smith et al. 1987). Calibration should be over the entire range of fluxes for which hindcasts are to be made and should cover a variety of sediment types (oozes, clays, and hemipelagic sediments) and a range of bottom boundary layer flow regimes and oxygen concentrations. Ideally, several promising methods would be intercalibrated to assess relative precision and accuracy. Furthermore, such a set of observations would allow multivariate statistical analysis (e.g., multiple regression) to assess the added value of using several independent measurements. In addition to alkenone biomarker concentrations in bulk sediments and  $\delta^{13}\text{C}$  and Cd/Ca ratios in foraminiferal tests, more traditional measurements (TOC, total carbonate, reactive silica) should be taken for objective multivariate evaluation of their utility.

### Development of Additional Paleoflux Estimators

The demonstrated utility of using benthic foraminiferans suggests that additional species indicators of fluxes and seasonal variation in fluxes should be sought. The basic natural history of foraminiferans is poorly understood. The exciting possibility exists, however, that horizontal as well as vertical fluxes can be bracketed by species composition. It is likely, for example, that *C. wuellerstorfi* is responding to horizontal fluxes or turbulent vertical fluxes since it resides above the diffusive sublayer (Fig. 3). The limited studies of living forams (Altenbach et al. 1987 and references therein) already indicate that some combination of paleo-flow and paleo-carbon rain rate reconstruction for the bottom boundary layer is feasible.

Xenophyophorans should also be examined. This phylum of protozoans inhabits the deep-sea floor and secretes barite that may be fossilizable (Schulze 1905; Tendal and Gooday 1981). This biological production of benthic barite and its effect on the sedimenting Ba flux (see Bruland et al., this volume) needs to be evaluated. The exciting possibility exists that xenophyophorans may preserve or even amplify the seabed-arriving Ba

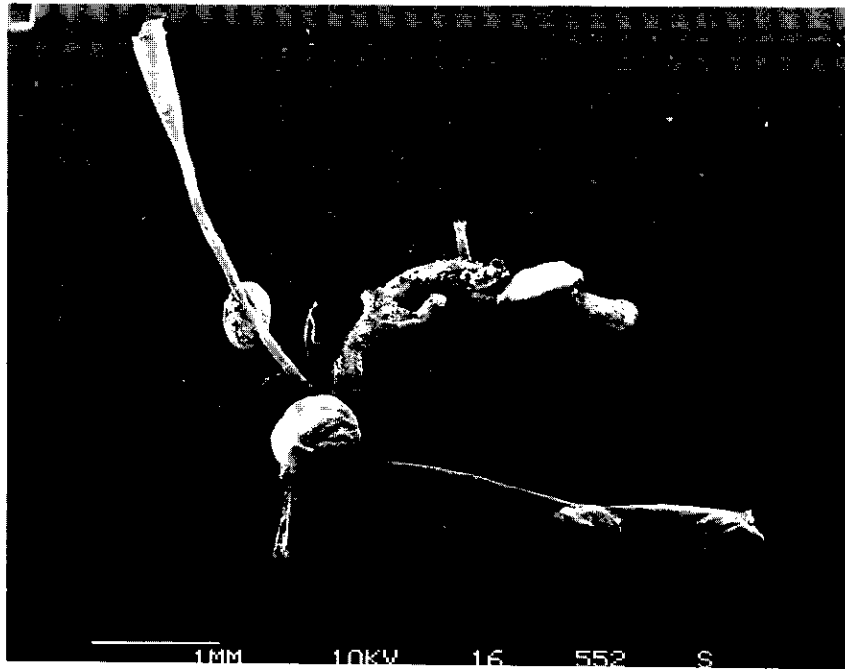


Fig. 3—A scanning electron micrograph of five individuals of *Cibicidoides wuellerstorfi* attached to a hydrozoan (photograph provided by A. Altenbach).

signal. The long-known association of barite, organic matter, and opaline silica has now been identified as largely due to syngenetic formation of  $\text{BaSO}_4$  precipitates during aggregation, aging, and settling of siliceous phytodetritus (Bishop 1988). Previous interpretation favored direct biological production by siliceous phytoplankton, but culturing experiments consistently have failed to show it. Marine haptophytes (*Pavlova lutherii*) are known to secrete barite along with energy storage products in their intracellular vacuoles (Fresnel et al. 1979). Little is known, however, about the contribution of microflagellates to total primary production. Syngenetic formation within decomposing particles explains several of the characteristic features of dissolved and particulate Ba patterns in the water column as well as an increase in Ba flux with water depth. The mechanism proposed by Bishop (1988) also encourages, albeit circuitously, application of Ba accumulation as a paleoproductivity indicator (Schmitz 1987).

