

Responses of Benthos to Changing Food Quality and Quantity, with a Focus on Deposit Feeding and Bioturbation

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Abstract. Deposit feeding is the process that accounts for most bioturbation of particles most of the time because there is selective pressure on deposit feeders to feed on generally nutrient-poor sediments at high rates and to separate sites of ingestion and egestion. Conversely, burrowing has substantial energetic cost, and there is strong selective pressure to minimize the amount and distance of sediments moved. The most rapid advances in understanding deposit feeding and thus bioturbation have and will come from examining the selective pressures of changing food quality and quantity on individuals. Comparatively little predictive value has been or can be gleaned from empirical, ecosystem level examinations of detrital processing. In particular, predictive models are needed of deposit feeder size, abundance, and activity as functions of food quality and quantity variation over a broad range of time scales. The roles of deposit feeder digestion in geochemical reactions are conspicuously underexplored either with models or measurements.

Community level responses to varying organic input are best known in cases of near-shore, anthropogenous organic inputs, where a succession from small, shallowly burrowing to large, deeply burrowing species is usually seen after loading ceases. In the deep sea, population responses of meiofauna to seasonal and episodic inputs of fresh phytodetritus have been noted, but the importance of such inputs to macrofauna is unknown. Exceptionally deep burrowers are characteristic of regions in which sedimentation has buried substantial organic carbon. Tranquil deep-sea sites under oligotrophic oceans are characterized by very sparse and small individuals of motile, deposit-feeding infauna, but inference of vertical flux of organics from standing stocks and community composition of benthic animals is confounded by the as yet poorly understood effects of horizontal sediment transport.

Depth of mixing by animals is surprisingly invariant and may be set by rapidly mounting costs of burrowing with increasing sedimentary overburden. Bioturbation intensity also varies less than one might expect, because animal density falls off with decreasing sedimentation rate and organic flux, but individuals in food-poorer regions presumably must feed at greater rates to

meet similar metabolic needs per gram of body mass. We also suggest that bioturbation intensity is much greater in the horizontal than in the vertical and accounts for surprisingly rapid disappearance of surface traces. Edges of communities (ecotones) and regions of unsteady sedimentation (in particular turbidite zones) are understudied in terms of the insights they could provide into benthic organism responses to varying food supply.

INTRODUCTION

Separating dependent from independent variables in the system of organisms, sediments, and boundary-layer fluids is certainly difficult and perhaps unwise. In systems with feedbacks, that separation must be arbitrary. At the risk of being both unwise and arbitrary, but for the sake of organizational simplicity, we adopt the point of view of benthic organisms and ask how they respond to changes in the quality and quantity of food supplied to them. We then switch perspectives to ask how these responses may affect the sedimentary record. We do not begin with the latter perspective because without an understanding of the selective pressures driving animal responses, organisms would appear both capricious and arbitrary in their effects on the sedimentary record. We endeavor to express and support strong opinion rather than to present a balanced review.

Our focus on feeding in general and on deposit feeding in particular may appear excessive, but there are several reasons for it. Feeding is the animal activity that under nearly all circumstances is responsible for the overwhelming majority of biogenous movement of sediments. A common misconception, due to such prominent structures as fossilized escape burrows across strata of strongly contrasting lithologies, is that organisms spend a great deal of time burrowing. Even when they do move from one place to another, there is strong selective pressure on organisms not in life-threatening situations to minimize the amounts of sediment displaced; burrowing is the most expensive means of locomotion, including flight (joules per body length moved, cf. Trevor 1978). Because water is so much easier to move than denser solids, it is no accident that apparent eddy diffusion coefficients of fluid bioturbation exceed by an order of magnitude or more those of particulate bioturbation (Aller 1982). Animals do erect tube and burrow structures within the seabed and move about within them: the anthropomorphic analogy is to digging subway tunnels rarely but using them frequently once built. The prime exceptions are a few: comparatively rare subsurface burrowers that combine the costs of ingesting sediments with the costs of burrowing, eating their ways along (e.g., heart urchins and large ophelliid polychaetes). Even these exceptions are better understood by focusing on feeding rather than burrowing, for there is still strong selective pressure to minimize the amounts of sediment moved but not ingested. Furthermore,

the kinetics of deposit feeding are counterintuitively rapid due to the short gut residence times (30 min to 2 hr being often seen in shallow-water representatives) and large gut volumes (typically 30–80% of total body volume) imposed by the generally low food quality of sediments.

To relate these ideas about animal activities to the usual biodiffusion coefficient (D_b in units of length squared per unit of time) Wheatcroft et al. (in preparation) have decomposed it into a step length and a frequency. Because step length is squared, this term dominates D_b . In burrowing, the typical distance moved by a sediment particle is small: a fraction of a burrow or body radius. In feeding, by contrast, gut length (more precisely mean distance from point of ingestion to point of egestion) is the appropriate length scale. Not only is the typical displacement distance by feeding thus much greater, we suggest that feeding is also the more frequent activity, assuring its dominance over burrowing in determining D_b .

This bioturbation formalism can be applied to either conservative or reactive chemical species (Aller 1982). To date, however, reaction terms inside animal guts have not been examined in the detail they deserve. What makes the deposit feeder gut a unique sedimentary environment is the otherwise rare combination of low gut oxygen levels (produced by microbial activity) with mechanical agitation. This combination is rare outside animal guts and is effective at speeding reactions over rates normally encountered in more tranquil anaerobic environments outside animal guts (Kristensen and Blackburn 1987).

A secondary purpose of ours is to challenge a virtually automatic focus on successional time scales when dealing with benthic biological response to varying organic input. The reason for this automatic focus is the relative abundance of data on these scales characteristic of anthropogenous organic inputs and scarcity of data on both larger and smaller spatial and temporal scales. In particular we question the notion that mechanistic, *predictive* understanding of aggregate phenomena, such as bioturbation, can be achieved without a focus on the selective processes that operate on individuals. We will examine both steady and unsteady responses over a much broader range of scales than those encompassed by most studies of organic loading—to highlight the lack of data and potential utility of models on these shorter and longer scales.

