

## 7: Gourmands of Mud: Diet Selection in Marine Deposit Feeders

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### INTRODUCTION

Deposit feeding, a subset of detritivory, is the eating of sand and mud. The central question in deposit-feeding research remains largely unanswered: What biological and chemical components of sediments are assimilated by deposit feeders? Candidates in specific settings and in spatially and temporally varying combinations include bacteria and their exudates, protozoa, (both benthic and sedimenting planktonic) microalgae, non-living particulate detritus, and interstitial solutes. Examinations of shallow-water sediments suggest that bacteria cannot constitute the principal carbon source for deposit feeders (Cammen 1989) but may be important or even dominant in reduced nitrogen supply. To date it has been established that bacteria are digested efficiently in many deposit feeders, that a few intertidal deposit feeders specialize on digesting and assimilating the contents of microalgae, and that at least a few deposit feeders can absorb organic matter from non-living, organic detritus (Lopez *et al.* 1989). Nitrogen rather than carbon limitation of growth rate seems more likely in this detritus-based system, so nitrogen would appear to warrant more focus than carbon. The inherent, intertwined problems in identifying the resources used by deposit feeders are that at their prodigious feeding rates a volumetrically and gravimetrically very small component of ingested sediments could yield the bulk of assimilated energy or matter (Cammen 1989) and that sediments are physically, biologically and chemically heterogeneous. Despite the fact that precise, accurate and general answers to the central question are still elusive, the range of possibilities for the unstudied majority of deposit feeders has been narrowed considerably by growing knowledge of sedimentary organic chemical characteristics and kinetics of deposit feeding.

The purpose of this chapter is to examine existing data on selection by deposit feeders in the context of both these constraints and any

constraints that can be imposed from general foraging theory. The time constraints imposed by large volumetric and gravimetric throughputs seem very different than for the macrophagous vertebrates treated by early foraging theory (Stephens & Krebs 1986). An analogy suggested by this examination of possibilities and constraints is of a rapidly operating machine that balances largely fixed and mechanical selective abilities with very flexible volumetric processing rates to make a nutritional profit under the majority of natural circumstances. This analogy also raises the pointed question of whether naive predictions of what should be preferred for ingestion fall within the capabilities of the machine. Testing of the machine analogy provides perhaps the most fundamental reason for study of deposit feeders; they appear to represent an extreme foraging strategy in rate of processing of food, fraction of their time devoted to food processing and importance of digestive and absorptive kinetics to their fitness. The marginal value and its variant, the principle of lost opportunity (Stephens & Krebs 1986), prove especially useful for understanding the limits on selection set by the need for a fast rate of throughput. Some gestalt for this evolutionary focus on feeding can be gained from the epithet 'roving gut' that has been applied to deposit feeders (especially the worms) by vertebrate zoologists. Indeed, up to 80% of apparent body volume can be taken up by the gut.

#### DEFINITIONS AND SUBDIVISIONS OF THE GUILD

Since assimilated food has not been identified with certainty for many deposit feeders, the definition of deposit feeding must be based instead on characteristics of ingested material. The most commonly accepted definition includes those animals that **frequently** ingest sedimented material of low **bulk** food value (Jumars *et al.* 1984; Lopez & Levinton 1987). The terms in bold are exceedingly important in applying the definition, but use of these discriminant variables remains very subjective for want of quantitative data. Few predators living in sediments can avoid ingesting sediments incidentally to prey capture, yet they clearly cannot be considered deposit feeders. Likewise, few meiofauna (animals retained on a 40- $\mu\text{m}$  sieve but passing a 300–1000- $\mu\text{m}$  sieve) that specialize on ingesting bacteria, microalgae or protozoa can avoid incidental ingestion of sediments. For kinetic reasons that will be elaborated below, however, it is doubtful whether meiofauna – or any animals with gut volumes much smaller than about 0.1 mm<sup>3</sup> – can be deposit feeders.

Two subcategories of deposit feeders are recognized frequently on the basis of the sedimentary horizon from which particles are ingested. Surface deposit feeders feed at the sediment-water interface, while subsurface deposit feeders feed below it. Although this definition seems clear enough, there is an intermediate category of deposit feeders, called funnel feeders, that feed with their anterior ends below the mean position of the sediment-water interface and thereby cause sufficient slumping of material downward to create, at least on occasion, funnel-shaped depressions in the sediment-water interface. An advantage to subsurface and funnel feeders in intertidal settings is that they can continue to feed after the tide is out if capillary water remains. Surface deposit feeders can do so only if overlying water remains or else must feed from void (e.g. burrow) surfaces below the plane of the sediment surface. If funnel feeders eat fast enough, they get mostly surficial deposits, with deposition of some kinds of particles from suspension enhanced by the presence of the pit itself (Nowell *et al.* 1984; Yager *et al.* 1993). A further potential problem with the surface-subsurface dichotomy is that animals may feed on surfaces, such as burrow walls, below the sediment-water interface with the aid of appendages much like those that are seen in animals that feed at the sediment-water interface. Pectinariid polychaetes (ice-cream-cone worms), protobranch bivalves and even some terebellid polychaetes (Nowell *et al.* 1989), for example, feed with tentacles below the sediment-water interface. Thus the morphological characters normally used to assign feeding guilds (e.g. Fauchald & Jumars 1979) may not be reliable indicators of feeding stratum.

Motility categories are also sometimes recognized (e.g. Fauchald & Jumars 1979). There are so few data, however, on the movements of individual deposit feeders that such classifications can be neither very detailed nor very accurate.

#### THE CHEMICAL, PHYSICAL AND GEOLOGICAL ENVIRONMENT AS A DETERMINANT OF FOOD QUALITY AND QUANTITY

Although the character of absorbed food remains poorly identified for marine deposit feeders in general, the form of organic matter for detritivores is certainly very different in terrestrial vs. open-ocean marine settings. Labile, nitrogen-rich plant protoplasm rarely arrives in the terrestrial litter community; plants resorb much of these valuable components before leaf abscission. In the marine realm, however, whole

microalgal cells seasonally or routinely do arrive at the sediment-water surface, even in deep water (Billett *et al.* 1983). The most labile material for open-ocean deposit feeders thus is newly arriving.

Cellulose (with lignin) clearly dominates terrestrial inputs of organic matter. Foregut fermenters (e.g. ruminants) and hindgut fermenters (e.g. termites) have evolved morphologically obvious means to tackle structural carbohydrates directly, but most litter organisms have not. Thus while available calories per mole of carbon must eventually decline with time after food inputs in either the marine or terrestrial realm, food value per gram of terrestrial organic matter for most litter organisms probably has peak value at some intermediate time after litter fall when microbes have degraded the polymers and have added at least their own masses of labile nitrogen. With the caveat that a few important exceptions (i.e. cellulose, chitin and structural carbohydrates from macroalgae) may be more useful after some ageing (Tenore & Hanson 1980) and may foster fermentative associations (e.g. Fong & Mann 1980), the bulk of organic inputs to marine sediments would appear most valuable to deposit feeders immediately upon input. Microalgae have much less mass in structural, polymeric carbohydrates than do terrestrial plants. Geochemical studies support this argument by documenting that a substantial part of the bottom-arriving particulate organic flux degrades quickly (Reimers 1989). This observation suggests strong natural selection for using or sequestering labile organic matter as soon as possible after its arrival.

Two major and strongly interacting physical differences between terrestrial litter communities and marine deposit-feeding communities involve excess density and the capabilities of the respective fluids to move both particles and solutes. The force required to lift a particle is linearly proportional to its excess density, i.e. its particulate density minus that of the fluid in which it is immersed. Moving water, by virtue of both its greater inertia and greater viscosity, is far more effective at transporting and redistributing particles of even the same excess density than is moving air. It is easy to forget when viewing sediments exposed at low tide that immersed sedimentary environments are scenes of constant, periodic or episodic particle motion. Newly arriving organic material at the seabed has lower excess density on average than the mineral grains that compose the gravimetric bulk of the deposit and thus is more easily redistributed. Density separations with surficial sediments immersed in high-density fluids reveal that the low-density fraction ( $<1.9 \text{ g cm}^{-3}$ ) is enriched by a factor of 10 to 100 in organic content per unit of weight (L. Mayer *et al.* in review). Mayer (1989) has

suggested that ageing of organic matter at and in the seabed corresponds, with due accounting for the material lost to mineralization, with a transition from labile organic particles to refractory, monomolecular coatings on mineral grains.

