PHILOSOPHICAL TRANSACTIONS OF THE ROYAL SOCIETY A MATHEMATICAL, PHYSICAL & ENGINEERING SCIENCES

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Deep-sea deposit-feeding strategies suggested by environmental and feeding constraints

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[Plate 1]

The principle of lost opportunity from optimal foraging theory, coupled with recent information about fluxes in the deep sea, allows prediction of feeding behaviours potentially specific to deep-sea deposit feeders. One possible strategy, thus far documented only indirectly, is to 'squirrel' away rich food from the seasonal or episodic pulses that recently have been shown to fuel meiofaunal growth. Echiurans and sipunculids show morphological and faecal handling patterns consonant with this suggestion. Where it is prevalent, this foraging strategy can have profound effects on stratigraphy. Autocoprophagy is another expected behaviour across a wider taxonomic spectrum, but one that is especially difficult to document.

The principle of lost opportunity also predicts highly selective ingestion, not necessarily accomplished by the assessment of individual particles but possibly through pit building in areas where fluids move near-bed material. Under many depositional régimes, small but abundant feeding depressions may be the primary sites where deposition occurs. Conversely, digestive utilization of heterogeneous refractory substrates like humic acids seems as unlikely as an effective municipal waste recycling system that starts with mixed garbage. High gut:body volume ratios in deep-sea deposit feeders, rather than representing an adaptation to use this heterogeneous and refractory end of the food spectrum, instead may allow (through greater residence time of ingested material) greater conversion and absorption of the labile fraction of sediments as it becomes scarcer. Intense natural selection for particle selection ability in fact is one possible reason for the prevalence of meiofauna in the deep sea, and for the diminutive size of macrofaunal taxa there. This selective pressure probably imposes a very restrictive bottleneck on the initial developmental stages of deposit feeders.

Introduction

Most of the 70% of the globe that is covered with seawater is underlain by fine-grained sediments that are food for deposit feeders. Most of that sediment-covered sea floor, in turn, is in the deep sea. Virtually all sediment grains pass through the guts of deposit feeders, usually many times, before they are buried as part of the geologic record. These feeding activities place limits on the resolution that can be gained from that record. In feeding and burrowing, deposit feeders can grossly alter the erodibility of the uppermost 10 cm of sediments (Rhoads & Young 1970). In pumping water through their open tubes and burrows for respiratory exchange, deposit feeders change spatial patterns of pore-water solute concentrations within sediments and enhance rates of exchange of dissolved chemicals between sediments and overlying waters. Pollutants that reach the sea bed usually arrive in particulate form or tightly adsorbed to particles. Whether they stay in the sea bed, enter food chains, or are released into the overlying water depends in large measure upon the activities of deposit feeders.

Thus there is abundant need to know about deposit feeders in general and deep-sea deposit feeders in particular. For logistical reasons, this need has been met to date primarily by direct observation of shallow-water deposit feeders and the drawing of analogies (hopeful homologies) between directly observed intertidal species and their deep-sea relations. This approach is a spatial analogue of the geological principle of uniformitarianism. It continues to be valuable, but we believe that knowledge of the environment of deep-sea deposit feeders and the capabilities of foraging theory have advanced to the point where a new approach can complement this traditional one. Namely, we combine foraging theory with features of the deep-sea environment to predict deposit-feeding behaviours that might be unique to the deep sea. We then look for evidence in the literature that such behaviours may be realized. The workhorse of our theoretical efforts is the principle of lost opportunity (Stephens & Krebs 1986). The idea is a simple one, yet it underlies most of the counter-intuitive results achieved with foraging theory. Namely, an animal should not engage in an activity (e.g. ingest a particular kind of food) if doing so is likely on average to prevent it from engaging in another activity (ingesting a better item) that will return more calories or moles of limiting nutrient per unit of time. It perhaps is not surprising, because of the special environmental conditions of the deep sea, that this exercise predicts deep-sea behaviours that have not been observed in the intertidal. What convinces us that the exercise is even more worthwhile, however, is that the approach also predicts new behaviours to be expected of shallow-water deposit feeders and allows new interpretations of previously observed behaviours in various environments.

Pulses of food to the deep sea

The easiest place to start with this exercise is with the most remarkable recent changes in understanding of the food environment of the deep sea. The concept of a steady drizzle of more or less refractory leavings of the water column has had superimposed upon it episodic 'downpours' or windfalls of highly labile material that find short circuits to the bottom (Deuser *et al.* 1981; Billett *et al.* 1983). Bacterial, microfaunal and meiofaunal populations respond to these pulses (Lochte & Turley 1988; Turley *et al.* 1988; Gooday 1988 respectively), and total community metabolism shows seasonal variations very much in phase with surface-ocean productivity (Smith & Baldwin 1984).

If it is true that the majority of usable food for deposit feeders arrives in such pulses of labile matter and that otherwise food is scarce, one might expect to see means of sequestering the windfalls. Caching would appear to be the simplest of such means, but where or how can material be sequestered from other heterotrophs? By far the majority of heterotrophs are concentrated near the sediment surface, so one means would be to bury the cache below the sediment–water interface. This strategy should also be of interest because the associated sedimentary structures – removed from the zone of greatest bioturbation – should be preserved preferentially in the fossil record. Another, not necessarily independent, means would be to modify the material so as to make it physically unavailable or chemically repellent.

There is evidence of caching. Sipunculids at abyssal depths in the Atlantic appear to be abundant and active enough to produce subsurface maxima of the most recently arriving materials (Smith *et al.* 1986), i.e. those carrying the greatest activity of short-lived radionuclides.