BIOLOGICAL STRUCTURE AND FUNCTION

Concepts of Food Quality and Quantity

Semantic difficulty runs rampant in discussions of organism response to food differences. To be useful, however, the amount of food supplied or available to an individual, population, or community must be expressed per unit of

time. Any unit of biomass requires a rate of supply in order to maintain itself or to grow. Fundamentally, an individual requires a given number of mol s^{-1} of some limiting nutrient in order to survive. Confusion often results, however, because at steady state the standing stock of food and its rate of supply can be related through a simple constant, leading to the assertion (true under steady state but not in general) that biomass of food is a perfectly valid indicator of food availability. Another special case in which standing stock of food can serve as an empirically, if not conceptually, satisfactory surrogate for rate of food supply to an individual is when the individual's utilization rate is swamped by the rate of supply, i.e., by advection or microbial growth. What is not always apparent is that growth is still rate-limited, but in this case it is limited by the animal's processing rate rather than by the rate of supply afforded by the external environment.

The latter point may seem subtle, but it must be treated explicitly if one is to determine an appropriate geometry for measurement of rate of supply. Rate of supply is often, and in general perhaps best, expressed in terms of $\text{mol m}^{-2} \text{s}^{-1}$, where the area is a horizontal plane representing the sediment-water interface. In reality, however, feeding volumes of organisms have more complex geometries. Among the simplest are those of surface deposit feeders having circular or cardioid areas reached by the feeding appendages, but even here some finite and not necessarily areally uniform thickness of sediments is accessible. In the absence of horizontal movement, organic matter sedimenting outside the geometry swept out by feeding appendages would remain unavailable; in the presence of horizontal sediment transport, due either to physical forces or to bioturbation, material deposited outside can become available, and conversely material initially deposited inside can become unavailable. Feeding geometries and transport interact, further complicating the situation; protruding animal tubes can create areas of scour (reduced deposition until some steady state is reached), and many animals build pits that increase deposition rates locally.

Flux geometry is perhaps most critical to suspension feeders. Passive suspension feeders—those that do not pump water past their capture appendages—depend upon the geophysically driven flux of material reaching the appendages. In the bottom boundary layer, horizontal fluxes of suspended particles typically exceed vertical fluxes by at least an order of magnitude. It is doubtful whether a suspension feeder could exist anywhere on the ocean floor if there were no turbulence or horizontal flow to provide a supply in excess of the net vertical sedimentation rate. An important corollary is that the same net vertical flux of organic matter from surficial waters may support varying proportions of suspension-feeding versus deposit-feeding animals (including the foraminiferans discussed by Altenbach and Sarnthein, this volume); a faunal change need not signal a change in vertical flux. Even under steady state transport, both suspended particle concentration

and horizontal velocity show very strong gradients near the bed, producing diverse and often strongly vertically varying flux profiles (concentration \times horizontal velocity = horizontal flux). At first it would appear that active suspension feeders (such as clams) would be sensitive only to ambient concentration. Reinforcing the point made above this insensitivity to flux should be observed only when supply overwhelms demand. Interactions of the flux rates and geometries produced by pumping with the flux rates and geometries produced by the ambient flow become critical.

It is thus apparent that rate of food supply—food quantity—cannot be defined accurately without taking into account to what organisms this rate is being supplied. For example, a benthic bacterium may depend upon vertical sedimentation of organic particulate carbon for its supply of chemical energy and vertical turbulent and molecular diffusive exchange of inorganic nitrogen to supply building blocks for proteins. A critical and unanswered question for both suspension feeders and deposit feeders in the deep sea is the extent to which they feed on a renewable resource in the form of such bacteria attached to particles versus the extent to which they compete with bacteria for newly arriving and labile organic material. In the former case, their food supply is strongly buffered against short-term oscillations in rate of supply (with bacterial growth rate determining that supply), while in the latter these animals should be strongly keyed to vertical and horizontal sedimentation events of the most organically labile, new materials. Identifying precisely the food resources assimilated by deposit feeders is a key problem in shallow water as well as in the deep sea (Lopez et al. 1989); the problem is not straightforward because, at the high processing rates characteristic of deposit feeders, a minor sedimentary organic constituent might be a major source of assimilated energy or mass even if it were assimilated with only moderate efficiency. The problems raised by this lack of knowledge are pervasive: if a downstream individual assimilates a different component of sedimentary organic carbon from that assimilated by individuals of other species found upstream, then horizontal transport is all the more effective as a source of food.

Any biologically useful definition of food quality must be even more closely tailored to the organism in question, as is obvious from Aesop's fable of the dog in the manger. One component of sedimentary food quality is the proportion of potentially digestible material in the food. A more specific definition is the volumetric or gravimetric concentration of the growth rate-limiting component, yet only for a handful of shallow-water species are there data to suggest what such components are (Tenore et al. 1984). This handful of results gives some hope that growth in deposit feeders may be limited more generally by either available (labile organic) nitrogen or available caloric energy, depending upon the ratio in which these two key ingredients are provided. To an organism, however, time is energy (or

mass that contains energy), and food quality must deal in net return to the animal per unit of time. Consistent descriptions would be the functions that describe net rate of gain to a metazoan versus residence time of a food in its sensory field (detection, pursuit, and capture) and gut or that describe net rate of gain to a bacterium versus time exposed to its exoenzymes. From such plots (Fig. 1) it is readily apparent that food quality and quantity are