There is a long- and well-established relationship between grain surface area and several other variables important in determining food quality for deposit feeders: organic content (Longbottom 1970), microbial metabolic rate (Hargrave & Phillips 1977) and microbial abundance (Dale 1974). DeFlaun and Mayer (1983) have refined the latter relationship by pointing out that bacteria tend not to attach to particles smaller than about 5  $\mu\text{m}$ ; while their study is limited to one intertidal location, it seems logical that the value to bacteria of attachment in general would fall as the size of the particle approaches their own cell size. This surface-area relationship implies that food value per unit of volume of food ingested scales roughly as grain diameter<sup>-1</sup>, at least down to the grain size at which microbial attachment per unit of grain area declines.

Implicit in this discussion is that the sediments in question are non-cohesive. Watling (1988) points out, however, that muddy sediments are much more like a complex sponge or lumpy gel than they are a collection of easily separable grains. An unsolved problem, then, is the extent to which sediments behave like and are perceived as (by deposit feeders) individual grains rather than as aggregates of grains. In the latter case, it is the properties of aggregates and not individual grains that limit selectivity. In general, it can be expected that cohesion and adhesion among grains will decrease the ability of animals to select among particles that constitute such aggregates.

Physical, chemical and biological components of the environment interact to set limits on the rate of supply to, and thus the potential for selection among particles by, deposit feeders (Fig. 7.1). At one extreme of possibilities is the now classic view of marine detritivory developed by Newell (1965) and extended by Levinton & Lopez (1977) based on the observation that fecal pellets after ageing and disaggregation yield particles worth eating again. In this situation fluxes in and out of the individual's ambit are ignored (i.e. implicitly assumed to be minor or of equal magnitude and opposite sign); this closed-system view does accurately portray the laboratory experiments on which these studies have largely been based. Food abundance (number of particles) is set primarily by the ratio of the rates at which sediments are ingested to the rate at which pellets disaggregate (Levinton & Lopez 1977), while food quality is set by the extent of microbial addition of labile organic nitrogen to the

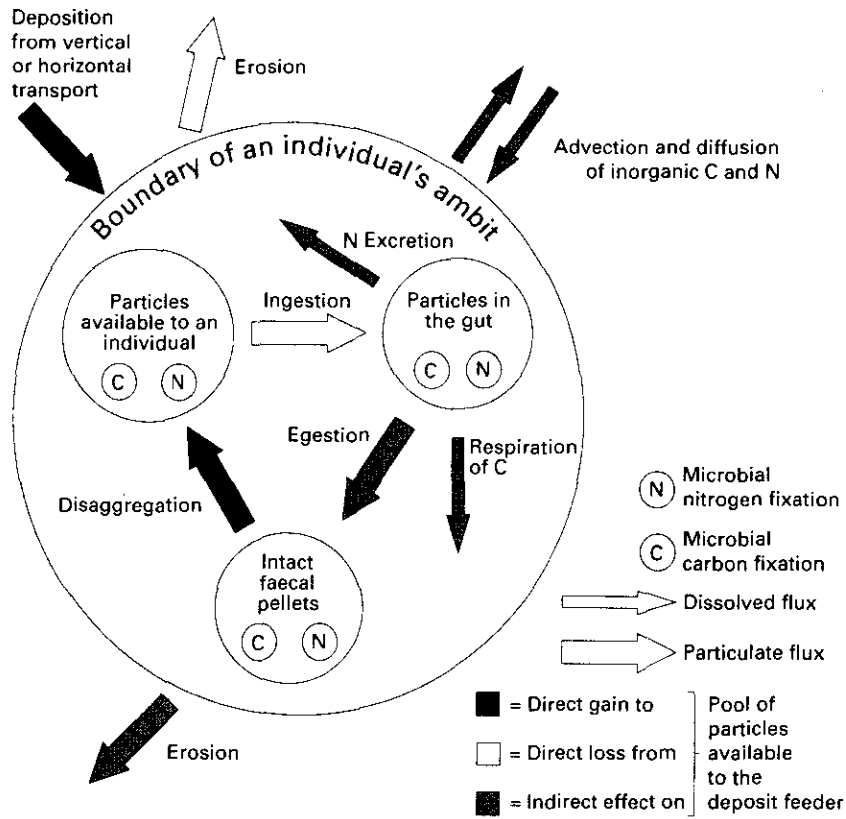


Fig. 7.1 The ability of water to transport particles and solutes makes food availability within the ambit of an individual marine deposit feeder far more dynamic than one might expect from experience with a terrestrial litter community. Not only are erosion and deposition frequent, but microbial (including microalgal) nitrogen and carbon fixation are also influenced by fluid transport.

disaggregating pellets (Newell 1965). This extreme falls close to what can be expected of terrestrial litter communities, where the time scale of particle inputs greatly exceeds that of fecal pellet breakdown. To provide much choice among particles at a steady state, the disaggregation rate must exceed the ingestion rate.

At the other extreme, physical transport constantly delivers or exchanges particles, swamping ingestion rate in magnitude and providing substantial food supply rate and potential choice to the deposit feeder. Because of the ability of combined waves and currents to move sediments on scales approximating those of individual ambits, intertidal communities in which sediment transport measurements have been

carried out (Grant 1983; Miller & Sternberg 1988) fall much closer to this extreme. There is reason, then, to expect diet selection by at least some deposit feeders. This perspective also raises a critical difficulty in evaluating selectivity by surface deposit feeders; at one extreme they may simply use the ambient sediments as a residence and feed on the flux of material going by, making comparisons of ambient sediments and diets of little relevance to the issue of diet choice. In this scenario, the flux (a rate) of particles may also determine feeding rate (Brandon & Miller, in preparation).

#### STATICS, KINETICS AND SIZE SCALING OF DEPOSIT FEEDING

Although studies of item and patch choice dominated early research on diet selection by deposit feeders as they did with macrophages, feeding rate so pervades these issues that considerable space is saved by treating this often overriding constraint first. In treating ingestion rate, it is tempting to create an implicit analogy with large grazers (Chapter 3). Herbivores on poor forage are well known for the prodigious rates at which they process food (Van Soest 1982), but they pale by comparison with deposit feeders. Deposit feeders typically ingest three times their own (dry) weight in (dry weight of) sediments per day (Fig. 7.2); even with allowance for the high bulk density of sediments, that figure translates to a volumetric rate in excess of a full body volume per day. Their maximal gravimetric rates of  $10^2$  body weights per day (Fig. 7.2) correspond with animals that ingest food particularly dilute in organic content.

Some of the high gravimetric and volumetric ingestion rate is achieved via a gut volume that exceeds in proportion of total body volume that of closely related animals (Fig. 7.3, *see* page 132), but the extreme volumetric and gravimetric throughput rates of deposit feeders are achieved primarily via short gut residence times. There is no strong correlation among species (Fig. 7.3) between body size and proportion of the body occupied by the gut. Similarly, with the important proviso that small juveniles were not sampled, Penry & Jumars (1990) found within deposit-feeding species that the proportion of the body occupied by the gut generally changes isometrically with body size. Figures 7.2 and 7.3 combine to provide a strong contrast with ruminants. Larger ruminants have greater fractions of their metabolic weights ( $\text{weight}^{0.75}$ ) devoted to digestion (Table 1 in Hoppe 1977). Poorer forage characteristic of large

