

Two Roads to Sparagmos: Extracellular Digestion of Sedimentary Food by Bacterial Inoculation Versus Deposit-feeding

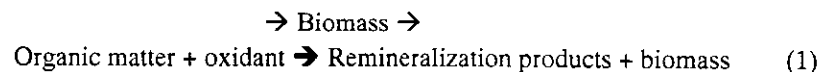
Lawrence M. Mayer*, Peter A. Jumars, Michael J. Bock, Yves-Alain Vetter,
and Jill L. Schmidt

Abstract: Extracellular digestion is a frequent mode of dissolution of dispersed organic detritus in marine sediments. Two geometric modes of deploying this digestive attack are extracorporeal: prokaryotic unicells, and intracorporeal: metazoans with flow-through guts. Enclosed digestive geometry gives metazoans greater ability both to retain digestive agents and to obtain digestive products, allowing them to create digestive conditions more intense than are generally found with communities of sedimentary bacteria. Metazoans hence can dissolve food substrate more quickly. Extracellular hydrolytic enzymes are sorptive for bacteria and dissolved for animals, enhancing both speed and net digestive gain for their respective geometries. Experiments showed little evidence for mass loss of digestive agents to sediments transiting deposit feeders. Standing stocks of sedimentary bacteria—ubiquitously on the order of 10^9 bacteria (cc pore water)⁻¹—set a cap on digestive rates by bacterial inoculations of sediment, and provide metazoans a further kinetic advantage at food concentrations greater than the bacterial biomass. Metazoans therefore have digestive advantage on substrates amenable to concentrated, quick dissolution, suited to their role as high wattage consumers of sedimentary food. Deposit feeding shows strong analogy to laundry technology.

The Opportunity

Particulate organic matter settles as planktonic detritus from the water column. It may be converted into biomass and energy, if successfully rended, dissolved, and hydrolyzed to oligomer size (*sparagmos*; “nature grinding down and dissolving matter to energy,” Paglia 1990) and then absorbed into cells. This nutritional detritus is mixed, by physical and biological means, into the top several centimeters of sediment, becoming increasingly diluted (if averaged over size scales of > 1 mm) by the indigestible sedimentary matrix.

In chemical terms, a dilute fuel, or reductant, is available for combination with an oxidant. Metabolizable organic matter in the presence of oxidants forms a galvanic cell, or battery waiting to discharge. Heterotrophic prokaryotes and eukaryotes are catalysts capable of physically and then chemically combining the oxidants and fuel—discharging the battery. A conceptual chemical reaction for this process is



The battery discharges with a voltage determined by the relative redox states of the oxidant and reductant, and with an amperage governed by the amount of reactants. This reaction is partially autocatalytic, in that its progress yields additional catalyst that can accelerate the reaction, as evidenced by an induction of biomass after deposition of bloom material (Graf et al. 1982; Lehtonen & Andersin 1998). Modeling of organic matter decay must, therefore, explicitly take into account the concentration or activity of biotic catalyst, especially if this catalyst term varies among sites or times being considered.

The heterotrophic opportunity requires a sequence of processes including encounter between organism and food particle, digestion of the food, digestate transport to and absorption by the consuming cells, and subsequent cellular metabolism. Two organismal plans adapted for responding to this opportunity are dispersed microbes (unicells) and multicellular animals. Each plan has various advantages with respect to the several tasks involved in using detrital substrate. Here we emphasize the digestive step, comparing two strategies designed to digest the largely polymeric food substrates available in sediments.

Digestive Response Strategies

FRAME OF REFERENCE

Digestive optimization can result from enhancing dissolution of the polymeric substrate and restricting costs of doing so. Digestion rate will be some positive function of the activity of digestive agents and substrate concentration and lability (ease of dissolution). One schematic possibility that relates substrate mass (M), time (T) and volume (V), in Michaelis-Menten form, is

$$\text{Digestion Rate} = \sum \left[\{DA\} \frac{k_Q S_Q}{(K_Q + S_Q)} \right] \quad (2)$$

where,

k_Q is the lability (T^{-1}) of a polymer substrate of quality Q in the food mixture,

S_Q is substrate concentration ($M V^{-1}$),

K_Q is a half-saturation constant ($M V^{-1}$), and

DA is the amount of the digestive agent(s) deployed against the substrate.