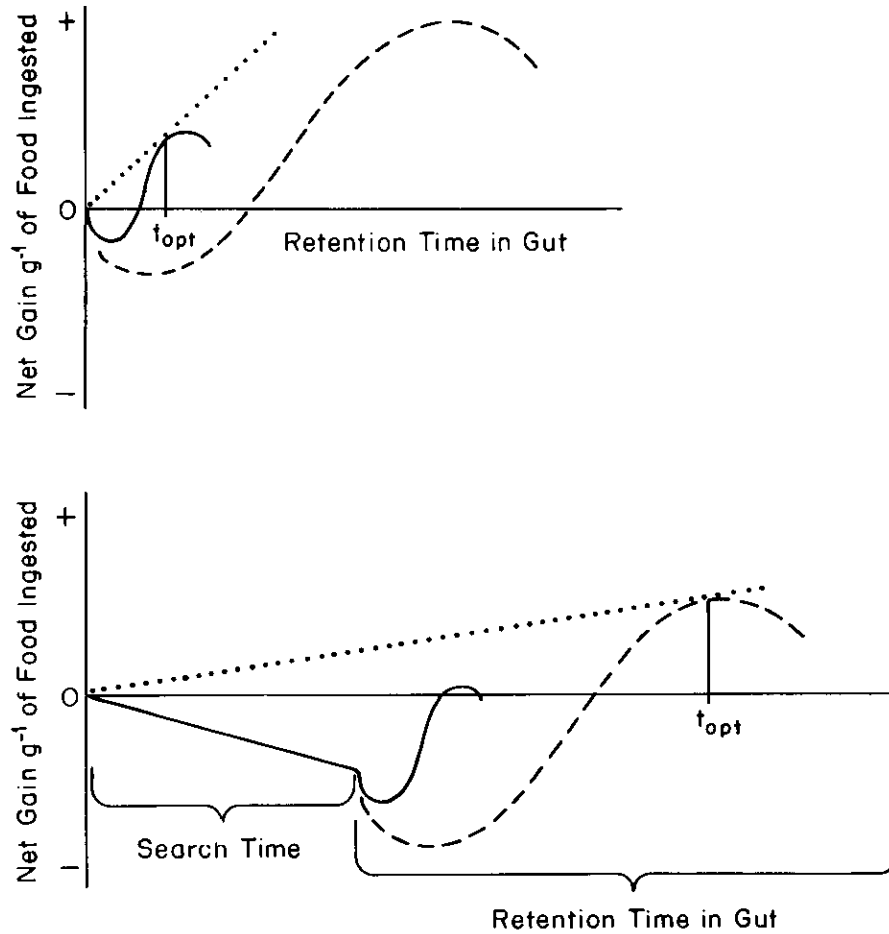


Fig. 1—Interaction of food quality (described by the solid line for a food type giving rapid return after ingestion and the dashed line for a food type giving slower but eventually greater return) with food quantity. The upper graph is for the case of unlimited food while the lower graph is for a lower abundance (supply rate), requiring a finite search time to locate a given item. The dotted tangents through the origins represent the maximal rates of gain possible (at the optimal retention time, t_{opt}), showing that the favored food type should change with food abundance. Modified from Sibly (1981).

not independent; in general, it is not possible even to ordinate food quality without specifying rate of supply, since rate of supply and quality interact in determining the foraging strategy that can maximize net rate of gain of mass or energy.

Clearly, there is a long way to go in determining food supply rate and food quality for deep-sea organisms. Sediment trap data provide apparent vertical fluxes expressed in total weight, carbon content, or nitrogen content per unit of area per unit of time. Over the range of C:N ratios seen in the deep sea, it seems safe, despite considerable scatter, to say that the trend is toward higher food quality the lower the ratio. Similarly, there is a tendency for food quality and quantity to covary. Much supply to the benthos seems to be from unsteady events in overlying waters, with consequent pulses of relatively labile material. Given this tendency towards covariation of quality and quantity and the present state of knowledge, we will subsequently not spend much effort (beyond a quick look at individuals' responses) to resolve quality from quantity. As the utility of specific biomarkers increases, however, this distinction will become crucial.

Responses of Individuals and Populations to Time-varying Food Supply

Feeding rates of active (spending energy to obtain new water parcels by swimming or pumping) planktonic suspension feeders and benthic bivalves have been much studied with respect to the rate of food supply. Foraging theory and empirical observations agree (Fig. 2) in illuminating individual responses to short-term changes (\leq mean gut residence time) in suspended food concentration, which acts as a surrogate for food supply rate since food is maintained at a given level while the response is measured. Data are consistent with the idea that suspension feeders act in such a way as to maximize their individual net rates of gain of energy or limiting nutrient. A plot very much like that of Fig. 2 can, in fact, be generated from Fig. 1 by means of continually shifting the origin in order to change the time between ingestion events.

Exercising Fig. 1 in this manner also demonstrates the predictive value of examining biological phenomena at the level of ecological organization where selection takes place, i.e., on individuals that constitute populations. As food becomes scarcer (time between ingestion events increases), a shift toward a new, longer optimal retention time will increase digestive efficiency. The ecosystem result will be greater retention of nutrients by organisms and more efficient recycling. In the past, such phenomena have been considered to be intrinsic features of "mature ecosystems" (Odum 1969), but it is now plain (Miller et al. 1984; Penry and Jumars 1987) that predictive theory at the level of the individual is much better poised to provide an understanding of them.

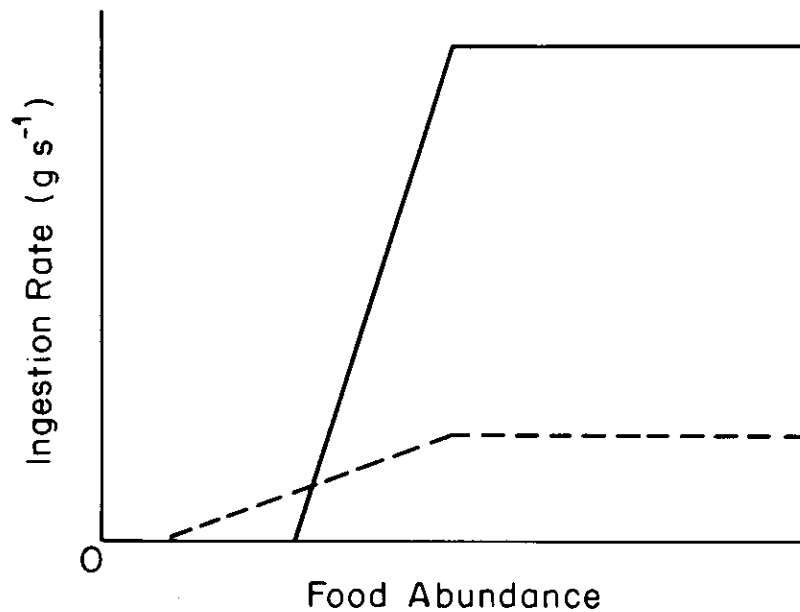


Fig. 2—Ingestion rate and food supply rate (as indicated by food concentration in the case of suspension feeders) on the two different types of food of Fig. 1, offered separately. The plateaus occur when search time of Fig. 1 drops to zero.