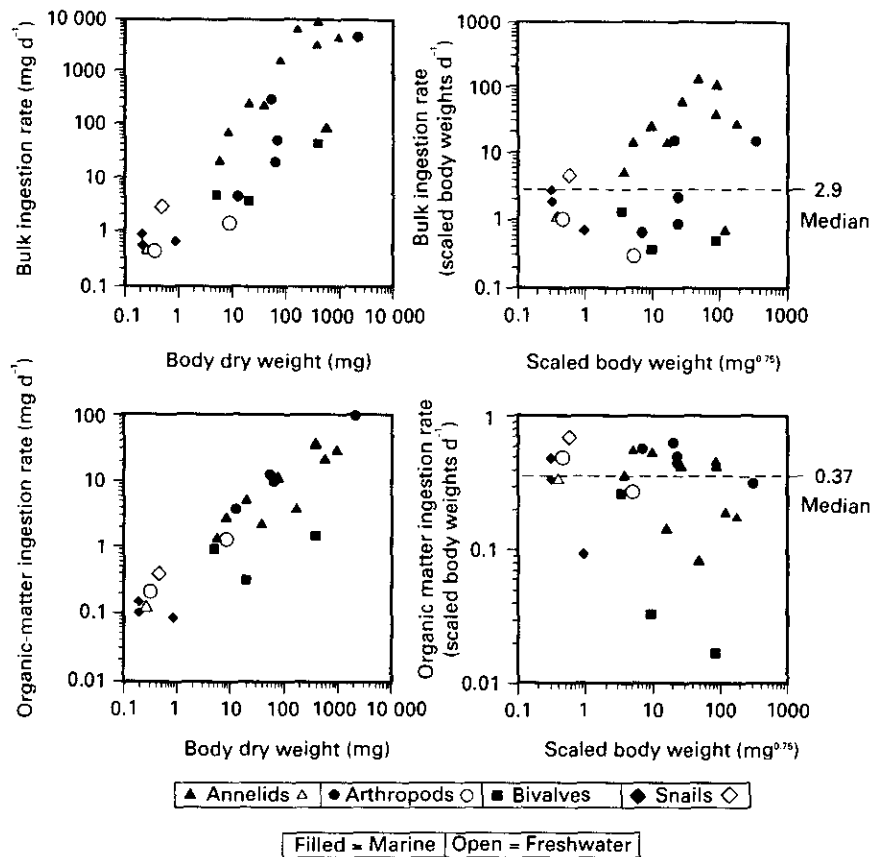
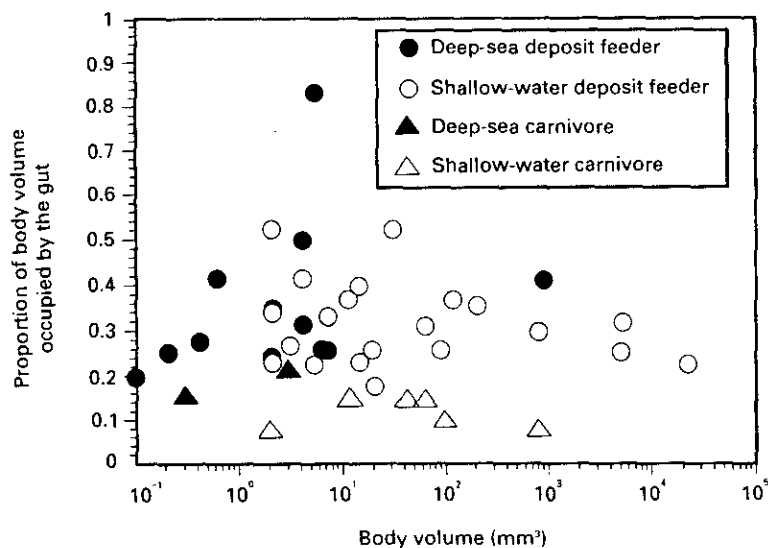


Fig. 7.2 Bulk ingestion rate of sediments and organic-matter ingestion rates (both as dry weights) versus body dry weights of deposit feeders, plotted from the data tabled by Cammen (1980, 1987). He was careful to select data from animals observed near 15°C, with each datum representing an average for individuals of one species and one average size. In the panels on the right the value of (body weight)<sup>0.75</sup> rather than unmodified body weight is plotted to remove the expected trend with body size and to reveal that the extremes of rapid ingestion rate correspond with food poor in organic matter.

grazers takes longer to ferment, and this residence-time constraint (Dement & Longhurst 1987) necessitates the greater volume (Chapter 8). By contrast, poorer food for deposit feeders drives faster feeding when species (not individuals) are compared over a large range in food quality (Cammen 1980).

When closely related deposit feeders are compared, there is some evidence of greater gut volume in animals living on poorer food, and isometry of gut and body volume coupled with the usual scaling of



**Fig. 7.3** Proportion of the body volume occupied by the gut versus body volume for a range of marine polychaetes, drawn from the data tabled by Penry and Jumars (1990). Deposit-feeding polychaetes typically have about  $\frac{1}{3}$  of the body volume occupied by the gut, but  $\frac{1}{2}$  is not unusual, and one species, the cirratulid *Tharyx laticastellus*, devotes over 80% of its body volume to the gut. There is no dramatic correlation of body volume with proportion occupied by the gut.

ingestion rate with body weight ( $\text{weight}^{0.75}$ ) does imply somewhat longer gut residence times in larger individuals and species. Feeding rates of the larger deposit feeders (e.g. the larger holothuroids) are not well studied enough, however, to allow their placement on Fig. 7.2. Characteristic gut residence times of deposit feeders in the range of sizes represented in Figs 7.2 and 7.3 are 0.5–6 h. To bring the fermentation contrast down to more comparable body size, a termite that feeds on **refractory but ultimately digestible** lignocellulose spends up to 48 h processing before releasing the particulate residue (Bignell 1984). Paradoxically, the short residence times of material in the guts of deposit feeders must make these animals specialists on digesting and absorbing relatively **labile** organic components of their food. The contrast is between a dilute and labile food resource in deposit feeders and a concentrated but refractory resource in fermenters that repays the costs of mutualism (Plante *et al.* 1990). This conclusion suggests that replacing the ordinate of the lower right panel of Fig. 7.2 with a measure of labile rather than total organic matter would both lower the median amount ingested per day and remove much of the scatter.

Scaling of nutrition in early life is a widespread problem. It is acute in deposit feeders because of the switch from relatively rich larval resources to the exceptionally dilute ones that deposit feeders utilize. Forbes and Lopez (1990) documented such a break in allometry for the polychaete *Capitella* sp. I. Cammen (1980, 1987) found no deposit feeder of <1 mg dry weight ingesting <13% organic matter. Gallagher *et al.* (1990) found strong circumstantial evidence that juveniles of the deposit-feeding (as an adult) polychaete *Hobsonia florida* specialize on diatoms. Individuals of the fiddler crab *Uca longisignalis* show a switch from discrete zooplankton prey as zoea to more dilute diatoms of sediments as adults (Weissburg & Zimmer-Faust 1991). The insoluble problem at small body size if the food is dilute is that there is not sufficient gut volume to provide a substantial throughput rate (volume per unit of time) with sufficient residence time to allow adequate digestion and absorption.

Although consensus has not been reached on the controls governing feeding rates in even adult deposit feeders, numerous experiments reveal great variability among individuals in feeding rate on identical foods as well as great flexibility in feeding rate of individuals from diet to diet. It is not known whether the variability among individuals is due to variability in prior diet vs. diversity in genetic composition. Whatever its source, this variability constitutes part of the scatter in the relationships of Fig. 7.2, but flexibility on varied diets is expressly avoided in the choice of data shown here, and among-individual variation is limited by using only means for each species. One way of looking at the trend in Fig. 7.2 is that it summarizes the mean rate of feeding in deposit feeders of a given size on the sediment to which they have adapted over evolutionary time. The inverse relationship between feeding rate and organic content of ingested sediments over several decades in both variables is a reflection of the absence of a free lunch; to support an average amount of organic matter (body size) takes an average rate of throughput. Since the plot is of means for given species and thus represents among-species patterns, however, it bears little direct relevance to the issue of the rate at which an individual does or should feed when food value is changed from the mean of the environment to which it is adapted. Because species adapted to sediments of lower organic matter must in the mean feed faster to make ends meet says little about what they should do when presented with an enriched food resource.

Taghon and Greene (1990) presented a set of data for one lugworm species (*Abarenicola pacifica*) and a detailed analysis of fit to the broad

suite of models that have been proposed to explain or predict individual feeding rates as a function of the quality of food presented to an individual. They analyzed individual feeding and growth rates on sediments of varying protein contents and two very different protein sources, finding maximal feeding rate at a sediment protein concentration of approximately  $0.1 \text{ mg protein (g sediment)}^{-1}$ . Growth rates, on the other hand, showed monotonic increase with increasing protein concentration. It is extremely important that this unique data set, combining data on individual growth and feeding rates, be replicated with additional species. Among extant predictive models for deposit feeders (i.e. Taghon 1981; Phillips 1984; Penry & Jumars 1987; Kofoed *et al.* 1989; Dade *et al.* 1990), their results are consistent with only the formulation of Dade *et al.* (1990), who coupled Michaelis–Menten kinetics of digestion with Michaelis–Menten kinetics of absorption, adopting the premise that animals adjust ingestion rate to maximize the rate of absorption. For any anticipated digestive kinetics and absorptive kinetics at one set food concentration (moles of food per unit of weight of sediments) and unlimited food quantity (weight of sediments) there is an optimal throughput time. Longer residence times produce lower rates of absorption because they result in slowed rates of digestive reaction (Penry & Jumars 1987), while shorter ones drive rapidly produced products out of the gut before they can be absorbed. For the complex (higher-order Michaelis–Menten in the terminology of Dade *et al.* 1990) digestive kinetics of deposit feeders, these optimal ingestion rates should be slow at low food concentrations because it takes time to produce enough digestive products to drive absorption, should rise until the absorptive system is saturated, and then should fall again as longer throughput times suffice to maintain absorption rate at its maximum (Dade *et al.* 1990). Net absorption rate, however, should increase with increasing concentrations, as suggested by the growth rates seen by Taghon and Greene (1990). To avoid confusion in the face of terminology that varies considerably among authors it is worth underscoring that concentration of food here is taken as a measure of its quality and that the model predictions assume that food of the indicated quality is available in unlimited amount.