If it were not for caching of the most recent and most radioactive material, one would expect such reverse conveyor-belt feeding to be more diffusive in its effects of radionuclides. Some echiurans, although they too probably draw most of their food from the surface, show an apparently different means of hoarding. They package recently egested material in large (*ca.* 1 mm diameter) faecal pellets and store it as either burrow linings (Kershaw *et al.* 1984; P. A. Jumars, personal observation) or as surface and subsurface piles of material (Smith *et al.* 1986*a*), possibly returning to them episodically, presumably to feed upon the renewed or stockpiled resource. Additional indirect evidence for downward transport of faecal material comes from extensive photographic studies of several species of deep-sea echiurans (Ohta 1984) that never show their faecal pellets on the sediment surface. This piling and unpiling of recently deposited material or burrow lining with newly arriving material wreaks havoc with local radionuclide profiles (Kershaw *et al.* 1984; Smith *et al.* 1986*a*). It is not known whether size of the pellets alone, or chemical content as well, inhibits use of the resource by other animals. In both sipunculids and echiurans, nitrogenous wastes are excreted where they could be utilized by faecal symbionts; in sipunculids the nephridia open very close to the anus, while echiurans have nephridia like those of sipunculids plus nitrogenous waste excretion directly into anal sacs that connect to the rectum. X-radiographs (for example, figure 1, plate 1) demonstrate what may be caching by sipunculids. It is tempting to speculate that the anal sacs of echiurans provide either an antibiotic or a specific microbial inoculum to their faecal pellets. It is also tempting to speculate that the ichnogenus *Zoophycos* represents this same sort of faecal caching strategy (Kotake 1989).

There may be some economy of scale in hoarding; the sipunculids and echiurans responsible for these alterations of the more normal stratigraphic sequence are among the largest infaunal deposit feeders observed at the depths where they occur. At the northeast Atlantic sites (4000–5000 m depth; 45–47° N, 16–18° W), where radionuclide data suggest caching, sipunculids are biomass dominants containing over one-half of the total biomass collected in cores (Smith *et al.* 1986*b*). We predict that sipunculids and echiurans will be found to be far less dominant where blooms are less prevalent, such as under the subarctic Pacific.

Although restriction of inputs of good food to pulses should select for hoarding in long-lived animals, caching of labile foods is not the only possible hypothesis to account for subsurface peaks of high radionuclide activity and young organic matter. Structural carbohydrates from land and nearshore plants and chitin from insects and zooplankton contain considerable chemical energy that can be released microbially. It is difficult to account for the distance of transport or fate of terrestrial and nearshore inputs, but not less than 20% of the organic carbon buried in deep-sea sediments is now thought to be land derived (Prahl & Muehlhausen 1989). Use of macrophytic debris by deep-sea animals (Suchanek *et al.* 1985) and burial of macrophytic debris in biotubated deep-sea sediments (Reichardt 1987) are documented, but no evidence of a link to caching has been presented. Despite assertions (Reichardt 1987) that ‘gardening’ is well documented for shallow-water species, in no case has the adornment of tubes by algae or stimulation of bacterial activity around animal burrows been shown to be of any energetic importance to a marine animal. Gardening thus remains an undocumented notion.

A contrasting means of sequestering labile material is by rapid assimilation and population growth. This strategy is clearly most effective for small organisms with growth rates rapid enough to achieve population growth before all the labile material is gone, i.e. k/r must be sufficiently small that the newly arrived organics are not all gone by the time that population growth begins (where k is the first-order degradation constant and r is the first-order population growth constant). To date this strategy is documented only for organisms of meiofaunal size and smaller (Gooday 1988; Lochte & Turley 1988; Turley *et al.* 1988). An estimate of 10 per year for k of the labile fraction (Reimers 1989) appears compatible with meiofaunal population growth responses. A hidden but perhaps even more important advantage is the macrophagous nature of these small organisms. (A macrophage generally eats food items one at a time, and is usually no more than about two orders of magnitude (equivalent spherical diameter) larger than its food items; microphages usually handle more than one food item at a time and are much larger than their prey.) By virtue of their sizes relative to newly arriving food particles, macrophages presumably are able to ingest these particles far more selectively than can larger, microphagous deposit feeders. A further advantage of most meiofauna is that they are motile; by allowing access to a wider spatial range of resources, greater motility allows greater selectivity as well.

Deposit feeders by definition ingest material of low bulk food value and are constrained by this strategy to feed at very rapid rates. For example, shallow-water lugworms ingest 10^2 times their ash-free dry weights of sediments per day (Taghon 1988). The principle of lost opportunity explains the apparent paradox. Selectivity based on evaluation of individual food particles takes time, and deposit feeders must lose more mass or energy by expending the effort to select than they would gain from avoiding the ingestion of inert material. By selecting individual particles, the opportunity to process sediment at a high volumetric rate is lost. A necessary corollary is that this high rate of processing must, when averaged over a generation time (the natural period for fitness arguments) return some dividend that meiofaunal macrophagy does not. Otherwise, evolution would drive deposit feeders to retain their small juvenile sizes so as to retain an ability to be both motile and macrophagous. Mechanically selective means that do not require evaluation of individual particles allow some selection to occur without major slowing of ingestion rates. Adhesive mechanisms, for example, allow rapid collection of small particles of low bulk density (Khripounoff & Sibuet 1980; Jumars *et al.* 1982; McKenzie 1987; Self & Jumars 1988).

The evidence that common deposit feeders of intermediate size (between echiurans and meiofauna, i.e. macro-infauna) can sequester pulses of sedimenting organic matter effectively is circumstantial and not yet convincing. Surface deposit feeders are known to contain large amounts of pigments soon after a settling event (Christensen & Kanneworff 1985), but it would be hard for surface deposit feeders to avoid this pattern even if they did not utilize the newly fallen material as their dominant source of food. An open question is whether they can reach and sequester any significant amount of the recent fall during $1/k$ (*ca.* one month), where k characterizes the labile components to which meiofauna are known to respond, or whether they benefit more and over a longer period of accrual from components with slower kinetics of degradation. Good evidence for utilization of the labile or refractory components could come from the content of body storage products (lipids) against time over the interval after against just before an event. It seems highly unlikely that fresh, intact phytoplankton settling to the sea floor would be either selected against or pass undigested. The relevant and unresolved issue for macrofaunal surface deposit feeders is whether these labile pulses are dominant, less important but still significant, or unimportant sources of the matter and energy shunted into production of this group of animals.