At first it might appear that deposit feeders are never limited by food quantity, since mud or sand is always available and nearly invariably has some organic coating. This intuition is wrong, as can be seen by doing the thought experiment of allowing an animal to feed in the absence of advection and positing its digestion to be highly efficient. If feeding rate exceeds resupply rate, food content of the sediments can be driven so low that feeding provides no net gain. While one could argue that only quality has changed, it seems more consistent to argue that rate of supply is a primary determinant of this food quality. Whether one argues on the basis of quantity or quality, the empirical observation is that surface deposit feeding rates of sedentary deposit feeders rapidly decline (order of one gut residence time) in the absence of advective resupply and removal of accrued fecal material. Again, further resolution is unlikely until the foods that deposit feeders digest and assimilate are better identified and quantified (Lopez et al. 1989).

Experiments that vary only the concentration of one pure food material covalently bonded to artificial sediments have been conducted using deposit feeders. Sufficient quantity has been provided to preclude change of quality by the animal. The general result with the handful of species thus far examined is for more rapid feeding ($\text{g dry weight sediments ingested s}^{-1}$)

as food quality (protein g^{-1} dry weight of sediment) is increased, as would be predicted from a plot like that of Fig. 1 tailored to this situation (Taghon and Jumars 1984). There is a hint from work with more complex mixtures of food that at some (perhaps unnaturally) high concentrations, feeding rate turns down (Taghon 1988); this downturn may, however, be due to diffusional constraints in such a thick stew of nutrients.

That faster feeding individuals among one species of a deposit feeder actually do gain mass at a greater rate (or lose it at a lower rate) has now been established (Taghon 1988). Given the same food quality and quantity, the faster feeding individuals showed greater net gains in weight. Presumably some other selective pressure, such as greater exposure to predation during feeding, prevents selection from proceeding to produce a population of uniformly high feeding rate. This established link between short-term feeding behavior and potential reproductive gain is a critical one in optimal foraging theory, so Taghon's study and new ones like it are extremely important. The idea underpinning optimal foraging theory is that the individual gaining energy at a greater rate has a greater excess over its own metabolic needs to place into its somatic growth or defenses and into enhancing the robustness or numbers of its offspring. Thus, this individual under steady food supply is better able to sequester available material, while under fluctuating food supply is better able to channel food into population growth. In the former case, investment in rarer, larger individuals is likely; in the latter, rapid population growth is the expected channel for available resources. The natural time scale for these population phenomena is the generation time, whose minima range from the order of an hour in bacteria to decades in the largest animals. There is now evidence that meiofaunal populations at shelf and deep-sea depths respond by rapid population growth to seasonal or episodic inputs of labile organic matter (Gooday 1988; Cammen, in preparation; Fleeger, in preparation). It is not clear whether larger, longer-lived organisms—particularly deposit feeders that by definition frequently ingest material of low bulk food value—depend similarly on this labile fraction or are keyed instead, or also, to slower but steadier yields from more refractory material. The finding of a few species that do depend upon the most labile material should not draw attention away from the question of whether these species are typical or unusual.

Succession

Changes in species composition due to organic enrichment in benthic communities are better documented, at least for intertidal and shallow subtidal cases. There is a repeatable succession from small, dense (number m^{-2}) shallowly burrowing species with rapid population increase toward large, sparse, more slowly growing, deep burrowers (McCall 1977; Pearson

and Rosenberg 1978). Exactly this kind of succession in population dynamics would be predicted, as the rate of food supply from the enrichment diminished, causing a transition from advantage in allocating resources toward population growth to advantage in allocation to individual maintenance and maintenance of a constant population size. In ecological terms, populations undergo *K* selection as food supply diminishes and becomes more steady and predictable. Since metazoans of organic-rich sediments must pump in their own oxygen, from the surface (or from neighbors' ventilation tubes), there is a general correlation between body size and depth of burrowing. If the severely disturbed area is large enough, new recruits near its center must come from the water column, so it is logical that shallow dwellers arrive and (since they on the average are smaller) mature first. The time scale for recovery from an organic enrichment depends upon the area covered by the enrichment and upon the intensity and time variation of the organic input. Clearly no steady state can be reached in less than the generation time of the longest-lived species in the latest stage of succession.

Most of the data on responses to organic loading come from anthropogenic events, and their relevance to nature is difficult to discern. Natural organic loadings rarely drive the sediments to a condition in which metazoans are absent and rarely occupy the size scales of these anthropogenic events. Nonetheless, there do seem to be parallels in nature. Floods of rivers sometimes cause similar conditions. Natural anoxia of continental shelf sediments and bottom waters from intense blooms has been observed, and successional recovery does appear similar to that observed in sediments affected by organic wastes (Boesch, in preparation). As expected, recovery from disturbances of large physical scale in which all fauna are removed is fastest among those species that have planktonic larvae. Recent results call into question, at least for disturbances of small spatial scale, the slow pace of recovery previously measured or assumed from deep-sea disturbances (Smith et al. 1986).