Tentatively, the accumulation of barite in the sediment would be some function, as yet unknown, of total supply of siliceous phytodetritus and residence time in the water column. Bio-barite produced by haptophytes would modulate such a function but would not be expected to be an independent source of significant magnitude. Excretion of bio-barite and its incorporation into tests by Xenophyophora might affect accumulation of barite in those areas where increased supply of detritus also stimulates the growth of xenophyophore populations. It is intriguing to pursue the utility of bio-barite as a proxy for productivity because, unlike any of the other indicators ( $C_{\text{org}}$ , opal,  $\text{CaCO}_3$ ) which suffer extensive loss during transfer from the sea surface to the ocean floor, barite abundance actually increases during transfer.

Systematic means of identifying additional biomarkers for studies of high- and low-productivity regions of the ocean are beginning to become evident. Lipids are generally the most structurally diverse biochemicals and hence display the greatest source specificity to the organisms that produce them, allowing in the ideal situation unique identification of the species that produce them. Lipid components traceable to protective coatings or cell walls of autotrophs are typically the most refractory biochemicals in organisms and as such are found preserved in sediments. Although most reported biomarkers are for organisms at the base of the food web (de Leeuw 1986 and references therein), too few studies have been conducted to generalize that distinctive lipids are restricted to organisms of low trophic position. In addition to the alkenones of coccolithophorids, compounds such as 4-methylsterols of dinoflagellates (de Leeuw 1986) and the hopanoids of cyanobacteria (Rohmer et al. 1984) should be investigated as biomarkers of paleoflux in the geological record. Given the above patterns and their physical presence in the fossil record, the resting cysts of dinoflagellates and spores of diatoms would seem to be promising candidates as sources for

new paleoenvironmental biomarkers. Nearly unexplored is the potential of bottom-dwelling bacterial or animal species to produce diagnostic biomarkers that persist in the sedimentary record. Functional groups of bacteria produce distinctive lipids (Goosens et al. 1987), but refractory components remain to be found, with the exception of ether lipids of Archaeobacteria in ancient sediments and Recent hydrothermal environments (Comita and Gagosian 1983). Animals produce a range of antibiotics to prevent bacterial attack of their bodies and structures (tubes and burrows). Despite these ideas on potentially good candidates for sources of biomarkers, the search is still largely empirical, and new biomarkers are found primarily through serendipity.

Use of the carbon isotopic ratio in benthic foraminiferans for estimating past gradients in  $\delta^{13}\text{C}$  of marine pore waters would benefit if additional species (beyond *U. peregrina*) could be identified that cover a greater depth range within diagenetic chemical gradients. Species that appear to occupy the stratum where oxygen falls to undetectable levels (Corliss 1985) may be useful for estimating paleoceanographic bottom water oxygen levels (McCorckle and Emerson 1988) if they are abundant enough geographically and can be calibrated using recent individuals and present  $\text{O}_2$  levels. If pairs of species that are widely separated vertically in life positions are used, however, care must be taken to determine that they are contemporaneous in the fossil record.

#### Assessment of Biological Responses and Effects

Rapid population response of benthic foraminiferans to seasonally enhanced flux in the deep sea (Gooday 1988) came as a surprise but may well be widespread. Metazoan meiofauna have shown similar seasonal responses at shelf or slope depths off both U.S. coasts (Cammen, in preparation; Fleeger, in preparation). Seasonal changes in sedimentation flux need to be linked to biological and geochemical changes occurring at the sediment-water interface. No deliberately seasonal studies have been initiated to correlate biological responses (changes in numbers, reproductive conditions, vertical distributions of organisms) or geochemical changes in particulate matter and pore water profiles to variable supply rates of particulate organic matter deposition (Reimers, this volume). In general geochemical and biological studies have been poorly coupled.

Experiments under actual or simulated *in situ* deep-sea conditions are needed to investigate the impact of invertebrate feeding and bioturbation on preservation of inorganic and organic material. The unique microenvironment (physically mixed and anaerobic) within some animal guts can create conditions for dissolution, precipitation, or degradation that do not occur in ambient sediments and are not yet reproducible in the laboratory. Animal

feeding should also stimulate microbial activity and thus increase the rate of organic matter degradation inferred from simple microbial incubations alone.

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