FIGURE 1. X-radiograph of a sipunculid in its burrow from 90 m water depth under the northern California upwelling régime (0.25 m^2 box core taken 21 April 1985 on a cruise of the R.V. *Thomas G. Thompson* near 38° 50′ N, 123° 40′ W); the X-ray dense material inside the animal is sediment in its gut. The centre of the animal is approximately 20 cm beneath the sediment–water interface, and the comparatively X-ray transparent material surrounding the animal is a suggested cache. (Scale bar = 2 cm.)

Mobile megafauna do appear to have substantial advantages over more sedentary macrofauna in utilizing fallen detritus when sediment transport is weak. Epibenthic, deep-sea holothuroids (Billett *et al.* 1988) show degradation of labile plant pigments during gut passage. When the detrital fall more or less uniformly covers the sea bed, its composition and that of holothuroid foregut contents match. When cover of the sea bed by newly fallen detritus is patchy, epibenthic holothuroids are effective at feeding from the patches of new detritus (Billett *et al.* 1988).

The notion that deposit feeders will not ingest their own faeces until some time has passed for microbial growth obscures several issues. Although this generalization may well be true for animals under steady food supply, it does not hold under unsteady conditions. *Eogammarus confervicolus*, an omnivorous amphipod, and *Pseudopolydora kempi japonica*, a deposit-feeding polychaete, routinely ingest faeces immediately upon defaecation when switched from a rich food resource to a poor one (P. A. Jumars and R. F. L. Self, personal observations). Re-ingestion as opposed to the alternative solution of longer retention probably is favoured by limited ability to change gut digestion or absorption kinetics on a short timescale (Dade *et al.* 1990) or by rapid growth of bacteria in the hindgut. Such rapid growth has now been documented in deposit feeders from both the deep sea (Deming *et al.* 1981; Deming & Colwell 1982) and shallow water (Plante *et al.* 1989). Lampitt & Billett (1988) have observed selectived feeding by *Echinus affinis* on holothuroid faecal material. Alternatively, re-ingestion may be due to limited ability to recognize that conditions have changed, with the egested material simply being of higher food quality than the new ambient level (see, for example, Khripounoff & Sibuet 1980). In any of these cases, however, deposit-feeder faecal pellets after an influx of high-quality material may still represent an important food resource for deposit feeders and other heterotrophs.

This line of reasoning immediately drives reassessment of metazoan feeding strategies in the most food-poor benthic regions, the red clays under mid-ocean gyres. Because of an interest in diversity, Hessler & Jumars (1974) distinguished those taxa that are normally members of the macrofauna in shallow water as 'macrofaunal taxa.' Although this distinction is useful for issues of species diversity within major taxa, it tends to obscure the fact that the overwhelming majority of individuals collected at their central North Pacific sampling site are meiofaunal in size. They also are motile (Jumars & Fauchald 1977). Hence we conclude that deposit feeding as commonly defined, i.e. the frequent ingestion of material of low bulk food value (Jumars *et al.* 1984; Lopez & Levinton 1987) may not be prevalent at this site. This tentative conclusion needs to be tested; the fact that dead specimens contain some clay particles is insufficient to discard it, for nearly any mode of ingestion is likely to take some of these tiny particles with it. Increasingly selective feeding with reduced food supply in the deep sea is supported by the observations of Allen & Sanders (1973), who found relative enlargement of feeding palps in protobranchs with diminished body size and, at least in one case, gut contents composed primarily of diatom remains. We suggest that these animals are verging on macrophagy, wherein each potential food particle is evaluated before ingestion. The reward for small body size must be phenomenal to repay some of the risks taken by evolution to achieve it. Individuals of some deep-sea protobranch bivalve species are so small as adults (not greater than 1 mm in maximal length) that only a single egg can be extruded at a time (Sanders & Allen 1973).

This line of reasoning also leads to questions and potential answers concerning diets during ontogeny of those deep-sea animals that are bona fide deposit feeders as adults. It also suggests the potential advantages that deposit feeders might have over macrophages. The larger body size of bona fide deposit feeders allows a greater gut volume than can be achieved in meiofauna. Across closely related species pairs, deep-sea species have comparatively more gut volume than their shallow-water relatives (Allen & Sanders 1966; Penry & Jumars 1990). Penry & Jumars (1990) found that deposit-feeder gut volume for both deep-sea and shallow-water deposit feeders increases roughly linearly with body volume. Ingestion rate increases less steeply with body volume; across species Cammen (1980) found that ingestion rate increases as body mass to a power of 0.7. Because (assuming insufficient digestion and absorption to affect volume) gut residence time is gut volume divided by ingestion rate, gut residence time thus increases with body volume. Across species of deposit feeders, smaller ones tend to be more selective (Self & Jumars 1988). This pattern is seen in many other groups of animals that feed on low-quality forage (for example, Sibly 1981), and the usual interpretation is that there is not enough of the higher-quality material to fuel bigger individuals. We suggest instead that smaller animals are constrained to eat more labile foods.

There are clear breaks, for example, in the allometric ratios of egestion rates (which roughly equal ingestion rates) to body volumes during ontogeny of *Capitella* (Forbes 1989), with the youngest post-settlement juveniles departing most radically from Cammen's (1980) generalization. Up to a capitellid body volume of 1.72 mm^3, Forbes (1989) finds that ingestion rate increases with body volume to a power of 1.2; above that body volume ingestion scales as body volume to a power of 0.8, much closer to the general trend found by Cammen among species. Other lines of evidence also suggest that juvenile and adult food resources may differ for deposit feeders. There is strong evidence of competition between intertidal oligochaetes and juvenile ampharetid polychaetes for diatoms (Gallagher *et al.* 1990). Digestion theory (Penry & Jumars 1987) suggests that these patterns will be general, i.e. that small juveniles of deposit-feeding adults will be found to be macrophagous specialists on labile foods. To achieve significant gains, residence time of material in an animal's gut must match digestive and absorptive kinetics (Dade *et al.* 1990). As residence time and gut volume determine ingestion rate, small gut volume therefore coincides with selective pressure toward specialization on foods that can return high digestive dividends rapidly (figure 2). Major dietary changes during ontogeny are thus likely for subsurface deposit feeders and for 'caching' species.