In most shallow-water environments a seasonal cycle is imposed on longer-scale trends. Seasonal reproductive periodicity certainly is seen in some benthic populations (e.g., Tyler 1986), but there is not a single published, deep-sea time series of quantitative samples that addresses the degree to which seasonality of reproduction in some deep-sea species is reflected in seasonally changing community structure. As a consequence, we do not know whether seasonality in population density and structure in the deep sea is an oddity or the norm.

Given that most sequences of deep-sea environments preserved on land come from bathyal depths and that many are of turbidite origin, successional patterns after major burial events are grossly underexplored. We have no idea how long complete recovery from a turbidity flow might take. Turbidity currents do bury organic-rich sediments and appear to allow deeply burrowing

species to make a net profit from deposit feeding at a depth below the sediment-water interface, where the costs of producing burrows otherwise would not repay the costs of making them (Griggs et al. 1969). Animals in effect "mine" the "coal seams" produced by the event. There is not a piece of benthic sampling gear in existence that is well designed to capture large and deep burrowers, but shallow-water representatives (e.g., thalassinid shrimp) easily can exceed 2 m depth below the sediment-water interface (Dworschak 1983), and we and other deep-sea biologists and geologists routinely see open tubes and burrows coming out the bottoms of 50 cm-long box cores taken from turbidites. An interesting question is whether these deep burrowers must be preceded by a sequence of shallower burrowers. Alternatively, they might find such events through the nonsteady state migration of pore waters (Sorensen et al. 1987). In either case it is not clear how the deep burrower grows large enough to reach the organic-rich deposit unless seams outcrop. It would appear profitable in view of all these unknowns to study living faunas and trace fossils in turbidites having varying vertical and horizontal structures and oxygenation histories.

Evolution

Clearly the most underexplored time scale for paleoceanographic purposes is the evolutionary one (from generation time upward). The level of resolution in most stratigraphic records gives little information on shorter-term phenomena (Schindel 1980). The key issue is whether one can identify characteristics of individuals, populations, and communities that reflect the local mean and variation of organic input. The goal from a biologist's perspective would be to predict the sizes, abundances, and types of organisms expected to evolve at or invade a site given its vertical inputs and horizontal transports of food. That goal is very distant, but as it is approached it will provide a strong means of converting paleontological evidence into paleoproductivity estimates. Despite the distance of the goal, it is clear that effects of millennial increases in productivity over broad reaches of the ocean floor do not parallel anthropogenous loadings. Equatorial deep-sea benthic faunas are neither dramatically low in diversity nor do they comprise exclusively small, shallow-burrowing individuals.

This empirical approach of comparing present-day faunas from disparate vertical and horizontal flux regimes, assuming that these faunas have evolved to some near-equilibrium with their present food supplies, can provide other insights as well. For the deep sea, however, this effort is hampered by lack of published information on geographic distribution of infaunal species. Community structure appears similar under the oligotrophic gyres of the North and South Pacific and quite different from that of the equatorial zone

(Hessler, personal communication), but the number of distinct communities and the characteristic lifestyles of their members are very poorly known, and one must invoke many arguments by analogy with shallow-water results.

In a compilation of feeding rates in 19 shallow-water, deposit-feeding species, Cammen (1980) corrected for the fact that metabolic rates generally, and deposit feeding rates in particular, scale as body weight or volume raised to a power near $2/3$ to $3/4$. He then found that ingestion rates (organic matter ingested per unit of time per size-corrected gram of flesh) are roughly constant across a thousandfold range in organic content of ingested sediments. That is, there is no free lunch. Species that live in organic-poor sands process much greater sediment volumes per unit of time than do species that live in organic-rich muds. Note that this among-species comparison is not at all in conflict with foraging theory predictions that an individual exposed to normal within-environment variation will feed faster on higher-quality foods; this response is simply behavioral noise in Cammen's empirical relation. Unfortunately, there is no *in situ* measurement of feeding rate in any deep-sea deposit feeder for comparison with Cammen's empirical findings for shallow water, but direct extrapolation of Cammen's results would predict feeding rate (volume or mass per unit of time) to be relatively high in deep-sea deposit feeders because organic content of deep-sea sediments is usually low. The only evidence thus far of this selective pressure is the relative increase in volume of guts of deeper-dwelling (water depths) species when closely related taxa are compared (Allen and Sanders 1966). Such an adaptation allows a greater flow rate of sediments without a decrease in residence time or an increase in residence time without a decrease in flow rate. Furthermore, there is less body (versus gut) volume to support.

Biomasses of macroscopic metazoans and their numerical abundances decrease roughly exponentially with water depth. Below continental shelf depths the overwhelming majority of metazoan macroscopic organisms are deposit feeders. This seeming overdescription is needed to hide the fact that much of the total biomass in the deep sea is in poorly known and often large-bodied protozoans. There is some suggestion, from observations reported by Altenbach and Sarnthein (this volume), that protozoans may comprise more suspension feeders. While some foraminiferans are known to be mobile, they almost surely account for a much smaller amount of movement of sedimentary particles than do deposit-feeding metazoans. Body size of deep-sea infauna characteristically is small and is smallest where the flux of food is smallest. This general tendency makes the few larger animals among the infauna all the more important (Smith et al. 1986), but their abundances are poorly known because rare, deep-burrowing animals are the least well sampled components of the deep-sea fauna.

In looking at these patterns one sees a peculiar melange of theory and empirical pattern analysis, with little direct connection between the two. One exception that soon should emerge will be the issue of body size. One might expect deep-sea deposit feeders to be larger than their shallow-water counterparts, because metabolic cost per gram of flesh goes down with body size. Body size models such as those of Sebens (1987), however, show that this cost must be balanced against gain, i.e., one must know how rate of collection or digestive production scales with body size. Hessler and Jumars (1974) suggest that small deposit feeders can better focus food collection on interfacial sediments and thus get food of higher quality than can a bigger animal with a bigger collector. Penry and Jumars (1987) suggest that small body size avoids diffusional constraints on rates of digestion and absorption. Body size models have the potential to explain and to predict how biomass will be distributed among body sizes and how fast each of the individuals will process sediments. There are certainly strong patterns to explain (Schwinghamer 1985); the challenge is to couple mechanistic, predictive theory to them.