Digestion Rate and DA can be normalized to either biomass or system volume (if normalized to system volume, then the units would be $M V^{-1} T^{-1}$ and $M V^{-1}$, respectively). The measurement and parameterization of DA are problematic and depend on interactions among various enzymes and other digestive agents such as surfactants. The lability parameter (k_Q) is a rate constant that results from an interaction between the digestive agents and substrate. It could be dependent on factors such as susceptibility of substrate bonds to hydrolysis by DA , or physical access such as the amount of surface area of food substrate available to DA . In the latter case, k_Q can be enhanced by grinding, which may be significant in animals with muscular digestive chambers or jaws.

This formulation can be thought of as a normal Michaelis-Menten expression in which the V_{\max} term has been decomposed into a rate constant (k_Q) times the total concentration of digestive agents ($\{DA\}$), the latter being dependent on biomass or digestive agent secretion. This equation also makes explicit the substrate compartmentalization of the well-known multi-G models (Berner 1980). Thus

Eq. (2) accounts for organismal participation in organic matter decay, as did the multi-B model of Smith et al. (1992), albeit in different form. Digestive optimization, then, requires increasing the $\Sigma^o k_o S_o / (K_o + S_o)$ term and decreasing the cost of the {DA} terms.

This paper examines dispersed unicellular prokaryotes and metazoan deposit feeders that utilize primarily extracellular digestion. However, the former digest extracorporeally and the latter digest intracorporeally. There are other digestive approaches (primarily intracellular, e.g., protozoans, mollusks), but this paper will focus on comparative aspects of the extracellular types. An important reason for this focus is that the terms in Eq. (2) have received more attention for extracellular digesters, and quantitative examination of these terms for intracellular digesters has not begun.

In terms of biomass distribution, bacterial and animal populations differ in the degree of patchiness of cells. They can have similar total biomass in sediments (Schwinghamer 1983); however, bacterial cells are highly dispersed and animal cells are aggregated into larger units that are in turn dispersed. To access food substrate, bacteria spread into (inoculate) the sedimentary food matrix, whereas animals gather and concentrate food matrix inside their multicellular bodies. Each may secrete cell-free, extracellular enzymes and perhaps other digestive agents into the food matrix, and absorb the resulting dissolved hydrolyzate. Additionally, each probably performs some hydrolysis with external but membrane-bound enzymes, to complete the more distant hydrolysis performed by the cell-free enzymes (Ugolev 1972). In energetic terms, there is advantage to the organism in restricting the loss of digestive agents (DA) to the environment and enhancing the capture of hydrolyzate that they create. There are strong contrasts between abilities of animals and bacteria to achieve each of these goals.

BACTERIA

Assuming cell-free enzymes, bacteria will rely on diffusion to transport both secreted digestive agents and the resultant hydrolyzate. Bacteria's small cell sizes and high surface area:volume ratios set them up for transport limitation by diffusion (Koch 1990). Extracellular bacterial enzymes diffuse spherically outward from the secreting cell but adsorb strongly to particles, such as their target substrate, which promotes local action that most benefits that cell (Vetter et al. 1998). Diffusion of hydrolyzate will be spherical from the point of hydrolysis, resulting in only partial return to the organism that secreted the enzyme (Fig. 1). The inefficient procurement of nutrition due to these sequential, spherical diffusion steps probably restricts net cost-effective foraging ambits to ca. 10 μm for individuals (Vetter et al. 1998). Dependence on diffusion, coupled to high partitioning to the solid phase (of enzymes, at least), implies slow transport for enzymes and hydrolyzates.

This inefficiency must lead to sharing of digestive effort and gain, by both individual cells and conspecific clonal populations (or genets, Andrews 1991), with other bacterial species in a mixed-species bacterial community. Mucus envelopes may enhance retention of both DA and digestive product for bacteria (Plante et al. 1990). Alternatively, monoclonal "swarming" of bacteria, for example, myxobacteria found in soil (but not marine) environments, can enhance net benefit to the genet from free extracellular enzymes (Reichenbach 1984). The lack of water in soils also allows bacteria to concentrate enzymes locally. The higher diffusivity of digestive agents and products in sediments, however, must reduce the marginal return on digestive agent secretion to sedimentary bacterial genets.