An interesting ontogenetic question for deposit feeders is whether the food resource that is digested and absorbed changes with animal size and increasing gut residence time. Longer gut residence time may simply allow greater digestion and absorption of the same food resource (cf. fig. 3*b* of Penry & Jumars 1986), or it may in addition allow digestion and absorption of material that inherently is more refractory and takes longer to digest. In the former case, the poorer food of larger individuals is simply more dilute, whereas in the latter case it is of a broader range of chemical compositions. We suggest that the latter case might be more important in shallow water than in the deep sea, because shallow-water sediment concentrations of non-living materials with intermediate decomposition rates are higher than they are in deep-sea sediments (Rice & Rhoads 1989). Phrased alternatively, we suspect that living components dominate deep-sea deposit-feeder diets (absorbed materials) to a greater extent than in shallow water. This potential for added gain must, however, be balanced against the higher overall humic contents of shallow-water sediments, which lower the efficiencies of hydrolytic enzymes (L. M. Mayer, unpublished data).

We suggest that the uncomfortable transition between macrophagy and microphagy as

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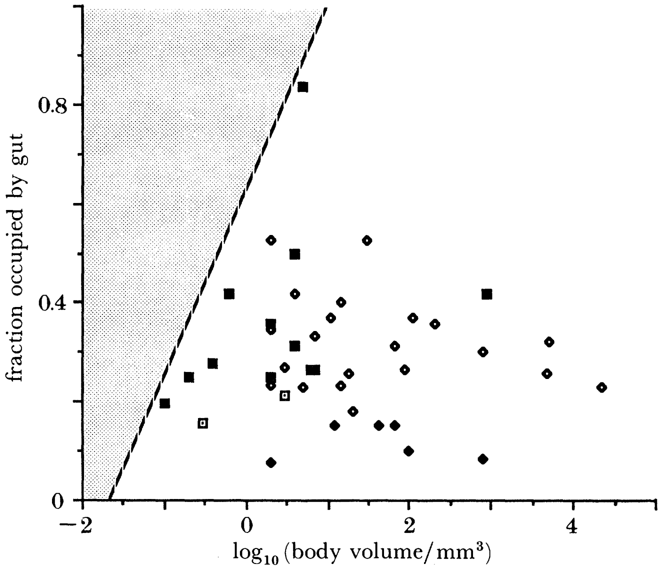

Figure 2. Body volume against proportion of the body volume occupied by the gut in a range of polychaetes from deep-sea and shallow-water sediments (drawn from table 3 of Penry & Jumars 1990). Here we suggest that the absence of deposit feeders from the shaded region may indicate a limit that small gut volume places on volumetric processing rate and hence on residence time of material. The kinetic constraints of small guts are likely to lead to highly selective ingestion, i.e. to macrophagy, and thus to replacement of deposit feeders by macrophagous meiofauna. ⊡, deep-sea carnivore; ◆, shallow-water carnivore; ■, deep-sea deposit feeder; ◇, shallow-water deposit feeder.

deposit- (and perhaps suspension-) feeding animals mature coincides with the minimum in biomass and species abundance seen at body sizes of about 1 mm (equivalent spherical diameter) at most benthic sites (Warwick 1984; Schwinghamer 1985). Getting through this bottleneck, then, might again depend upon windfalls of labile material. To the extent that such windfalls are unpredictable, they might explain the frequent observation among deep-sea populations of a few mature ova present in some population members at any time (see, for example, Rokop 1974) and the even more general observation of few juveniles present on average at any time (Grassle & Sanders 1973). If juvenile survival is highly variable, then it is advantageous to spend more time as an adult and to have many reproductive events with little energy (few offspring) invested in each (Schaffer & Gadgil 1975). An alternative labile food resource that also deserves exploration as a means of passing this suggested bottleneck in the deep sea is the comparatively high standing stock of benthic foraminiferans found there (see, for example, Gooday 1986).

The importance of particle transport

Despite the recent revelation of active sediment transport in the deep sea (Nowell & Hollister 1985), the importance of horizontal physical transport to deposit feeders remains grossly underrated. One reason is that people visualize a rain of particles, whereas windblown snow or cottonwood fluff would provide a more accurate impression. Almost anywhere in the world ocean the typical particle arriving at the sea floor has a greater horizontal than vertical velocity. Nowhere in the deep ocean have currents been found to be constant. Particles landing under one set of conditions may be resuspended or rolled along the seabed under others (Lampitt 1985). Some of us have had the opportunity repeatedly to revisit Santa Catalina Basin at a depth of 1200 m in the southern California continental borderland. It is a common 'test basin' for deep-sea ideas and equipment, and extensive current observations reveal no flows of sufficient magnitude to be considered erosive by geologists. Yet in six out of 19 dives spread over four years, observers on our *Alvin-Atlantis II* cruises noted aggregates of surface fluff rolling in tumbleweed fashion along the sea bed during at least parts of the 6–8 h (bottom time) dives.

Horizontal transport favours particular species well adapted to catching newly deposited material or to inducing material to deposit, but it would not at first appear possible for horizontal transport greatly to enhance overall community standing stocks or production. There are well known patterns of animal abundance with depth, and they appear in general to be well correlated with vertical flux of organic matter (Tietjen *et al.* 1990). In the area of the Scotian rise influenced by strong bottom currents, however, both bacterial and animal abundances are anomalously high (Thistle *et al.* 1985). The reason is not clear. Epifaunal predators may be reduced in abundance, allowing other animals to proliferate, but this explanation fails to reach the bacterial level. Alternatively, abundances may be high because physical transport removes the need for expenditure of organisms' own energy stores in finding and gathering food. This argument is extended if transport events also significantly enhance the supply of oxidants to sedimentary organic matter; oxic metabolism yields more energy per mole of organic matter mineralized. Further, the food budget for this Scotian rise may get both its normal (for this water depth of about 4600 m) vertical flux of food and a subsidy via near-bed horizontal transport from adjacent regions. The finding of Tietjen *et al.* (1990), that meiofaunal abundance correlates better with near-bottom sediment-trap fluxes than with higher sediment-trap catches unaffected by resuspension, underscores the importance of redistribution.