Motility patterns also change with water depth and distance from shore. Frequent and intense sediment transport precludes sessility, as does a food flux so low that an animal cannot encounter sufficient food to sustain itself by staying put. Hence, an intermediate-depth maximum in sedentariness of the fauna is expected and observed (Jumars and Fauchald 1977). One also sees the anticipated demise of active benthic suspension feeders and decreasing abundance of passive suspension feeders with depth, except where horizontal fluxes of seston are unusually high. Feeding type changes can be much more subtle, however, as a look at the life habits among the tube-dwelling polychaete worm family Ampharetidae demonstrates (Fig. 3). In the high-energy intertidal, ampharetids build no special devices for capturing sediments and show no special adaptations for getting rid of their fecal matter; the former are supplied in abundance while the latter are removed regularly by waves and currents. In lower-energy subtidal to bathyal and abyssal sites, ampharetids make pits that enhance sedimentation locally by inducing settlement or retention of horizontally transported material, and they show much more care in keeping such feeding pits free of their own feces (Nowell et al. 1984). At the deepest, most food-poor abyssal sites, ampharetids disappear altogether. One gets the impression that it may be possible in the next decade to build models that predict what lifestyles will occur under what rates of organic rain and horizontal transport.

A striking anomaly in the typical pattern of abundance change with depth has recently been discovered at the base of the continental rise (approx. 4800 m) off Nova Scotia (Thistle et al. 1985). This region, studied under the HEBBLE (High Energy Benthic Boundary Layer Experiment) program,

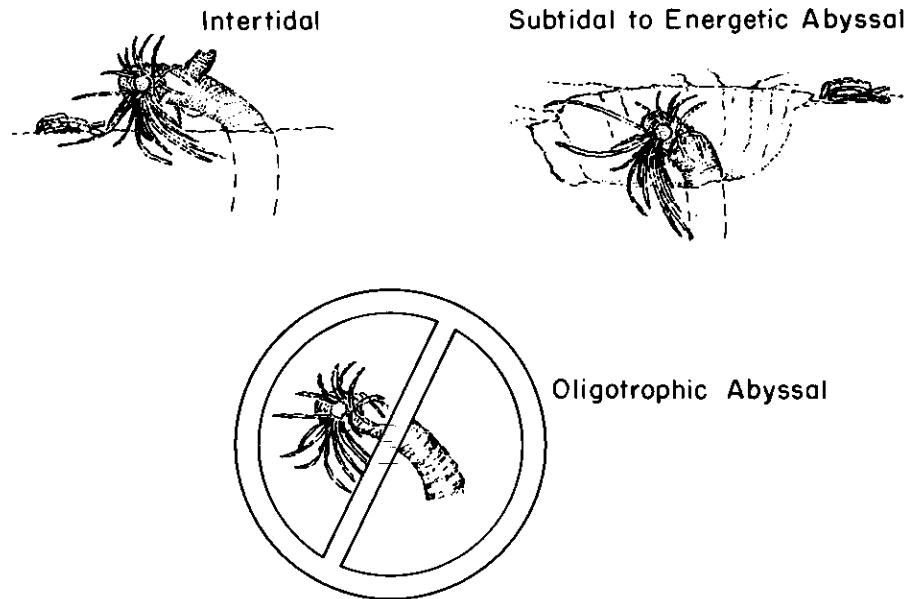


Fig. 3—Sketches of ampharetid polychaete lifestyles as the flux of food from local production, waves, and currents decreases. Intertidal ampharetids deposit their fecal wastes in the feeding area, relying on current and wave energy to remove them. Where wave and current energy is reduced, ampharetids often make pits that enhance sedimentation, and they take care to deposit fecal wastes outside the feeding area (helping to maintain the pit). At most food-poor abyssal sites, they and other sedentary tube builders are rare or absent.

is characterized by high horizontal sediment transport rates in “storms” that occur roughly five times per year and are now thought to represent geostrophically trapped edge waves along the rise. Bacterial and faunal abundances are an order of magnitude larger than otherwise would be expected at this depth. The storm events apparently are effective at stimulating bacterial production sufficient to fuel this enhanced standing stock. The numerically dominant macroscopic infaunal species uses the food-gathering method of the second panel of Fig. 3, and a tube of the adult size provides shelter within the sediments from storms of the magnitudes observed. The high organism abundances are not consistent with the idea that the deep-sea fauna is fed with little lag directly by the labile components of phytodetritus falling vertically. If the latter notion were true, then it would not be apparent why areas with large horizontal fluxes of sediments should yield such high standing stocks. Epifaunal species are extremely rare, however, and so part of the standing-stock increase might be explained by reduced predation from epifauna.

**SEDIMENTARY CONSEQUENCES OF BIOLOGICAL
STRUCTURE AND FUNCTION****Stratigraphic Resolution**

If one accepts the argument that deposit feeding is the principal component of bioturbation, then can one rationalize the biological patterns noted above with observed stratigraphic resolution? Moreover, can one suggest particularly good places (outside anoxic basins) to look for improved resolution? Unfortunately, the most obvious answer—to look where suspension feeders that do not rummage through the sediments for food dominate—is not a good one. Metazoan suspension feeders simply are too rare in the deep sea ever to dominate soft bottoms. The best one can hope for is to find variations in the abundances, sizes, and activity levels of deposit feeders.