Earlier thinking that failed both to distinguish and to couple digestion and absorption suggested (Taghon 1981; Penry & Jumars 1987) that faster ingestion rate would always produce a higher gross rate of gain because Michaelis–Menten digestive production rates decrease monotonically with gut residence time. The idea and problem are still typical of optimal foraging approaches. The apparent rate of gain

(digestive production) could be formulated relatively easily, but poorly specified or unknown and non-linearly increasing costs of increased feeding rate had to be invoked to avoid the absurd prediction of infinitely fast feeding. Two possibilities that seemed likely in view of the prodigious feeding rates of deposit feeders were the costs of mechanical processing (weight of sediments moved a given distance and height per unit of time) and costs of digestive enzyme production. Taghon (1988) devised a means to partition these two variables and anabolic costs (specific dynamic action) in a system of three equations in three unknowns. His surprising experimental result, again with the lugworm *Abarenicola pacifica*, was that even for individuals feeding on sediments of no food value the mechanical and enzymatic costs of feeding were insignificant. Taghon's (1988) and Taghon and Greene's (1990) results appear to support the idea that deposit feeders, for which quality rather than quantity of food seems to be the principal limitation on growth rate, are free to set their throughput rates at the absorption-rate maximum suggested by Dade *et al.* (1990). If digestive costs or mechanical costs of feeding were large, then this absorption-rate maximum might not correspond with maximal rate of energy or mass gain. A corollary (Dade *et al.* 1990) of feeding at a rate set by absorption is that gut residence time becomes a far more important determinant of diet choice than does pre-ingestive handling time.

Ingestion rate of deposit feeders clearly is flexible (e.g. Taghon & Jumars 1984), but it is not yet clear what signals the animals use to set this rate. Dade *et al.* (1990), to derive their model, assumed that deposit feeders maintain a full gut but respond with ingestion (and egestion) rate changes to their rate of absorption of digestive products. It seems very likely, however, that at least four sets of stimuli operate to affect ingestion rate, since they do in many other animals from insects (Bernays 1985) to ungulates (Illius & Gordon 1990). These stimuli are, in sequence, smell, taste, distension of the gut and internal detection of the levels of absorbed products in body fluids. Here smell is defined operationally as chemical detection of food prior to its contact by an appendage. Although working with intertidal organisms during emersion precludes ready separation of smell from taste and the 3-h duration of experiments includes time for feedback from absorbed food, the most complete data on chemical stimulants of feeding rate are for the sand fiddler crab *Uca pugilator* (Robertson *et al.* 1981). L-serine, sucrose and maltose proved highly stimulatory, consistent with the crab's dietary specialization on benthic diatoms. Qualitative experiments easily reveal

that smell does affect ingestion rate of at least some deposit feeders. In experiments with selection on valueless particles (glass beads), for example, in Jumars' laboratory seawater extracts from complex food mixtures (the commercial aquarium preparation Tetramin®) are routinely applied to elicit adequate ingestion rates. The normal procedure (e.g. Self & Jumars 1988) does not distinguish smell from taste, but it has been observed (unpublished observations) that the dissolved form alone when dispensed near the polychaete *Pseudopolydora kempji japonica* immediately stimulates feeding palp activity.

There are phagodepressants as well. Valiella *et al.* (1979) documented that cinnamic acids at natural concentrations inhibit detritivore ingestion. The experimental protocol again made separation of smell from taste impractical. A common observation of laboratory and field feeding traces and bottom photographs is that feeding marks (e.g. grooves from deployment of tentacles) avoid fecal pellets of the same species. Forbes and Lopez (1986) found that recently egested, disaggregated fecal material depressed feeding rates in the snail *Hydrobia truncata*. Miller and Jumars (1986) similarly showed that accumulation of pellets of *Pseudopolydora kempji japonica* in its feeding area slowed its feeding rates. It may be more practical from the standpoint of sensory capability for a detritivore able to gain nutrition from a diversity of foods to recognize lack of resupply (accumulation of fecal pellets) rather than carrying all the detectors necessary to recognize resupply. Perhaps the most bizarre situation, however, has been seen in the subtidal and deep-sea polychaete *Amphicteis scaphobranchiata*. Nowell *et al.* (1984) documented that it literally slings its fecal pellets outside its feeding zone, thereby creating a feeding pit that traps material in suspended and bedload transport. In the slinging activity the worm is at great risk to predation, since two-thirds of its body is extended from the protective tube. A reasonable scenario for the evolution of this behaviour is that individuals that ejected pellets from their feeding area both removed a phagodepressant and enhanced food supply by making a pit, contributing sufficiently to rate of nutrient gain to outweigh the predation risk.

Feeding appendages of surface deposit feeders constitute major components of the diets of many bottom-dwelling fishes, and thus predation also modulates feeding rate by affecting time spent feeding. Levinton (1971), for example, established that *Macoma tenta*, a tellinid bivalve, was active only at night when visual predators were less effective. Such periodicity may not be limited to surface deposit feeders alone, since many subsurface feeders place the opposite ends of their bodies at risk

when they come to the sediment surface to defecate. Fuller *et al.* (1988), for example, report greater nocturnal feeding rate in the capitellid polychaete *Mediomastus ambiseta*. Some deposit feeders reduce the risk of predation and thus ameliorate the time constraint by incorporating toxins in their feeding appendages and other structures that often protrude from the tube (e.g. Gibbs *et al.* 1981).

Another modulator of feeding rate is resupply of high-quality particles. Nichols *et al.* (1989) found that the heart urchin *Brisaster latifrons*, that normally burrows several centimetres below the sediment surface, emerged in apparent response to modulation by current reversals of the supply of rich surficial particles. Jumars and Self (1986) documented enhanced feeding rate in one species of surface deposit feeder just after a sediment transport event but found no evidence of a similar effect in a sympatric species. Both of the tentacle feeders studied by Jumars and Self (1986) are constrained mechanically to feed only when immersed, but a substantial fraction of the flat is covered by shallow pools at low tide. Conversely, intertidal ocypodid crabs, like the fiddler and sand bubbler crabs discussed below, are constrained to feed at low tide. Penry and Jumars (1987) have suggested that animals constrained to feed less frequently should choose for digestion items that continue to give gain until the animals are able to feed again.

#### PATCH EXPLOITATION

Feeding rate thus should in part be determined by the ability of deposit feeders to locate or produce (by affecting sediment transport or microbial growth) patches of high food quality. Most deposit feeders, however, are quite restricted in mobility compared with cruising predators and scavengers. A major component of habitat choice is therefore associated with larval or juvenile settlement at a site. Deposit feeders have long been known to recognize and prefer bacteria-coated sediments to cleaned ones (Meadows 1964), a preference that makes good sense with respect to food value. A more recent suggestion that has stimulated considerable debate is that a major component of site selection may be passive (Butman 1987). To overstate the case, a deposit feeder might find its way to a good feeding environment by mimicking in sediment dynamic properties (i.e. settling velocity) the characteristics of its preferred food. While this null model is an interesting one, departures from it already are known (Butman *et al.* 1988), and more can be expected. One problem is that the bulk sediments represent responses primarily to extreme

conditions that may exist only episodically during spring tides or major seasonal storms, and it is not clear, therefore, that larvae responding to physical conditions at one time would end up reliably in the proper regime. A further problem is that food for recently settled juveniles may not match food for adults, but resuspension and resettlement of juveniles may alleviate both these problems (Emerson & Grant 1991). At the very least, however, the null model has injected some physical realism and controversy that is spurring research on the issue of larval habitat choice. Analogy with ballooning gives a vivid impression of the difficulty of habitat choice. Control is primarily in vertical position in the winds or currents and is limited by the fuel onboard or energetic reserves. Thus, the decision is not where to go, but when to stop. Marine larvae are well known to become less selective of settlement sites as time proceeds. The problem is eminently suited to dynamic programming as a theoretical approach (Mangel & Clark 1988), but has not yet been formulated in the context of a choice that affects subsequent foraging success.