Sedimentary geologists care most about flows that are sufficient to cause large net horizontal transport over kilometre and greater spatial scales and over periods important to a net deposition budget. They care little about the movement of organic particles that will not remain in the sedimentary record. Surface deposit feeders have a much different perspective (Miller *et al.* 1984). The benefits to deposit feeders of specializing on newly depositing and transporting material are many. It tends to be material of low bulk density, which correlates very well with high food quality (Mayer 1989). Deposit feeders have mechanical means (Jumars *et al.* 1982; Self & Jumars 1988) of selecting this low-density (grams per cubic centimetre) material without evaluating individual grains and thus without slowing their processing rates. Simple devices are effective at enhancing capture. Shallow feeding pits (see, for example, Nowell *et al.* 1984; Mauviel *et al.* 1987) capture essentially all the material in bedload transport and under deep-sea conditions roughly double local deposition rates of material from suspension (Yager *et al.* 1990). Conversely, if sediment transport is infrequent yet food arrives in pulses, mobile epifauna capable of gathering it may be favoured (Khripounoff & Sibuet 1980). The mobility and gut capacity of large epifauna may be reasons for the clear functional separation of megafauna and macrofauna (Lampitt *et al.* 1986).

The absurdity of coupling individual feeding rates tightly with regional net deposition rates even for sedentary fauna is seen by examining the feeding geometry of a surface deposit feeder. A contained gut volume of 1 mm^3 (cf. Penry & Jumars 1990) and a foraging radius of order 1 cm (judged from personal observations (P.A.J.) of tentacle length of living and dead deep-sea specimens) are not unusual for a bathyal deposit feeder. Net sedimentation rates are roughly 1 cm ka^{-1}. Feeding once on each permanently deposited particle would imply a gut residence time of 0.3 years! While there are few published values, a more realistic figure for gut residence time in deep-sea species is two orders of magnitude less (Rowe 1974; Deming & Colwell 1982; Penry 1990; M. Sibuet, personal communication). Mineral grains are re-ingested many times, either incidentally because of their presence in organic aggregates, because of imperfections in the mechanically selective devices used by deposit feeders (Self & Jumars 1988), or because the resources on those mineral grains are renewed. Organic particles that do not survive to constitute a net sedimentation rate are ingested with or in preference to them.

Surface deposit-feeding animals that extend feeding appendages from a more or less permanent tube or burrow are major community components at all depths in the ocean except where sediment transport is so severe (e.g. exposed beaches) as to make burrows impermanent. The only known exception (Jumars & Fauchald 1977) in the deep sea is the region underlying central gyres, where it seems that few if any animals can make a living on the resources they can reach from one tube or burrow; motility is the rule, and deposit feeding may be exceptional.

Perhaps the reason that the importance of sediment transport to the day-to-day life of deposit feeders is not more obvious to people is that subaerial sediment transport is so ineffectual in moving food-rich particles. Given the excess density and water surface tension that hold food-rich terrestrial particles down and the vegetation that keeps wind forces from reaching the soil–air interface, the entire guild of surface deposit feeders that sit still and feed on transported particles within reach is missing. The closest analogue is in the form of earthworms that drag down leaves by night.

Surface deposit feeders in the sea are a harmless guild as far as stratigraphers are concerned. They move material mostly horizontally (Wheatcroft *et al.* 1990). In fact, their horizontal redistribution of material may be the major reason why vertical movement of sediments by subsurface deposit feeders does not greatly complicate stratigraphy over small horizontal distances (Wheatcroft *et al.* 1990). They are probably a major reason, however, for the geochemical fact that a substantial amount of the bottom-arriving flux of organic carbon cannot be found in the sediments. If deposit feeders of ordinary size can make use of windfalls of labile material, it is surface deposit feeders that do so. Typically one-half the macrofaunal individuals at deep-sea sites are thought to be surface deposit feeders (Jumars & Gallagher 1982). Based upon our arguments concerning their dependence upon particle transport, however, one might expect both their biomasses and productivities to vary with the local extent of horizontal particle transport. Horizontal particle transport, whether by deposit feeders or by currents, also makes it quite unlikely that a given particle laid on the sediment surface by a conveyor-belt species will be subducted back into its own feeding pocket. Anything but extraordinarily rapid subduction (relative to the characteristic dispersion time from geophysical and biological transport in the horizontal), then draws down material of average surficial composition rather than material previously ingested by the subducting individual. Thus physical or biogenous sediment transport is important for subsurface as well as surface deposit feeders.

Subsurface deposit feeding

Just how important horizontal transport may be to subsurface deposit feeders may be indicated by the absence of terrestrial analogues of head-down or conveyor-belt species that spend a good deal of time feeding in one place (e.g. molpadiid holothuroids or some maldanid polychaetes). What is known about marine subsurface deposit feeding is perhaps best summarized, however, by the cliché 'out of sight, out of mind.' The observational problem is very real. Sediments scatter acoustic energy so well that resolution of individual subsurface deposit feeders *in situ* is not yet practical. As a consequence, most of what is known about the behaviour of individual subsurface deposit feeders comes from 'ant farms,' thin aquaria through which direct visual observation is possible, from X-radiography of slabs of material that are not much thicker, or from less direct analysis of traces (e.g. after making resin casts of burrows). Students of biology perhaps have been too shy of γ-ray methodologies.