ANIMALS

Animals enhance transport of food particles, digestive enzymes, hydrolyzate, and consuming cells by advective means. Animals' gut enzymes are largely dissolved (Mayer et al. 1997), increasing

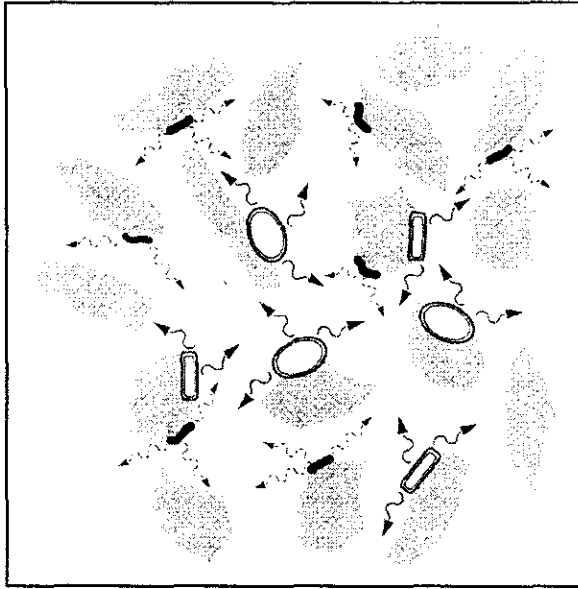


Fig. 1. Inoculation of food-containing sediment by two species of bacterial cells (rods and ovals), forming two genets. Each cell secretes cell-free enzymes (arrows with solid lines), which diffuse spherically, encountering food patches (black coatings on gray sediment grains) from which then diffuses hydrolyzate (arrows with dashed lines). Hydrolyzate is shared among the two genets. Figure adapted from Fig. 1 of Vetter et al. (1998).

effective foraging distance between food substrate and the secreting and absorbing cells well beyond the 10 μm viable for bacteria. Upon absorption at the gut wall, advection in the circulatory system takes over the transport of hydrolyzate to absorbing cells throughout the individual. This combination of partitioning into the fluid phase and fluid advection implies faster transport of enzymes and hydrolyzates than for bacteria, and routinely increases profitable foraging distances between digestion and consuming cells to centimeters in macrofauna—three orders of magnitude greater than bacteria.

The enclosed digestive geometry of animals provides an opportunity for greater retention of secreted digestive agents. Losses in a flow-through digestive system may be in dissolved or adsorbed form (i.e., adsorbed to transiting sediment). Loss via dissolved form is likely restricted through resorption, as evidenced by strongly lower enzyme and surfactant activities in hindguts relative to midguts (Mayer et al. 1997), or control of fluid transport. Gut

fluid retention (Jumars 1993; Mayer et al. 1997) is currently being quantified in our lab. Adsorption to transiting sediment, which is poorly understood, was addressed here in two ways.

Experimental Methods and Results

In order to evaluate export of enzymes from macrofaunal digestive systems, we measured enzyme activities in ambient sediments and fecal material of *Arenicola marina* (Sheepscot estuary, Maine). Ten paired sediment samples from feeding pits and fecal mounds were collected and stored at -80°C until analysis. Activities of three enzymes—esterase, lipase, and protease—were measured by fluorescence assay (Mayer 1989; Mayer et al. 1997). Fecal ejecta had the same or lower enzyme activities as the ambient sediments (Fig. 2), indicating no significant export of gut enzyme activity by the animals. In the case of protease there was a significant decrease in activity in the feces.

In a second series of measurements, we examined changes in enzyme activity and surfactant concentration after gut fluid incubations with different size fractions of sediments. Subtidal estuarine sediments were collected from the Damariscotta estuary, on the mid-coast of Maine, and size-separated by wet sieving into < 10 , 10–63, and 63–250 μm fractions. Digestive fluids of two deposit feeders, *Arenicola marina* (from Lubec, Maine) and *Parastichopus californicus* (from Puget Sound, Washington), were obtained as described in Mayer et al. (1997). Each species commonly inhabits sandy environments. The sediment size fractions were incubated with aliquots of the two gut