As one of the two initial problems addressed by (optimal) foraging theory, it is not surprising that more information is available with respect to the more classically defined patch choice. Attention among students of trace fossils to rules for space utilization in fact predates foraging theory by nearly forty years. Richter (1928, cited in Raup & Seilacher 1969) observed that many fossil traces seemed to conform to a simple, three-part algorithm: turn approximately  $180^\circ$  after going approximately a given distance, avoid recrossing (i.e. avoid previous tracks), and keep close proximity to previous tracks. More recent computer simulations of trace fossils have shown that slight changes in these very simple rules can generate diverse patterns (Papentin 1973). More importantly for the present context, some of the most frequently observed patterns (e.g. Fig. 7.4a) of burrowing or crawling traces are consistent with the marginal value theorem, i.e. that an individual should forage in a patch only until its mean rate of gain falls to the mean level that can be expected from the environment as a whole (including the search time needed to find a new patch). Another suite of observations consistent with foraging theory of patch choice is those of Scheibling (1981) concerning a microphagous seastar. It apparently uses flow direction as a cue to avoid recrossing already foraged territory. An explicit, experimental test of patch choice for deposit feeders was that of Robertson *et al.* (1980) on the fiddler crab *Uca pugnax*. They indeed found that crabs spent more time foraging in patches that had been manipulated to have higher concentrations of benthic diatoms and by probing with sensory setae on their legs could

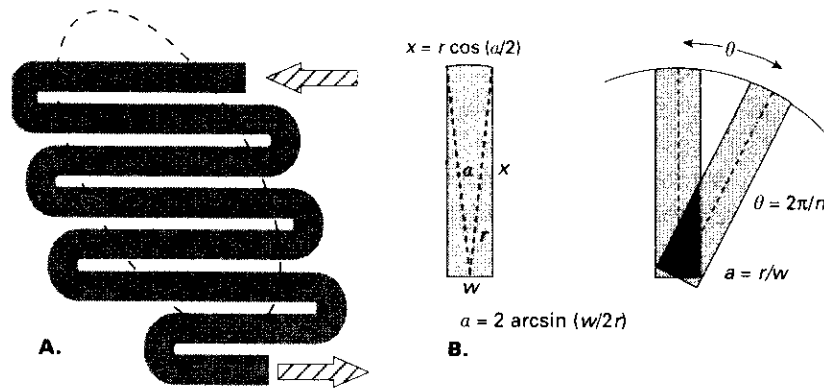


Fig. 7.4 Two variants of Richter's (1928, cited in Raup & Seilacher 1969) rules for patch utilization by deposit feeders. (A) A hypothetical trace of a mobile deposit feeder encountering a food-rich patch (dashed ellipse). It proceeds straight forward until a food-rich patch is encountered and doubles back whenever it leaves a rich patch. (B) Definition sketch for Ohta's (1984) model of patch utilization by an echiuran worm feeding by making radial strokes of a given aspect ratio,  $a$ , from a central burrow. Strokes are spaced evenly, i.e.  $2\pi/n$  radians apart where  $n$  is the number of strokes. Note that overlap (dark grey shading) is extensive near the centre of the circle for large  $\theta$ , while overlap of strokes is minimal at the distal portions of strokes. For simplicity, Equation 7.2 calculates the unharvested (white) area between adjacent strokes.

resolve patches of millimetre scale. Forbes and Lopez (1986) found similarly in the snail *Hydrobia truncata* that animals spent more time foraging in patches richer in chlorophyll. Snails slowed their rates of crawling when they encountered higher chlorophyll concentrations but did not change egestion rates significantly. An elegant analysis of patch utilization (Weissburg, in press) also has recently been completed that provides strong support for the existence of patch-leaving resource thresholds in deposit feeders.

These various patterns and experiments involve mobile animals and thus require no fundamental changes to the notions of patch choice for non-deposit feeders. In a very innovative contribution, Ohta (1984) added the geometric constraints of foraging with a single tentacle from a fixed burrow location to the idea of patch choice for deposit feeders. He analysed the number of strokes made by the single feeding proboscis of deep-sea echiurans (gutter worms) evident in bottom photographs and observed a remarkably strong relationship ( $r^2 = 0.95$  for a regression based on 14 points) between the maximal number of strokes seen ( $n_m$ ) and the aspect ratio,  $a$  (length/width or radius/width,  $r/w$ ), of the strokes and presumably of the appendage that produces them:

$$n_m = 4.86 + 2.39a \quad (7.1)$$

For the two extremes of  $a$  seen, i.e. 4 and 14, this equation gives  $n_m = 14.42$  and  $38.32$ , respectively. While the geometry of strokes is simple conceptually, it is messy computationally because of the single and multiple overlaps near the centre of the circle. These overlaps make it easier to calculate the fraction,  $f_u$ , of the circle that is left uncovered by  $n$  evenly spaced strokes than it is to calculate the fraction of area with overlaps. Specifically,

$$f_u = 1 - \frac{n}{\pi} \left[ \arcsin \frac{1}{2a} + \frac{\sin^2 \left( \frac{\pi}{n} - \arcsin \frac{1}{2a} \right)}{\tan \frac{\pi}{n}} \right] - \left[ \frac{\sin^2 \left( \frac{\pi}{n} - \arcsin \frac{1}{2a} \right)}{\tan \left( \frac{\pi}{n} - \arcsin \frac{1}{2a} \right)} \right] \quad (7.2)$$

Substituting for  $n$  the values of  $n_m$  calculated for  $a = 4$  and  $14$ , respectively, gives  $f_u = 0.18$  and  $0.32$  (not a constant value of  $0.24$  as suggested by Ohta). The number of strokes,  $n_c$ , that it would take to just cover the feeding circle completely (distal edges of strokes just touching) is calculated far more easily by noting that for such, just complete, cover  $a = \theta$  of Fig. 7.4b. It also corresponds with the number of chords of length  $w$  that would be needed to go fully around the circle:

$$n_c = \frac{\pi}{\arcsin \frac{1}{2a}} \quad (7.3)$$

Complete overlap (each spot touched by at least two strokes) would not occur until the number of strokes reached  $2n_c$ . Because of the uniform geometry of the problem (covering a circle with radially arranged rectangles), 75% cover of the circle by strokes ( $f_u = 0.25$ ) corresponds approximately with  $n_c/2$  for the full range of  $a$  documented by Ohta (1984). The generalization is approximate because the real number of strokes must be an integer, while Equations 7.1 to 7.3 in the simple forms written allow fractions. (The approximation gets far worse for  $a < 0.71$ .) There is rough correspondence between  $n_m$  of Equation 7.1 and  $n_c/2$  over the full range of  $a$  seen, but for high aspect ratios 75% cover is reached at higher numbers of strokes than are observed (Fig. 7.5);  $n_c/2$  overestimates the number of strokes observed (Equation 7.1) by about 15% at  $a = 14$  and equals  $n_m$  only for  $a = 6.49$ . While  $n_c/2$  and  $n_m$  both are linearly related with  $a$  over the domain of interest,  $n_c/2$  has a somewhat steeper slope.