Incentive to learn is reduced by the fact that one easily can be lulled into complacency by assuming that a great deal is known about earthworms and that marine subsurface deposit feeders are not very different. Both assumptions are false. Most research on the ecological functioning of earthworms has not dealt with individuals. Rather it has focused on measurements that do not require direct observation, e.g. production of earthworms over a given area of soil when supplemented or not by a given organic material (Satchell 1983). It has long been known that earthworms tend to be most active under rocks, leading to burial of the latter (Darwin 1881). The reason is that many invertebrates (and heterotrophic processes in general) in soils are rate limited by the supply of water. Activities of marine organisms certainly are not rate limited by the availability of water, and mixing may be more intense away from under rocks, actually buoying them up (Sanderson 1985).

Nor do the differences end with the availability of water. On land and in small bodies of fresh water, the dominant input of organic matter is as phosphorus- and nitrogen-poor (because of resorption before leaf abscision and the chemical structure of the remaining parts) particles too large and chemically refractory for most invertebrates to eat. Because of this fact, and the issue of water availability, it is not surprising that detritivore activities peak downstream (fresh water) or below the surface (soil) of litter inputs.

Virtually by definition, marine subsurface deposit feeders in régimes of slow and steady deposition also must subsist on relatively refractory material, i.e. on material that has not been remineralized by the time it reaches the feeding horizon of the animal. Phytoplanktonic production, however, entails little manufacture of refractory structural carbohydrates. What is the refractory material that deposit feeders get and how does it become available for their assimilation? The pat answer is 'humic substances', but their definition is so vague as to be practically useless. Further, one sees terrestrial plant fragments at all nearshore depths; their reliable arrival, even in the deep sea, is shown by the adaptation of hadal species to live on this substrate and substratum (see, for example, Wolff 1979). The percent contribution of terrestrially derived matter to carbon burial rates far from land is surprisingly poorly constrained even in the mid ocean (Prahl & Muehlhausen 1989), and there is some evidence to indicate that bioturbation progressed to deeper sediment depths as land plants evolved (Seilacher 1978; Larson & Rhoads 1983). For a truly sessile animal, the only alternatives – under steady, slow sedimentation – to using refractory material would be some sort of short circuit whereby surficial material gets subducted (e.g. by subsurface feeding in one place long enough (Rice & Rhoads 1989)) or chemoautotrophic production provides the supply.

Regions of grossly unsteady sedimentation are often avoided for study because of complex stratigraphy, but there is reason to think that deposit feeders in turbidites are the best understood deposit feeders in the deep sea. Turbidites can bury labile material. This buried organic treasure is available to metazoans large enough to burrow to it and pipe in their own oxygen supply. Thalassinid shrimps and other deep burrowers (e.g. some opheliid polychaetes) appear able to locate and use these rich seams of material (Griggs *et al.* 1969). The extent to, and frequency with, which episodic burial of labile material occurs to depths below those accessible by smaller aerobic metazoans, however, is uncertain for much of the sea floor.

Again, almost by definition, it is highly unlikely that deep-sea deposit feeders can digest refractory organics directly. For lack of a better guess, assume a one day residence time of material in the gut of a subsurface deposit feeder. That interval certainly is long enough for efficient digestion and assimilation of bacterial matter, but would not seem to allow significant digestion of any but the most labile materials that have been characterized geochemically with a first-order rate constant (Reimers 1989), even after one considers that reactions may be rapid during part of the time over which this mean geochemical rate constant is calculated.

One path used by terrestrial invertebrates to gain matter and energy from otherwise refractory organics (i.e. cellulose) on similar timescales is microbial fermentation. That path would appear closed as a means to obtain food in deep-sea, subsurface deposit feeders, with the possible exceptions of chitin and cellulose digestion. It might be more practical for a mobile surface deposit feeder that could concentrate recently deposited chitin, for example (Deming 1985). Fermentation as a major source of food is open to terrestrial animals because one or a few enzymes secreted by their symbiotic microbes are sufficient to digest cellulose, and cellulose is abundantly available in relatively pure form. Fermenters so far identified in the sea similarly have sources of macroalgal (Fong & Mann 1980) or angiosperm (Foulds & Mann 1978) detritus of relatively uniform chemical structure. It seems unreasonable to expect marine deposit feeders to be able to use fermentation to obtain significant nutrition from humic matter; it is inconceivable that the poorly identified organics lumped as humic substances could be digested with any small suite of enzymes (Mayer 1989). The possible importance of fermentation as a source of food is difficult to discount entirely, however, because of the potentially subtle interactions of microbial consortia (see, for example, Tomel *et al.* 1985).

Fermentation may occur quite frequently in the hindguts of deposit feeders, and rapid microbial growth in animal hindguts (Plante *et al.* 1989) will drive down oxygen tensions. It may be very important for geochemical transformations without being important as a major source of food to the deposit feeder in which it occurs. Hindgut fermentation with passive absorption of volatile fatty acids may, in addition, be a fairly general means of recovering some of the material lost by constant, rapid turnover of midgut tissues (Plante *et al.* 1990).

The gutless individuals that use internal symbionts at hydrothermal vents and cold seeps suggest another deposit-feeding ploy than simply eating resident subsurface bacteria at their normal (unknown) growth rates. That diffusion rates of reductants in sediments remote from hydrothermal activity can be sufficient to fuel analogous feeding mechanisms where redox gradients are steep is substantiated in the shallow-water bivalve *Solemya*, for example (Cavanaugh 1985). There is a point of interest in these obligate symbioses for potential application to subsurface deposit feeding. Namely, the microbial members of the symbioses are species that in the body of the invertebrate obtain reductant–oxidant pairs that are usually not available in the classical sequence of oxidants and reductants used by bacteria in animal-free sediments (see, for example, fig. 1a of Aller 1982). The presumed advantage to the microbe and animal symbiosis is that a stronger oxidant yields more moles of adenine triphosphate (ATP) per mole of reductant.

There thus is every reason to expect that provision of stronger oxidants will, under some conditions, enhance bacterial growth externally. The existence of the internal symbioses demonstrates that a relatively small volume can contain sufficient bacteria to sustain the animal, and the needed volume of microbes is much reduced if they are not treated as a renewable resource. It is at this point that we refine or depart from the classic if poorly documented idea of microbial gardening in deposit feeders (Hylleberg 1975; Dobbs & Whitlatch 1982). Flash cooking might be a more accurate analogy. The undigested resource (sediment particles plus other remains in faeces) is not likely to return to the same individual, and the process is an inherently unsteady one not easily evaluated with typical microbiological or geochemical methods.