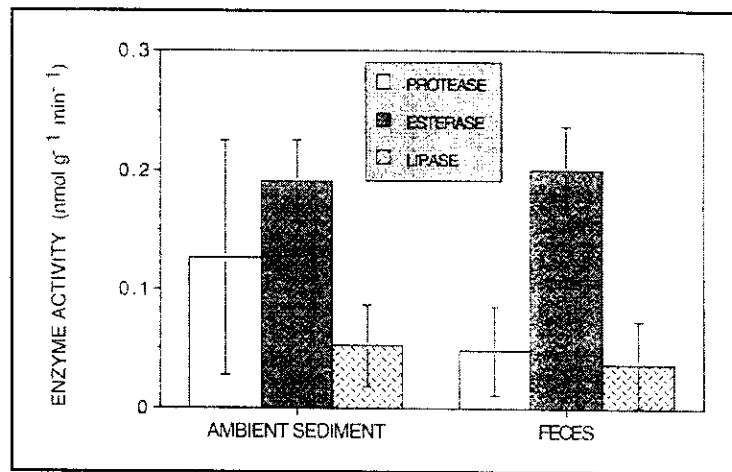


Fig. 2. Extracellular enzyme activities ($\text{nmol g}^{-1} \text{min}^{-1}$) in ambient sediments (feeding pits) and feces of *Arenicola marina*. Bars are standard errors.

fluids for 0.5 h at room temperature, and then assayed for enzyme activity (protease, esterase, lipase, using the fluorescent substrate methods of Mayer et al. 1997) and surfactancy (using contact angle titration assays of Mayer et al. 1997). Gut fluid with no added sediment served as a control.

Minor, though measurable, decreases in most enzyme activities were found in the gut fluid from *A. marina* (Fig. 3). These losses increased with the amount of sediment surface area added to the gut fluid. The role of surface area (or a correlate such as organic carbon concentration, Mayer 1994) was separated from other factors potentially varying among size fractions. This was achieved by adding different mass amounts of various size fractions of sediment to obtain the same surface area per milliliter of gut fluid. The greatest fractional loss of activity occurred with lipase. With *P. californicus* gut fluid, there was no loss of any enzyme activity except for lipase. The relatively high losses of lipase are consistent with the need for this enzyme to adsorb to lipid-water interfaces in order to function. Our enzyme assay results do not allow distinction between inactivation of enzymes and adsorption of enzymes onto the sediments.

Surfactancy was assessed with contact angles of gut fluid on Parafilm, and titrating with clean seawater to test for presence of micelles (Fig. 4). The *P. californicus* gut fluid showed evidence of micelles: in a two-phase titration plot the contact angle remained fairly constant with dilution below 100% gut fluid, until an inflection point at which the contact angle increased with further dilution. This inflection point is termed the critical micelle dilution factor (CMD), and represents the dilution at which all micelles initially present in the gut fluid disappear. Neither initial contact angles nor the shape of subsequent titration plots changed significantly as a result of the adsorption experiments. An exception was a small increase in the CMD in one of the triplicates using the $< 10 \mu\text{m}$ fraction at the highest surface area loading (Fig. 4C). This increase would correspond with adsorption on the order of 15–20% of the surfactant. *A. marina* gut fluid showed little evidence for micelles in the raw gut fluid, which is typical for individuals of this species. No changes in initial contact angles or titration plots were observed after sediment incubation, also consistent with little or no adsorption of surfactant. While the contact angle approach only crudely assesses surfactant concentration, these results do indicate a lack of strong adsorption of the compounds responsible for surfactancy.