Guinasso and Schink (1975) provide a nondimensional index (G) of mixing intensity that varies inversely with stratigraphic resolution:

$$G = \frac{D_b}{L_b S} \quad (1)$$

where S is sediment accumulation rate (thickness per unit of time) and L_b is the thickness of the layer in which bioturbation occurs. Variations in L_b and D_b are quite limited so that the best stratigraphic resolution to date has been observed in areas with highest values of S (Schindel 1980; Shiffelbein 1984). A modest increase in L_b with increasing flux of organic carbon and sedimentation rate (Berger, personal communication) is consistent with the idea that deeper burrowing costs can be repaid when fluxes and concentrations of organic carbon are higher at greater sediment depths. It is tempting to speculate that the relative invariance of L_b is due to rapidly increasing costs of deeper burrowing as the sedimentary overburden increases. L_b does not scale with the most deeply burrowing species found at a site; depth of deepest burrowing is nearly invariably larger. Note also that this mixing relation is developed only for regions free of obvious complications from turbidites. The range in G , nonetheless, is smaller than one would expect if D_b were independent of S . Over the full range of gradual sediment accumulation rates seen in the deep sea, one expects animal size and abundance to vary directly with S , but with a great deal of scatter due to variations in horizontal fluxes. The greatest apparent deep-sea values for D_b in regions of continuous sedimentation have indeed been measured in nearshore regions of high productivity. However, since individual feeding rate (evolutionary time scale) by Cammen's (1980) arguments varies inversely and animal abundance varies directly with sedimentary organic

content, the range in D_b is not as large as one might expect. Unfortunately, information to make a more informed guess as to where abundances, kinds, and activities of deposit feeders might permit stratigraphic resolution best to persist is still lacking. Clearly, if we better knew how to predict D_b and L_b from biological information we could better choose sites of higher potential stratigraphic resolution.

We would not expect similar invariance of the equivalent parameters to D_b and L_b with respect to pore water solutes. Animals pump water to meet respiratory needs for oxygen. Where sediments are richer in organic matter and animals are larger, volumetric pumping rates and pumping depths will have to be greater. In oxygenated red clays sparsely populated by small animals, molecular diffusion without pumping may meet metabolic oxygen demand.

Faunas of calcareous and siliceous oozes are particularly understudied. Digestive enzymes are highly pH sensitive, so it would be reasonable to anticipate some differences in digestive kinetics between the terrigenous-sediment feeders so far examined in feeding-rate relationships (Cammen 1980) and deposit feeders on calcareous oozes. Casual (personal) observations of equatorial Pacific radiolarian oozes and animals in them would suggest mechanical difficulty in ingestion and gut passage by deposit feeders. Perhaps Antarctic shelf sediments in areas of massive siliceous sponges also warrant stratigraphic attention for similar reasons, particularly if the sponges mechanically (by spicules fallen to the sediments) or competitively (by intercepting food for deposit feeders) decrease deposit-feeder activity or abundance.

Enough is known, however, to rule out some possibilities. It might be tempting to try, for example, to use apparently large D_b (or large G observed in a fossil sequence) as an index of paleoproductivity. The HEBBLE observations, however, suggest that the correlation of G is good with secondary productivity at the bed or with horizontal flux just above it but not with overlying water productivity. Interpretation is difficult because physical transport as well as biological mixing contribute to the apparent D_b values measured at the HEBBLE site, but the animal abundances and D_b values are comparable to those seen under much more productive overlying waters (DeMaster et al. 1985).

Surface Traces

Surface trace abundance has been suggested to be an index of animal abundance and hence a potential fossil index of paleoproductivity. To evaluate this suggestion, we recently have developed a model of surface trace concentration (fraction of surface area covered by traces) that demonstrates that at the highest animal abundances trace concentration

should be low; traces can be erased both by epifaunal movement and by horizontal mixing due to infauna (Wheatcroft et al. 1988). Since trace concentration is simply the areal production rate of new traces (ones that do not cover previous traces) times their residence times, there is not a monotonic relationship between animal abundance (surrogate for production further down the food web) and trace abundance.

We also suggest that bioturbation is generally much more intense in the horizontal than in the vertical. Feeding and defecation by surface deposit feeders (typically comprising one-half of all deposit feeders at deep-sea sites) move material horizontally to a far greater extent than it moves material vertically. The same will be true of horizontally burrowing subsurface deposit feeders. It is the horizontal component of bioturbation that is effective in erasing surface traces, and so disappearance rates of traces may be much faster than anticipated from D_b values estimated from vertical mixing of tracers.

Ecotones and Unsteadiness

We have focused implicitly on what occurs within a given community of benthic organisms and on how what goes on differs among benthic communities. It is also worthwhile to consider the edges of communities, the so-called ecotones. Inefficiency of utilization is often associated with rapid change, and productivity changes may also be associated with changes in the borders of high- and low-productivity regimes. Such regions of change often produce the most spectacular evidences of bioturbation, e.g., of exchange between brown clays and calcareous oozes (Nelson 1985). These regions have not been popular sites for estimation of mixing parameters because so many variables change downcore. The very fact that the sediments remain mottled rather than appearing completely mixed, however, gives impetus to further exploration. These sites would also appear to warrant attention from the standpoint of being places where one might expect some inefficiency in processing of sediments by an imperfectly adapted community. In fact, we do not know whether such border regions in the benthos contain "ecotone specialist" species—as is found in the oceanic zooplankton between major water masses—or whether one simply sees a mixture of two neighboring faunas.