For some period (since the last subsurface deposit feeding event), a volume of sediments remains anoxic, inaccessible to most small metazoans. Suddenly it is approached by a deposit feeder pumping oxygen and ammonium (its nitrogenous wastes) slightly ahead of its own advance. Anaerobically digested material is exposed to aerobes arriving with, or stimulated out of a resting state by, the oxidant stream, and facultative anaerobes begin to switch metabolic gears while strict anaerobes die or at least become inactive. Some material is stockpiled in the microbial cells, whereas other chemicals run short; growth is unbalanced. The invasion continues with aerobic protozoans and meiofauna (Reise 1981). What the subsurface deposit feeder gets in a mouthful is thus critically time-dependent, with local standing stocks, nutritional states, digestibilities and growth rates of microbes rapidly changing in the volumes recently exposed to oxidants by deposit feeders.

The previous paragraph might be taken as pure fancy. What makes us dare to suggest that important events occur during the time between enhanced oxidant supply to, and ingestion of, a given mouthful is that rapid growth is known for some deep-sea microbes from animal guts (Deming *et al.* 1981; Deming & Colwell 1982) and that we have recently documented 1 hr doubling times of sediment microbes in shallow-water deposit feeder guts (Plante *et al.* 1989). For one strain of *Aeromonas* that showed such rapid growth afterward Plante *et al.* (1989) observed 97 % digestion efficiency prior to the explosive growth. Thus there is also every reason to expect rapid microbial responses to the unsteady chemical conditions preceding ingestion by deposit feeders. B. Hentschel (personal communication) has found doubled bacterial abundance in the small, oxidized portion of the head shaft just in front of the current feeding void of the intertidal lugworm *Abarenicola pacifica* and nowhere else in the vicinity of the animal.

What is lacking to apply or test these ideas in the deep sea is just about everything. Namely, the relevant feeding rates and geometries are not known for any deep-sea subsurface deposit feeder. Likewise, we can only guess at the effects of quickly time-varying oxidants on subsurface bacteria. Direct assimilation of refractory organics seems so unlikely on kinetic grounds, and microbially mediated fermentation of heterogeneous humic materials in deposit-feeder guts seems so unlikely on grounds of the enzymatic diversity required that we are forced provisionally to discount these possibilities for subsurface deposit feeders. We cannot easily escape the conclusion that deep-sea subsurface deposit feeders depend for their energy and organic nitrogen either directly on microbes or on the accumulated external products of microbes.

A few pieces of circumstantial evidence dangerously put together from various oceans may serve to raise interest levels in what it is that the few seemingly bona fide subsurface deposit feeders of oligotrophic seas do for a living. Thomson & Wilson (1980) have reported fine, open burrows to depths of 1.5 m in the oligotrophic Atlantic. One of us (P.A.J.) has observed similar open burrows to depths of at least 30 cm (deeper depths not examined) in box cores from the site described by Hessler & Jumars (1974). At roughly 1 mm ka^{-1} of net sedimentation, the burrow spans material exceeding 3×10^5 years in age. In one of these burrows was found (P. A. Jumars, personal observation) a specimen of the third most abundant species at the central North Pacific site, a capitellid polychaete (Hessler & Jumars 1974). This worm is long and very thin, and no individuals were recovered intact to compare with burrow lengths. Fine, open burrows of similar length have not been reported at richer abyssal or shallower sites. Indeed, higher rates of bioturbation might make them impractical. We speculate that the worm might take advantage from some yet unidentified and perhaps rather local redox couple to garden or flash cook its food, but that the lack of steep gradients at these organic-poor sites necessitates a very long tube to make that couple.

General implications for deposit feeding

Digestive limitations on the minimal size of deposit feeders would seem to provide a fairly general bottleneck or constraint on nutrition of small juveniles. Within the euphotic zone, some or much of the need for labile food can be met by benthic photoautotrophs. At deeper shelf and slope depths, however, seasonal or episodic inputs of labile planktonic detritus might be important developmental constraints. Perhaps their importance to recently settled juveniles is the reason that larvae of many species seem to be released well before the time when a spring bloom can be expected (see, for example, Tyler 1986). The correspondence of dietary change during ontogeny through the 1 mm abundance minimum merits examination in shallow as well as deep water. Gut retention time and gut volume should change in reflection of changing food lability.

Similarly, the major effects of horizontal transport on food availability to individuals are still underrated in shallow water. One might categorize surface deposit feeders as well as suspension feeders as either passive or active. Instead of water, however, surface deposit feeders have either to move themselves or not to get continuously renewed resources. Horizontal movement of sediments either by currents or bioturbation has profound affects on what is subducted by subsurface deposit feeders and upon the stratigraphic record (Wheatcroft *et al.* 1990). With extensive horizontal transport relative to feeding rates, subduction continually draws down particles of average surficial sediment composition rather than generating local overturn.

Transport is an overlooked variable in the recent trend toward ‘microbe bashing’, or repudiation of bacteria as a major source of food for deposit feeders. There is still plenty of room for doubt. Resupply of a thin veneer of bacteria-rich sediment, for example, is a viable alternative to Tunnicliffe & Risk's (1977) conclusion that *Macoma balthica* in the Bay of Fundy is unable to survive on bacteria contained in the deposits. The idea that bacteria are minor sources of food for deposit feeders may be correct for some deposit feeders in intertidal environments where labile food is contained in diatoms, but failure to include sediment transport in the general consideration of whether bacteria can sustain deposit feeders surely pushes the general answer further toward ‘no’ than it belongs. It would seem unreasonable to regard the issue as settled until the chemical identity of the food in sediments that is assimilated by deposit feeders becomes known. We find it quite tantalizing that a subsurface deposit feeder from an intertidal environment, when fed Pablum (Taghon 1988), could not be grown at rates comparable to field growth rates. Nitrogen limitation due to the animal's dependence on microbial nitrogen sources and the experimenter's control of microbial growth seems the most likely explanation.