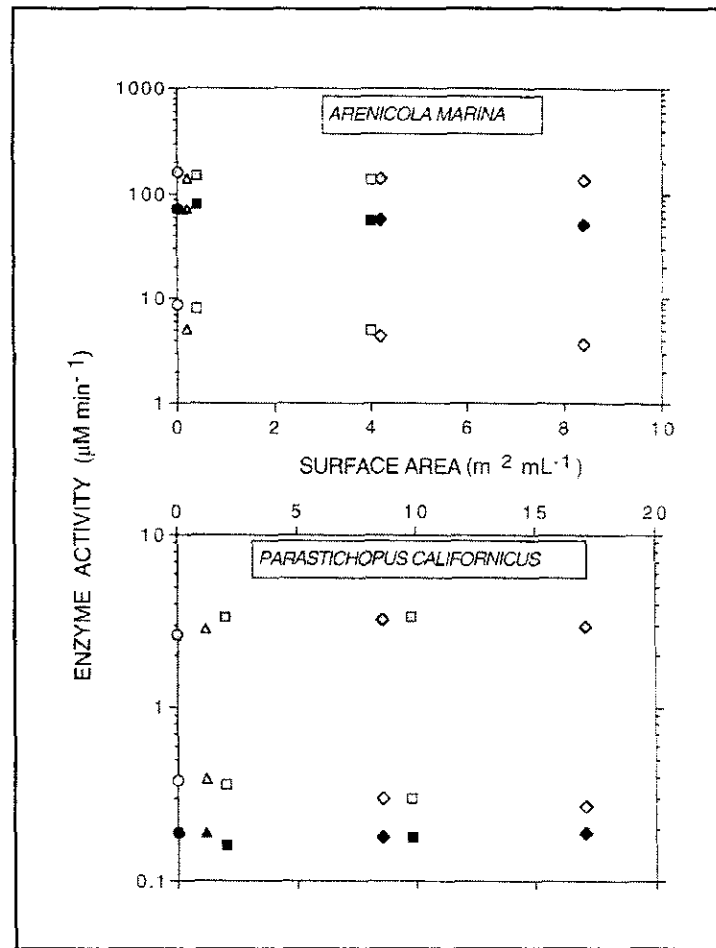


Fig. 3. Enzyme activities before and after incubation of midgut fluids of *Arenicola marina* (top) and *Parastichopus californicus* (bottom) with size fractions of a marine sediment. Gray symbols: esterase, white symbols: lipase, and black symbols: protease. Circles represent the control (no sediment), triangles are the 63–250 μm fraction, squares are the 10–63 μm fraction, and diamonds represent the < 10 μm fraction. Significant losses of activity after incubation were found for lipase in *Parastichopus* gut fluid ($p = 0.0024$) and protease in *Arenicola* gut fluid ($p = 0.013$).

With the finest size-fractions (i.e., 8–17 $\text{m}^2 \text{mL}^{-1}$), the amount of surface area incubated with these gut fluids likely exceeds the normal *in vivo* processing conditions of these animals by an order of magnitude. Furthermore, these experiments represent midgut conditions; hindgut concentrations of digestive agents are much lower (Mayer et al. 1997), which may allow desorption of material adsorbed in the midgut. Thus minimal loss of dissolved enzyme activity during gut passage probably occurs *in vivo*. These results are consistent with the fecal pellet enzyme activity assays and indicate that deposit feeders do not incur significant loss of enzyme proteins. As the same conclusion applies to the surfactancy, we conclude that little {DA} is lost by adsorption to transiting sediment in these species.