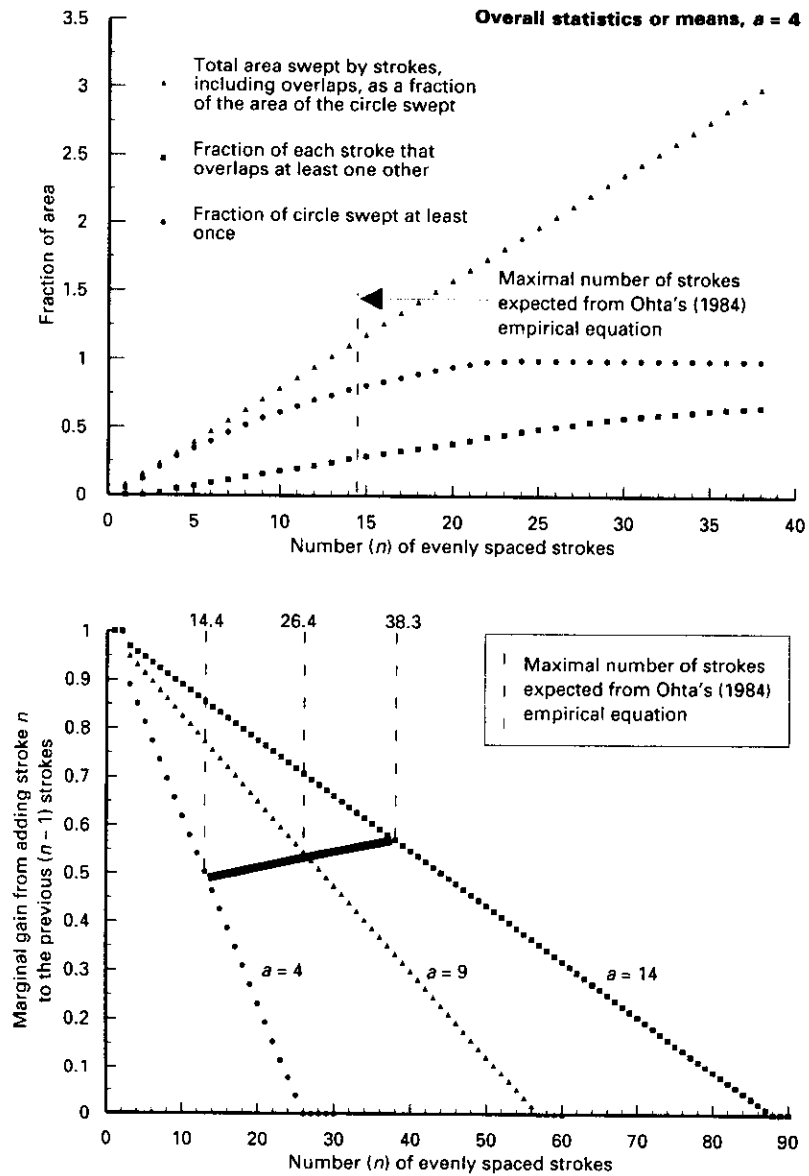


Fig. 7.5 An example for  $a = 4$  of the way that area of strokes rises linearly with number of strokes while fraction of the circle harvested (touched at least once) and average fraction of a stroke that consists of area overlapping another stroke both rise more slowly. Complete coverage of the circle is achieved at the number of strokes given by Equation 7.3, while complete overlap does not occur until twice that number of strokes. Evolution probably acts upon the marginal gain achieved by adding another stroke rather than upon the mean overlap per stroke. Shown are such marginal gains for the full range of aspect ratios (4–14) reported by Ohta (1984). The animal appears to stop adding strokes when about 50% of the added stroke constitutes previously unharvested sediments (heavy line).

The tight fit of Equation 7.1 as well as this departure from strict geometric similarity with changing aspect ratio still begs for evolutionary explanation. It is not clear that the animal has any way to evaluate mean quantities for the circle as a whole. It seems more likely that evolution has operated upon the marginal gain per stroke (Fig. 7.5) than upon integral measures for the circle, i.e. upon the difference in harvested area ( $b$ ), expressed as the fraction of an additional stroke's area that would contact previously unharvested sediments with increasing number of strokes ( $n$ ) or  $\Delta b/\Delta n$ . This function has no peak and declines linearly with  $n$  (Fig. 7.5). The previously untouched area contacted, when expressed as a fraction of the area of one stroke, drops to near 50% for  $n_c/2$  and thus also for low values of  $a$  in Equation 7.1, but stays higher at about 60% for  $n_m$  of Equation 7.1 when  $a = 14$  (Fig. 7.5). The disparity is probably due to imprecision by the animal in locating strokes exactly  $\theta$  radians apart, this imprecision compounding when  $n$  is large. The likelihood of some imprecision makes the estimates of harvested area and marginal gain under the assumption of perfectly evenly spaced strokes upper bounds and the estimates of overlap lower bounds, at least until full cover is expected (Equation 7.3). If there is a given variance associated with placing each additional stroke, then one would expect overall imprecision to grow approximately linearly with  $n$ , returning an increasingly lower marginal gain than predicted as  $n$  increases. Thus, the marginal gain for values of  $n_m$  given by Equation 7.1 and true values of  $f_n$  may be relatively constant if this imprecision of stroke placement is included in the problem.

There is reason to expect echiurans and sipunculans (peanut worms) to be particularly sensitive to this marginal gain. Jumars *et al.* (1990) and Plante *et al.* (1990) have argued that echiurans and sipunculans are likely to cache recently arrived deposits for later use. The cache may be in the form of the animal's own, microbially modified, fecal pellets. Although caching gives access for nutritional purposes to external volume in addition to gut volume or other somatic storage and thus also relieves some volumetric and temporal constraints upon digestion, cache volume must be limited and should not be filled with 'old' material of low bulk food value. The rule of spacing strokes at equal angles greater than the one that would yield complete coverage of the circle is an example of a simple way to achieve recovery of a reasonably large proportion of newly deposited material without recourse to sensory evaluation of particles one by one. The need for 'new' material also raises questions of risk sensitivity of the gathering strategy, since bloom sedimentation events on the deep-sea floor would appear to be less than exactly predictable (Billett *et al.* 1983).

Further, fascinating problems include the prediction of both aspect ratios ( $a$ ) and absolute reaches ( $r$ ) of feeding appendages. One might expect both to increase with decreasing flux of food since the radius is the reach and a greater aspect ratio gives a greater reach from the same material investment (area and presumably mass of tentacle). Imprecision in tentacle placement may set the upper bound on  $a$  for species that rely on contacting unharvested surface, but non-caching species, e.g. of spionid and terebellid polychaetes, have much larger values of  $a$  than 14 (and from 2 to  $10^2$  feeding palps or tentacles). High  $a$  is associated with multiple tentacles, presumably so that a reasonable fraction of the feeding area can be explored and harvested per unit of time. The lower bound on aspect ratio, on the other hand, probably stems from the limited gain in reach achieved and from acute overlap problems when  $a < 0.71$ . Nor should even coverage of the circle be considered always ideal. In a classroom experiment J. Grebmeier (personal communication) found the tentacle-feeding spionid *Pseudopolydora kempji japonica* to spend disproportionate time feeding in food-enriched sectors of its feeding circle. Such patch-selective capability is consonant with flow-induced heterogeneity in food quality (Eckman & Nowell 1984).

Perhaps the best example of strong constraints acting on patch exploitation, however, is in foraging by an intertidal crab that belongs to the same family as fiddler crabs but, unlike them, apparently foregoes evaluation of patches. Zimmer-Faust (1987, 1989) documented that the sand bubbler crab, *Scopimera inflata*, does not select patches of high food value. It lives in an intertidal sand zone where food concentrations are low and food presumably is redistributed by wind-wave induced sediment transport as the tide moves in and out, and it forages only during the daytime low tide. Predation by birds appears to be a major constraint as well (Zimmer-Faust 1989). Thus it seems that the costs of sensory mechanisms and time in selecting patches may outweigh the gains. The solution used to maintain rate of gain is geometrically very similar to that employed by echiurans (Fig. 7.4b). The crabs scuttle in swaths extending from the central burrow to a set distance, take a step forward and forage back, repeating the process around the compass. These swaths proceed either clockwise or anticlockwise, but are timed and spaced so as to cover the full circle in the one daytime low tide. The distance moved from the burrow thus is the minimum possible for the area of sand foraged. This foraging pattern represents an interesting variant on Richter's (1928) algorithm, and one that Zimmer-Faust (1987)

documents to be approximately optimal. It would be interesting to compare swath geometries (i.e. their aspect ratios and numbers around the circle) of the crabs with those of echiurans.

Overall, there are no clear violations of foraging theory in documented examples of patch exploitation by deposit feeders. In few cases, however, have rules of thumb or 'satisficing' (doing well enough but not optimally cf. Stephens & Krebs 1986) been tested explicitly against truly optimal solutions. Such tests would be instructive if for no other reason than to see how close the simple algorithms obvious to Richter (1928, cited in Raup & Seilacher 1969) come to optimality.

#### DIET SELECTION

Diet selection also reflects the need for means to collect material quickly in large volumes. Taghon's (1988) results discussed above show that there is no great penalty in ingesting food of low food value. Thus diet selection should be on the basis of opportunity lost (*sensu* Stephens & Krebs 1986) by not selecting high-quality items rather than on the basis of cost of processing poor items. If selecting high-quality items takes too much time, such selection results in loss of the opportunity to ingest a greater mass of food of lesser quality with potentially greater rate of absorptive gain. These volume and time constraints act on diet choice to produce the nearly universal observation of partial preference in particle selection. Most species show a bias toward smaller particles, at least down to the range of 0–10  $\mu\text{m}$  (e.g. Whitlatch 1980) yet ingest nearly the full spectrum of particle sizes below the morphological limit of mouth size. A few species show strong selection for larger particles (e.g. Whitlatch 1974), while others show little apparent selection. There are many reports of non-selective ingestion, but one must be careful to distinguish failure to find selection from convincing demonstration that selection does not occur. Since non-selectivity is the null hypothesis in virtually all these examinations, failure to reject it is not convincing evidence of the absence of selectivity without a formal test of statistical power. Thus most findings of apparent non-selectivity cannot be distinguished statistically from weakly selective feeding. The rates at which deposit feeders are constrained to feed may, however, make strong selection difficult or impossible in settings where sediment transport does not frequently renew the supply of particles.