The trend toward using carbon rather than nitrogen budgets for evaluating bacterial importance in deposit-feeder diets (Lopez *et al.* 1990) also seems to bias the case against microbial food. It is difficult to argue that any detritivore is limited in food acquisition rate by carbon availability. Hence we cannot reject the conjecture that the major fraction of most deposit-feeder nitrogen and energy budgets below the depth of the euphotic zone comes via bacteria. Another way to look at this problem is to ask whether bacteria represent primarily competitors or food for deposit feeders. We suggest that the problem may be primarily a kinetic one in oxic sediments. Microbial growth on an organic particle would appear in general to increase the lability of the resource to deposit-feeder digestion unless the particle already is a living cell, but the bacterium must extract chemical energy from solution or from the particle to grow. The resultant change benefits a deposit feeder if more of the food substance that currently limits deposit-feeder growth – probably not carbon – can be extracted from the microbially modified particle than from the unmodified particle during the gut residence time. The issue cannot be addressed definitively without experiments. One indirect line of evidence is whether antibiotics are used by either deposit feeders or bacteria feeding on detritus to sequester food, i.e. whether the chemical costs of the defence repay the gains of excluding the competitor. Bacteriocides manufactured by deposit feeders apparently are common (King 1986), but their use in sequestering food is not established.

We believe that it is premature to focus on non-living organic matter or phytoplankton falls as the immediate sources of organic matter for deposit feeders. So far, despite considerable efforts, we have failed to find a reasonably labile, non-living food that we can use for even a few hours in the laboratory to test digestion models quantitatively (beyond the ordinal level achieved by Taghon & Jumars (1984)). The apparent reason is that in seawater and sediments with natural bacteria, the bacteria get there and get them (the foods) first. Bacteria certainly have the growth-rate advantage. We have difficulty visualizing a means whereby bacteria do not have first access (relative to deposit feeders) to at least the exterior layer of non-living detritus arriving at the sea floor. Although sedimentary grain configurations (see, for example, fig. 25 of Aller 1982) and the structural matrices of organic particles may exclude bacteria until physical processes or animals mechanically remove this protection, structural barriers also may protect organic matter from metazoan digestion. Carbon source for deposit feeders seems a bit of a red herring, because carbon is not taken to be limiting for most benthic systems; the general issues for detritivores are sources of energy and available nitrogen. Until mass and energy balances show otherwise, we therefore retain the working hypothesis that deposit feeders in shallow water and the deep sea specialize kinetically upon digesting material that upon ingestion was contained in living cells, recently living microbes and their exudates. Consistent with this hypothesis, our preliminary measurements for intertidal species suggest that the carbon:nitrogen ratio of material absorbed from food is quite low, near 5 (L. M. Mayer, unpublished).

Bacteria clearly can use nitrogen (NO_3^- and NH_4^+) and energy sources (e.g. NH_4^+, S^0 and H_2S) that are unavailable to deposit feeders directly. These pathways provide food rather than competition for subsurface deposit feeders. The fraction of organic carbon that is degraded anaerobically in coastal environments approaches 50%, and early evaluations of this pathway in continental margin settings appear to have been substantial underestimates (Thode-Andersen & Jørgensen 1989). The bacteria that carry out these transformations are difficult to view as competitors with large deposit feeders that are capable of pumping oxygen, but they clearly can be food. It is tempting to think of anaerobiosis as protection for bacteria from pesky, macrophagous meiofauna in the absence of macrofaunal conduits of oxygen (Reise 1981). The net, long-term effect of this exclusion of small metazoa with respect to material or energy gain by subsurface deposit feeders is not clear.

The benefit to subsurface deposit feeders of unsteady biochemical and microbial processes induced by their feeding activities merits attention in shallow water as well as the deep sea. Importance of these interactions may be one reason that subsurface deposit feeders are so difficult to maintain in the laboratory; the disturbance of setting up aquaria for observation may eliminate the resource. There is nearly complete ignorance concerning the natural motility of subsurface deposit feeders, and the shapes and sizes of the spaces from which they feed.

Further, the number of subsurface deposit-feeding species may be severely underestimated. Terebellid, trichobranchid and cirratulid polychaetes generally are considered surface deposit feeders (Fauchald & Jumars 1979). The reason is that primarily those species that dwell in rock crevices and U-shaped tubes have been studied because at least their tentacles can be seen from the surface. We now know, however (Nowell *et al.* 1989; P. A. Jumars & R. A. Wheatcroft, personal observations), that at least some terebellids, trichobranchids and bipalpate cirratulids rarely appear at the sediment surface. Bipalpate cirratulids of the genera *Chaetozone* and *Tharyx* usually rank first in macrofaunal species abundance in deep-sea areas. The intertidal representative upon which we have the most observations (*Eupolymnia heterobranchiata*, cf. Nowell *et al.* 1989) pumps bottom water ahead of itself as it builds a continuous tube a couple of centimetres below the sediment–water interface. In the field, it does so in an environment where accumulation of the sea lettuce, *Ulva*, otherwise drives the redox discontinuity right up to the sediment surface. This interaction of steep and rapidly changing redox gradients with microbes and deposit feeders will be difficult, but probably very rewarding, to study in terms of understanding rate limitations that are removed when one considers unsteady as opposed to steady processes. For stratigraphic as well as geochemical issues, subsurface deposit feeders demand attention.

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FIGURE 1. X-radiograph of a sipunculid in its burrow from 90 m water depth under the northern California upwelling régime (0.25 m^2 box core taken 21 April 1985 on a cruise of the R.V. *Thomas G. Thompson* near 38° 50′ N, 123° 40′ W); the X-ray dense material inside the animal is sediment in its gut. The centre of the animal is approximately 20 cm beneath the sediment–water interface, and the comparatively X-ray transparent material surrounding the animal is a suggested cache. (Scale bar = 2 cm.)