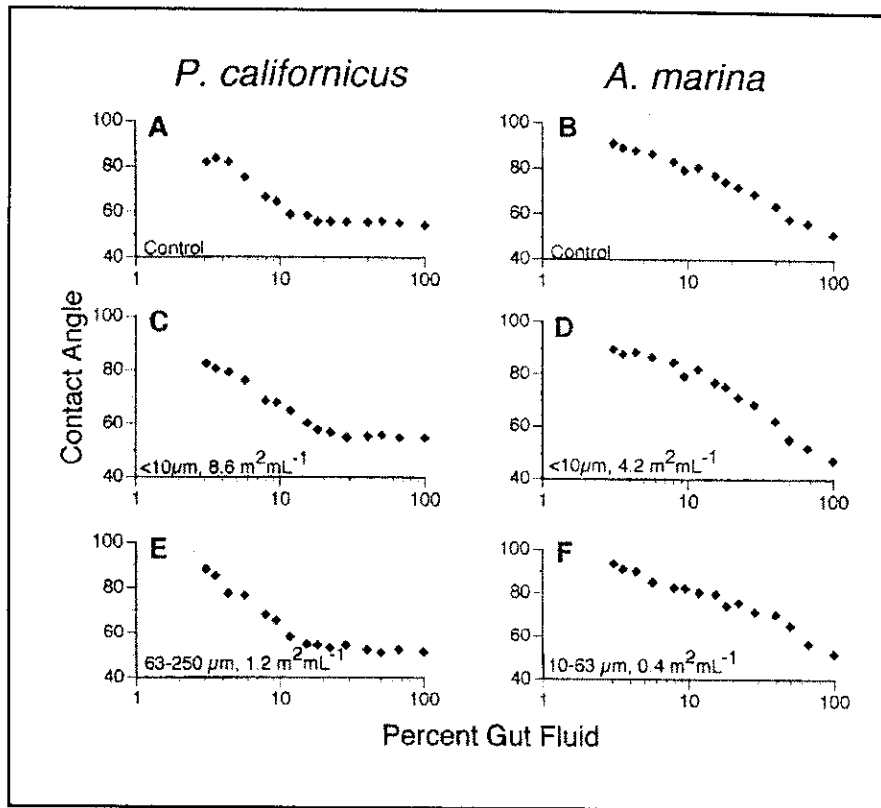


Fig. 4. Surfactant activity, as measured by contact-angle titrations, after incubation of midgut fluids of *A. marina* (C, E) and *P. californicus* (D, F) with size fractions of a marine sediment. Controls (no sediment) are given by A and B, respectively. The X-axis values represents dilution of original gut fluid; 100% is pure gut fluid and smaller values are after subsequent dilutions. C represents the most extreme case of apparent surfactant adsorption, with the change in slope (i.e., CMD) increasing from its control value of ca. 15% gut fluid to about 22% gut fluid. E represents the typical *A. marina* titration plot after sediment incubation, with no apparent change in CMD.

Animals have a similar advantage (relative to bacteria) in absorption efficiency of hydrolyzate: before releasing gut fluids to the environment the hydrolyzate is exposed to absorptive gut epithelia. By reducing dissolved hydrolyzate via gut wall absorption, re-equilibration between gut fluid and sediment will promote continued desorption of hydrolyzate that might have adsorbed onto sediment particles. Adsorptive loss of hydrolyzate onto transiting sediment should be especially reduced by lowered concentrations in the hindgut, again displacing sorption equilibria toward the dissolved phase, which facilitates further absorption.

A strong analogy exists between the digestive approaches of deposit-feeding animals and laundry technology (Fig. 5). Each seeks to dissolve a subset of the organic matter associated with particles. Each process has a wash cycle using enzymes and surfactants, that work together to dissolve, selectively, the desired organic compounds while leaving the rest of the particulate matrix

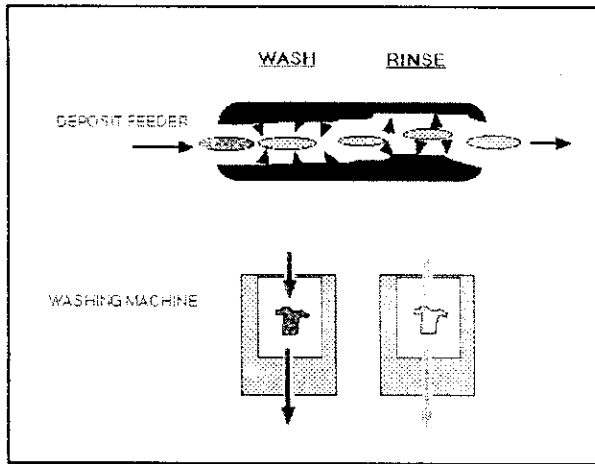


Fig. 5. "Wash-and-rinse" cycles in deposit feeders and washing machines. In deposit feeders the dirty material (pellets) is input at the mouth, with net secretion (arrowheads) of digestive agents in the foregut and midgut. Gut wall absorption occurs throughout the gut, but it is completed in the hindgut by rinse cycles induced either by bringing clean water from the posterior or by simple absorptive removal of dissolved materials that displaces sorption equilibria toward desorption from sediment surfaces. In a washing machine, digestive agents are physically introduced in the wash cycle and then physically advected away. Subsequent rinse cycles of advectively introduced clean water induce desorption of remaining adsorbed dirt and cleaning agents.

(inorganic and organic) intact. The selectivity of each process is less than perfect, resulting in faded clothes and bioavailable pollutants. Sorption equilibria will cause some desirable organic materials to remain stuck to transiting particles. Rinse cycles with clean water, which can be enhanced in invertebrate hindguts by anal inspiration, promote displacement of adsorbed material toward the aqueous phase. One adaptive result of rinse cycles in deposit feeders may be to remove chemical cues that would attract predators. Material in the aqueous phase is then absorbed in the animal system, which is in contrast to the laundry system where extracts are discarded. There are unexplored possibilities in this analogy. For example, commercial laundry formulations add chemicals to be adsorptively retained by clothes and stimulate responses from other biota after the laundry event; analogous deposits can be hypothesized for fecal ejecta from animals.