The impact of feeding rate on diet selection is perhaps most evident when feeding rates are expressed as number of particles ingested per second. The small marine deposit feeder *Corophium* (an amphipod), for

example, feeds at about 30 particles  $\text{sec}^{-1}$  (Miller 1984). Self and Jumars (unpublished) estimate that a 30-cm long *Parastichopus californicus* (a holothuroid) when feeding on even relatively coarse sand (125  $\mu\text{m}$  median grain diameter) ingests  $10^3$  particles  $\text{sec}^{-1}$ . The point of this quantification is to suggest that choice of individual particles may be difficult if not impossible. At 30–1000 particles ingested  $\text{sec}^{-1}$  it seems unlikely that evaluation routinely can be made particle by particle. Rather, mechanical means are becoming apparent that allow moderate bias toward smaller, less dense ( $\text{g cm}^{-3}$ ) or otherwise richer particles without greatly slowing the rate of ingestion. Particle selection can occur upon collection, after collection but before ingestion, or even after ingestion via selective gut passage.

The most widespread method of particle collection in deposit feeding is via mucous adhesives, often coupled with ciliary transport of the layer of mucus in which the particles are ensnared or muscular withdrawal or inversion of the sticky surface for ingestion. From 1 to  $10^2$  tentacles may be employed to enlarge the collection area with less predation risk than extending the whole body, but adhesion can act via the pharynx alone, as Jumars *et al.* (1982) documented in tentacle feeders that had lost their tentacles. Adhesion is used in particle collection by polychaetes, hydrobiid snails, protobranch bivalves, echiurans, sipunculans, holothuroids, echinoids, asteroids, enteropneusts, i.e. by nearly all soft-bodied deposit feeders and also by hard-bodied deposit feeders having soft appendages.

Mechanisms of contact of tentacle and body surfaces with particles have an inherent bias toward larger particles in the deposit (Jumars *et al.* 1982; Whitlatch 1989; Telford 1990). The bias is in direct proportion to particle radius if the collection device is modelled as planar but can approach the square of the radius in the extreme of a zero-width 'line' applied to sediments. Hentschel (in preparation) has predicted and shown that small, tentacle-feeding individuals, whose tentacle widths approach the diameters of particles that they encounter, experience an even greater bias toward large particles than do larger individuals of the same species. Jumars *et al.* (1982) demonstrated with analogue experiments that for spherical particles (and arguably for particles of any shape so long as shape remains constant across size classes cf. Weibel 1963) and for  $d_i < d_j$  where  $d_i$  is diameter of the  $i^{\text{th}}$  particle size class,  $n_i$  is the number of encounters of the  $i^{\text{th}}$  particle size class and  $Q_i$  is the number of beads of the  $i^{\text{th}}$  size class per unit of sediment volume:

$$\frac{n_i}{n_j} \leq \frac{d_i Q_i}{d_j Q_j} \quad (7.4)$$

Coming from the stereology of thin sections, this formulation underestimates the large-particle bias of appressing a flat plane on the sediment surface, from which larger particles will protrude further. This protrusion bias can be overcome by some combination of a layer of mucus (especially if it is thick enough to span the difference among particle heights), ciliation, papillation or rugosity of the collecting surface.

Rather than showing consistent bias towards large particles, however, mucous adhesive-using deposit feeders were found to ingest smaller spheres preferentially down to about 10  $\mu\text{m}$ , below which selectivity again fell (Jumars *et al.* 1982; Self & Jumars 1988). It is important to stress that the feed particles were clean glass and plastic beads of no food value. This unrealistic choice of particles was provided to allow more precise analysis of the mechanical workings of the selection process by eliminating complex geometries and variations in shape and limiting differences in surface properties. For this purpose spheres work all the better because they are out of the realm of organism experience. Little post-contact rejection behaviour was seen in the adhesive-feeding animals in these experiments. Jumars *et al.* (1982) proposed that adhesive failure to retain particles that were too heavy per unit of surface area contacted could account for the observed pattern of selection. Thus probability of contact multiplied by the conditional probability of retention given contact would give the observed, unimodal selection curves peaking at about 10  $\mu\text{m}$ . As predicted from their monotonically decreasing weight per unit of surface area, particles of decreasing specific gravity were ingested preferentially. Selection for large particles thus easily can be explained as a consequence of strong adhesives.

While it has not yet been tested rigorously, this two-step model still appears consistent with published results. More recently, Guieb, Jumars and Self (in preparation) have extended similar experiments with the polychaete *Pseudopolydora kempji japonica* to size-graded, natural sediment grains. As expected, natural grains with rougher surface textures than glass beads are easier to pick up (more surface area of adhesive per contact), shifting the most preferred grain sizes upward by a factor of 10 over the most preferred sizes of spheres. In addition, one size class at a time was coated selectively with a bacterial monoculture. Through a set of internal controls (glass beads of varying sizes interspersed with the natural grains), it was concluded that the animals were able mechanically to select preferentially the coated grains but showed no behavioural flexibility to change the strength of their adhesives to enhance retention of particular size classes rich in food.

This adhesive collection machine is elegantly simple and efficient; heavy, food-poor particles incur no cost of transport since they are not picked up, and great rates of collection are achievable since individual particles need not be evaluated. It is sensitive, however, to the ambient grain-size distribution (cf. Equation 7.3) in terms of selectivity achievable and would appear to be sensitive to cohesion among sediment grains. Sticking together of grains must reduce selective ability for individual components of the aggregate, but the effect need not be entirely negative. *Pseudopolydora kempji japonica*, for example, ceases to feed when there are no unattached grains at the sediment surface, while the sympatric tentacle feeder *Hobsonia florida* continues to feed by pulling grains from the bed so long as overlying water remains (Jumars & Self 1986). Although *H. florida* thus achieves a greater average rate of intake, *P. kempji japonica* presumably obtains richer, fresher organic matter. Similarly, adhesive feeders show great diversity in the degree to which particles are actively rejected after adhesive capture. By comparison with other spionid polychaetes (e.g. Dauer *et al.* 1981), *P. kempji japonica* shows comparatively little rejection after capture, again consistent with its pickup of unattached grains.

The next most prevalent means of particle pickup to adhesion is simple scooping, as seen in many crustaceans. Scooping up a volume of sediments eliminates or at least reduces the bias towards collection of larger particles. It is nearly always accompanied, however, by some mechanism for post-capture, pre-ingestive rejection. Post-capture sorting is perhaps most evident in the intertidal ocypodid crabs *Uca* and *Scopimera* that form discrete boluses of rejected material that volumetrically and gravimetrically grossly exceed the amount of material that is accepted into the alimentary tract for digestion. Their sorting is accomplished by elutriation and flotation. The mechanism has long been known qualitatively (Altevogt 1957; Miller 1961; Fielder 1970), but only recently has received quantitative mechanical analysis (Robertson & Newell 1982). It is clear, however, that great concentration of organic matter for ingestion is achieved, particularly by those species inhabiting sands (Robertson & Newell 1982; Zimmer-Faust 1987). The requirement of a chamber for elutriation limits this mechanism to relatively large-bodied species. In the much smaller amphipod *Corophium*, several sets of experiments document preference for smaller particles (e.g. Fenchel *et al.* 1975; Self & Jumars 1988). Miller (1984) suggested that at least part of the rejection is mechanical. He presented a Poisson model in which relatively coarse setae are used to 'rake' coarse particles into a rejection stream. The

probability,  $P_0$ , that a particle would not be dislodged (rejected) by  $n$  seta-particle contacts, where  $p = b \times d$  is the probability of dislodgement for each seta-particle contact,  $b$  is a coefficient of proportionality and  $d$  is particle diameter, is given by:

$$P_0 = e^{-bdn} \quad (7.5)$$

This model is consistent with Miller's (1984) observed linear dependence of selectivity on diameter. When coupled with a reduced ability to retain the smallest particles (Miller 1984) it is capable of producing a unimodal selection curve (Self & Jumars 1988) very similar to those of adhesive feeders. *Corophium* is also unusually efficient at choosing protein-coated glass beads from uncoated ones (Taghon 1982), suggesting some involvement of adhesion or more specific and behavioural, chemical selection. These crustacean mechanisms would appear to be less sensitive to ambient size-frequency distributions and to cohesion than are adhesive mechanisms, perhaps contributing to the increasing prevalence of crustacean deposit feeders in the abyss (Jumars & Gallagher 1982). Selection by crustacean mechanisms for a particular particle type or size also appears to be less sensitive than adhesive mechanisms to the composition of ambient particle mixtures (cf. Equation 7.3 vs. 7.4 and the results of Robertson & Newell (1982) and Miller (1984).