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REFERENCES

- Allen, J.A., and Sanders, H.L. 1966. Adaptations to abyssal life as shown by the bivalve *Abra profundorum* (Smith). *Deep-Sea Res.* **13**: 1175–1184.
- Aller, R.C. 1982. The effects of macrobenthos on chemical properties of marine sediment and overlying water. In: *Animal-Sediment Relations*, eds. P.L. McCall and M.J.S. Tevesz, pp.53–102. New York: Plenum.
- Cammen, L.M. 1980. Ingestion rate: an empirical model for aquatic deposit feeders and detritivores. *Oecologia (Berl.)* **44**: 303–310.
- DeMaster, D.J.; McKee, B.A.; Nittrouer, C.A.; Brewster, D.C.; and Biscaye, P.E. 1985. Rates of sediment reworking at the HEBBLE site based on measurements of Th-234, Cs-137 and Pb-210. *Marine Geol.* **66**: 133–148.
- Dworschak, P.C. 1983. The biology of *Upogebia pusilla* (Petagna) (Decapoda, Thalassinidae). 1. The burrows. *P.S.Z.N.I: Marine Ecol.* **4**: 19–43.
- Gooday, A.J. 1988. A response by benthic foraminifera to the deposition of phytodetritus in the deep sea. *Nature* **332**: 441–443.
- Griggs, G.B.; Carey, A.G., Jr.; and Kulm, L.D. 1969. Deep-sea sedimentation and sediment-fauna interaction in Cascadia Channel and on Cascadia Abyssal Plain. *Deep-Sea Res.* **16**: 157–170.
- Guinasso, N.L., Jr., and Schink, D.R. 1975. Quantitative estimates of biological mixing rates in abyssal sediments. *J. Geophys. Res.* **80**: 3032–3043.
- Hessler, R.R., and Jumars, P.A. 1974. Abyssal community analysis from replicate box cores in the central North Pacific. *Deep-Sea Res.* **21**: 185–209.
- Jumars, P.A., and Fauchald, K. 1977. Between-community contrasts in successful polychaete feeding strategies. In: *Ecology of Marine Benthos*, ed. B.C. Coull. Columbia: Univ. South Carolina Press.
- Kristensen, E., and Blackburn, T.H. 1987. The fate of organic carbon and nitrogen in experimental marine sediment systems: influence of bioturbation and anoxia. *J. Marine Res.* **45**: 231–257.
- Lopez, G.R.; Taghon, G.L.; and Levinton, J.S., eds. 1989. *Ecology of Marine Deposit Feeders*. New York: Springer, in press.
- McCall, P.L. 1977. Community patterns and adaptive strategies of the infaunal benthos of Long Island Sound. *J. Marine Res.* **35**: 221–266.
- Miller, D.C.; Jumars, P.A.; and Nowell, A.R.M. 1984. Effects of sediment transport on deposit feeding: scaling arguments. *Limnol. Ocean.* **29**: 1202–1217.
- Nelson, C.S. 1985. Bioturbation in middle bathyal, Cenozoic nannofossil oozes and chalks, southwest Pacific. In: *Initial Reports of the Deep Sea Drilling Project*, eds. J.P. Kennett and C.C. von der Borch, vol. 90, pp.1189–1200. Washington: US Govt. Printing Office.
- Nowell, A.R.M.; Jumars, P.A.; and Fauchald, K. 1984. The foraging strategy of a subtidal and deep-sea deposit feeder. *Limnol. Ocean.* **29**: 645–649.
- Odum, E.P. 1969. The strategy of ecosystem development. *Science* **164**: 262–270.
- Pearson, T.H., and Rosenberg, R. 1978. Macrobenthic succession in relation to organic enrichment and pollution of the marine environment. *Ocean. Mar. Biol. Ann. Rev.* **16**: 229–311.
- Penry, D.L., and Jumars, P.A. 1987. Modeling animal guts as chemical reactors. *Am. Natural.* **129**: 69–96.
- Schiffelbein, P. 1984. Effect of benthic mixing on the information content of deep-sea stratigraphic signals. *Nature* **311**: 651–653.
- Schindel, D.E. 1980. Microstratigraphic sampling and the limits of paleontologic resolution. *Paleobiol.* **6**: 408–426.

- Schwinghamer, P. 1985. Observations on size-structure and pelagic coupling of some shelf and abyssal benthic communities. In: Proceedings of the 19th European Marine Biology Symposium, Plymouth, Devon, UK, 16–21 September 1984, ed. P.E. Gibbs, pp. 347–359. Cambridge: Cambridge Univ. Press.
- Sebens, K.P. 1987. The ecology of indeterminate growth in animals. *Ann. Rev. Ecol. Syst.* **18**: 371–408.
- Sibly, R.M. 1981. Strategies of digestion and defecation. In: Physiological Ecology: An Evolutionary Approach to Resource Use, eds. C.R. Townsend and P. Calow, pp.109–139. Sunderland, MA: Sinauer.
- Smith, C.R.; Jumars, P.A.; and DeMaster, D.J. 1986. *In situ* studies of megafaunal mounds indicate rapid sediment turnover and community response at the deep-sea floor. *Nature* **323**: 251–253.
- Sorensen, J.; Jorgensen, K.S.; Colley, S.; Hydes, D.J.; Thomson, J.; and Wilson, T.R.S. 1987. Depth localization of denitrification in a deep-sea sediment from the Madeira Abyssal Plain. *Limnol. Ocean.* **32**: 758–762.
- Taghon, G.L. 1988. The benefits and costs of deposit feeding in the polychaete *Abarenicola pacifica*. *Limnol. Ocean.* **33**, in press.
- Taghon, G.L., and Jumars, P.A. 1984. Variable ingestion rate and its role in optimal foraging behavior of marine deposit feeders. *Ecology* **65**: 549–558.
- Tenore, K.R.; Hanson, R.B.; McClain, J.; Maccubbin, A.E.; and Hodson, R.E. 1984. Changes in composition and nutritional value to a benthic deposit feeder of decomposing detritus pools. *Bull. Mar. Sci.* **35**: 299–311.
- Thistle, D.; Yingst, J.Y.; and Fauchald, K. 1985. A deep-sea benthic community exposed to strong near-bottom currents on the Scotian Rise (western Atlantic). *Marine Geol.* **66**: 91–112.
- Trevor, J.H. 1978. The dynamics and mechanical energy expenditure of the polychaetes *Nephtys cirrosa*, *Nereis diversicolor*, and *Arenicola marina* during burrowing. *Est. Coast. Shelf Sci.* **6**: 605–619.
- Tyler, P.A. 1986. Studies of a benthic time series: reproductive biology of benthic invertebrates in the Rockall Trough. *Proc. Roy. Soc. Edinb.* **88B**: 175–190.
- Wheatcroft, R.A.; Smith, C.R.; and Jumars, P.A. 1988. Dynamics of surficial trace assemblages in the deep sea. *Deep-Sea Res.*