Retention of Digestive Agents Rewards Higher {DA}

Bacteria and animals apparently have developed fundamentally different extracellular enzymes, in terms of adsorbability, to improve the net rate of nutrition gained. Their different efficiencies at retention of digestive agents and products should result in different net returns of product per investment of DA (Fig. 6). Gross and net returns of hydrolyzate due to enzyme secretion should increase until hydrolysis sites are saturated (Fig. 6A, B). However, the net return should be greater for animals (Fig. 6A) than for bacteria (Fig. 6B), because of greater retention of both secreted enzymes and hydrolyzate. Sedimentary bacteria likely operate at enzyme activities below saturation of substrate, as evidenced by enhanced hydrolyzate release upon addition of fungal proteases (Mayer et al. 1995).

Surfactants should exhibit different net yield curves. The purpose of surfactants found in animal guts is not well understood (Mayer et al. 1997), but their common occurrence at levels above the critical micelle concentration (CMC) suggests that the micelle form is critical. They probably act to partition food substrates, digestive agents, and hydrolyzates into the solution phase. Hence gain should increase markedly above a secretion rate necessary to maintain the CMC, leading to a sigmoid gain curve (Fig. 6C). For an open hydraulic system, such as dispersed bacteria, a high rate of continuous surfactant secretion would be necessary to maintain these concentrations above the CMC. In a partially closed gut system, especially with fluid retention, the secretion rate necessary to

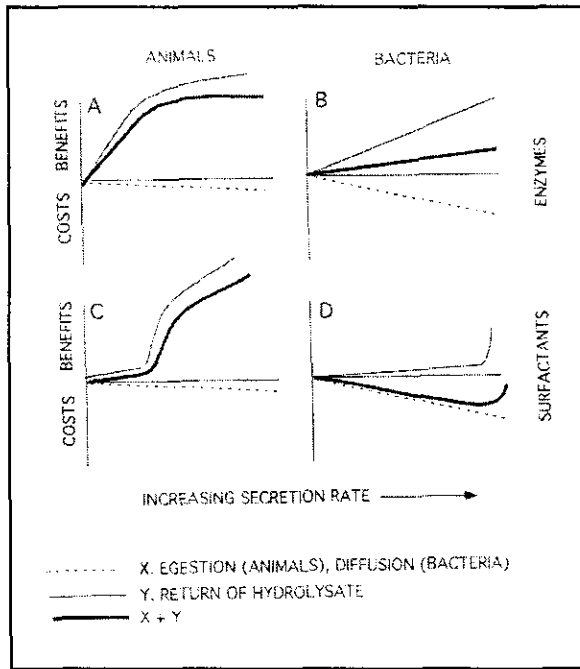


Fig. 6. Costs and benefits (mass time⁻¹) of secretion rate (mass time⁻¹) of digestive agents (enzymes or surfactants) to bacteria versus animals. Costs (dashed lines) result from spherical diffusion (bacteria) and fecal egestion (animals); animals suffer less cost because they recover digestive agents. Benefits include gross gain of hydrolyzate (thin lines) and net gain after loss of digestive agent (heavy lines). Special cases: (A) We assume saturation of hydrolytic sites at some high level of enzyme secretion; (B) Saturation of hydrolytic sites does not occur; (C) Gain increases only when critical micelle concentration (CMC, that concentration above which micelles form) is exceeded, due to increased transport of slightly soluble lipid digestates; (D) Achieving the CMC, and consequent gain in benefits, takes greater secretion rate for bacteria than for animals because of diffusive loss.

bacterial-protein cc⁻¹ (Mayer et al. 1995). If all members of the community are active and their maximum doubling time is on the order of 1 h with an anabolism:catabolism ratio of 0.25:0.75, then this community cannot eat more than 0.2 mg-protein cc⁻¹ h⁻¹. This figure is almost certainly an overestimate because of the inactivity of most sedimentary bacteria.

Deposit feeders have gut residence times similar to bacterial doubling times. However, their advective transport (gathering food, distributing digestate) and storage (e.g., goblet cells) systems allow them to apply the capability of a much larger biomass, in terms of digestive action and consuming cells, to a parcel of sediment than can the bacteria resident in that parcel. Thus animals should have a kinetic advantage in digesting food at concentrations above that of the resident bacteria on short time scales. At least some benthic animals are apparently "tuned" to grow positively only

maintain concentrations above the CMC should be lower. This advantage should be especially important for nutritional materials requiring micelles for solubilization or transport (e.g., lipids).