The only other major class of collection methods is suction, seen in the tellinid bivalves. It also appears to be relatively non-selective, i.e. to have sufficient power to draw in any particle that does not exceed the inhalant siphon's inside diameter (Self & Jumars 1988). As with scooping, pre-ingestive sorting after collection is the rule and is effective for both specific gravity and particle size (Hughes 1975; Hylleberg & Galucci 1975). Again, the ciliary tracts involved have been described qualitatively, but neither a quantitative mechanical analysis of the sorting mechanism nor a suggested dependence on particle size like Equation 7.3 or 7.4 has yet been published. The net result, however, is ingestion of particle spectra remarkably similar to those achieved with the other mechanisms (Self & Jumars 1988). Suction mechanisms of deposit feeding are not known from deep water.

It is easy to overlook some 'passive' means of selection. Since sediment grain sizes reflect extreme transport events more than they do the mean condition, there often is a thin veneer of recently deposited material or material being barely transported by the mean condition. A great advantage of surface deposit feeding is spatial access to this material. This material of low specific gravity and small grain size is available without any need

for sorting devices. Use of external physical processes to accomplish selection is less well known in subsurface deposit feeders, but the arrangement of sediments in trace fossils of subsurface deposit feeder activity provides abundant evidence of grain-size selective slumping (Seilacher 1986), and there is observational evidence on at least one species (Kudenov 1978) that such slumping is used to obtain finer grain sizes for ingestion.

Hydrobiid snails (Lopez & Kofoed 1980) and corophiid amphipods (Nielsen and Kofoed 1982) present another interesting variant on selection by diverging from deposit feeding *sensu strictu*. Over much of the sedimentary particle size range they show selection spectra and partial preferences much like those of other deposit feeders. For grains above about 40  $\mu\text{m}$  in diameter, however, they rasp off surface coatings for ingestion rather than ingesting grains. At this extreme, handling particles one at a time must be worthwhile. The gut space saved for ingestion of smaller particles, including the scrapings, must repay the time and energy costs. That this behaviour is prominent in small deposit feeders, for which an ingested large grain represents a substantial fraction of gut volume, again underscores the volume and throughput constraints of deposit feeding. It would be interesting to compare the limits on grain sizes ingested with corresponding limits on seed size in frugivores. In several ways, eating of fruit with large seeds represents an interesting analogy with deposit feeding.

Although chemical cues stimulating enhanced feeding rate are known, chemicals that induce active behaviours (e.g. ciliary reversals) that lead to preferential retention or rejection of particles coated with them have not been identified. Taghon (1982) showed enhanced selection of protein-coated glass beads over clean glass beads in most of the species that he studied. Without documentation of behavioural change, however, these data could be interpreted simply as a mechanical consequence of the greater 'stickiness' of coated beads. Observations do show behavioural rejection of individual particles and of particle boluses, the ciliary field of an entire tentacle sometimes being reversed, but the chemical or physical cues have not been identified.

There are trends towards less selectivity in larger-bodied species and subsurface deposit feeders (Self & Jumars 1988), for which rates of supply relative to feeding rates may limit selectivity. More generally, effects on rate of absorption as modelled by Dade *et al.* (1990), give a means for estimating maximal costs of selection: selection should occur only to the extent that the time taken to achieve it does not cause greater loss, in terms of the rate of absorption, than would be gained by that

selection. Individuals feeding at maximal rates, i.e. on food of intermediate quality, thus may forego particle selection to a greater extent than individuals feeding on either very low- or very high-quality food.

One means of diet selection not often considered is sorting in the gut. The time constraints imposed by plug flow (Chapter 3) can be relieved to some extent by selective retention of materials that continue to provide absorptive gain and selective passage of food-poor and rapidly utilized materials. Such selective retention is one clear advantage of intracellular digestion, seen notably in some molluscs. There is evidence in some deposit-feeding species for sorting in the gut lumen on the basis of physical properties (Self & Jumars 1978; Penry 1989) and correlated biochemical properties (Kofoed *et al.* 1989). Recent results of Decho and Luoma (1991) suggest that intracellular digestion in some deposit feeders may provide access to food with relatively slow digestive kinetics, though volumetric throughput rates cannot be large. The slowed kinetics of throughput via intracellular digestion may also help to explain the molluscan outliers in Fig. 7.2 (page 131). A particularly interesting question then becomes the means by which particles are selected for this digestive treatment.

Conversely, there are other species, such as *Capitella* sp. I (Forbes & Lopez 1990) that bind their particulate food almost immediately upon ingestion into pellets that preclude particle sorting in the gut. Yet to be determined in either kind of species is the relative passage rate of fluid and particulate phases, though one qualitative experiment (Jumars unpublished) suggests, as expected from experience with larger animals in which tracers are more easily employed, a longer residence time of the fluid. *Pseudopolydora kempji japonica* individuals were each fed (sequentially) anaerobic sediments, Sephadex<sup>®</sup> beads saturated with tetrazolium salts, and anaerobic sediments again. The salts are soluble until they are reduced, when they precipitate irreversibly. Particles travel in plug flow in *P. kempji japonica* (Jumars & Self 1986), providing a clear demarcation of sediments and chromatography beads. A front of precipitation often was evident anterior to the plug of Sephadex<sup>®</sup> but was not found posterior of it, implying generally anteriorward transport of fluid relative to particles. These results are consistent both with the greater fluid than particulate residence times known for large mammals (e.g. Van Soest 1982) and with the ongoing work of Mayer *et al.* (in preparation), who find that solubilization of large polypeptides from marine sediments occurs faster than their hydrolysis to assimilable oligomer size, making longer fluid retention advantageous.

## CONCLUSIONS

These various observations support the notion of rate (i.e. time) constraints as strong determinants of diet selection in deposit feeders and suggest that deposit feeding may represent the natural extreme of chronic limitation by dilute diet and consequent need for rapid, nearly continuous feeding. Time and sensory costs can preclude selection of patches and usually do yield partial preference for poor foods. There is an element of *déjà vu* suggesting caution, however, in the conclusion that individual particles probably are not evaluated for ingestion. This notion was prevalent in early studies of suspension feeders but has been tempered by direct observation (e.g. Price *et al.* 1982 and Chapter 6). Such direct observation is clearly needed in a diversity of deposit feeders, but most notably the subsurface ones, where such observation is the most difficult.

For very few species of deposit feeders is there an organized body of information on the entire foraging strategy. Rather, there are isolated studies of particle or patch selection or of feeding rate. The two most conspicuous exceptions are species from two genera, *Uca* and *Hydrobia*, both of which are intertidal and specialize on benthic diatoms as food. The various studies by Robertson and coworkers cited above show that a sand-dwelling species of *Uca* selects primarily on the basis of patches – and *Hydrobia* appears to do the same (Forbes & Lopez 1986). This generalization fails to hold, however, even for other mobile, intertidal deposit feeders. Knowledge of foraging strategies of subtidal deposit feeders is fragmentary. For few living subsurface deposit feeders – intertidal or subtidal – are frequencies and patterns of movement known. The situation is arguably better for the fossil record.

This dearth of integrated information is matched, again with one exception from Robertson's studies (as extended by Weissburg & Zimmer-Faust 1991), by particular lack of information on chemical cues that initiate ingestion and modulate its rates in deposit feeders. Given the demonstrable profitability of such information in understanding the foraging of insects (Bernays 1985), this lack is all the more glaring. Subsurface deposit feeders are well supplied with chemosensory equipment (e.g. the nuchal organs of polychaetes) whose capabilities might give good clues to the kinds of patches that subsurface deposit feeders prefer and thus to the resources that support them.

In summary, marine deposit feeding is seen to be an extreme digestive strategy, entailing rapid throughput of organically dilute, largely indigestible material. Marine deposit feeders contrast markedly with

fermenters (Chapter 3) that extract energy from refractory but ultimately digestible material and that hence have much longer gut residence times. The constraint to operate at high volumetric throughput restricts deposit feeders to relatively rapidly digestible material, limits minimal sizes of deposit feeders, selects for simple but effective means of patch utilization and results in the dietary inclusion of particles of low or zero food value. Machine-like methods of particle collection and sorting used by deposit feeders from diverse taxa converge in showing peak selection of lower excess density (density of the particle minus density of the fluid). The sorting 'machinery' thus converges evolutionarily on physical characteristics associated with geophysical transport and renewal of deposits, i.e. on newly arriving material.

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