The guts of deposit-feeder taxa such as polychaetes, echiurans, and sipunculids have enzyme activities that are 10²–10³ times higher than the extracellular bacterial enzyme activities found in sediments, although deposit-feeding holothuroids exhibit activities similar to bacterial levels (Mayer et al. 1997; unpublished data). All deposit feeders examined so far, however, show evidence for surfactant micelles (Mayer et al. 1997), so that the combination of enzymes and surfactancy in holothuroids may cause a {DA} that is more intense than that exhibited by sedimentary bacteria.

Biomass and Time Constraints

The standing stock of sedimentary bacteria is usually on the order of 10⁹ bacteria cc⁻¹ (Schmidt et al. 1998). This concentration is so common that it suggests a cap on biomass, although any firm explanation for its ubiquity is not settled. Nevertheless, this standing stock sets an upper limit to bacterial food utilization per unit of time. Expressed as protein, the major cellular constituent, 10⁹ bacteria cc⁻¹ is equivalent to ca. 0.05 mg-

above this threshold flux rate of 0.2 mg-protein $\text{cc}^{-1} \text{h}^{-1}$ (Taghon & Greene 1990; Tsutsumi et al. 1990). There is, as yet, no physiological budgeting that can explain minimum food quality requirements for deposit feeders. There may be other explanations, but it is possible that this threshold flux simply reflects an inability of animals to compete with bacteria at concentrations below this value. The ubiquity of bacterial densities of ca. 10^9 bacteria cc^{-1} indicates their ability to maintain biomass at input fluxes of < 0.1 mg-protein $\text{cc}^{-1} \text{h}^{-1}$.

Relative Success, Particle Selection, and Bioturbation

Obviously both digestive strategies lead to sparagmos in sediments, and many factors besides digestion control the relative biomass and activity of animals versus bacteria (Andrews 1991). Metazoans in soft sediments usually appear to account for less than half of secondary production (Gerlach 1978; Probert 1986; Riddle et al. 1990; Piepenburg et al. 1995), except in areas with energetic flow regimes (Dye 1981). However, estimates generally rely on biomass measurements coupled to production:biomass (P:B) ratios, and have considerable uncertainty due to ignorance of the percent of active bacteria.

Food disappears more rapidly under animal than under bacterial attack. *P. californicus* gut fluid digests protein more quickly than native extracellular enzymes (Mayer et al. 1995). Half-lives of proteinaceous materials are on the order of a gut residence time under metazoan digestion (Carey & Mayer 1990) and on the order of weeks to months under microbial attack (e.g., Mayer & Rice 1992). The differences in these half-lives are reduced only slightly by taking into account assimilation of some fraction of the protein by the metazoans.

If animals are geared, digestively, for high rates of substrate dissolution, then deposit feeding should succeed if the animals can obtain nutrients from a parcel of sediment more quickly than can bacteria. Their relative advantage must proceed from more rapid kinetics of dissolution (due to higher {DA}) than is possible by the standing stock of bacteria generally observed. One obvious implication for feeding strategy is to select microzones where food concentration, of a quality amenable to hydrolysis on time scales of 10^1 – 10^3 min, is particularly high. Such selection (reviewed by Lopez & Levinton 1987; Jumars 1993) occurs at particle to patch scales, utilizing physical and chemical attributes of the particles as well as natural sorting mechanisms such as resuspension (Muschenheim 1987). Many animals are observed to focus on regions of high-quality particles, mining the steady flux to the sediment-water interface or deeper deposits in turbidites (Griggs et al. 1969). The food source for many conveyor-belt, subsurface deposit feeders is more problematic, although it may represent either fresh material hoed down burrows or accumulated as adsorbed remains from fundamentally inefficient (Vetter et al. 1998) microbial action.

Surficial deposit feeding provides a temporary opportunity for patch selection in the vertical, before removal of surficial food enrichments by either bacterial inoculation from below or downward mixing. Kannevorff and Christensen (1986) accordingly found rapid feeding response to spring bloom detritus by macrofauna, followed by burial and subsequent utilization by bacteria. Burial of detritus has the dual jeopardy to animals of dilution plus the acceleration of bacterial inoculation (mixing the food into the inoculum rather than vice versa). The relative advantage of surficial deposit-feeding should be greatest in areas with relatively little sediment dilution of the food-fall—either by resuspended sediment mixing with food in the nepheloid layer or physical mixing of the upper 0.1–1.0 cm in the sedimentary bed. Animal ingestion causes sediment mixing and hindguts promote bacterial growth (Plante et al. 1989) so that animal feeding may shift advantage toward the

prokaryotes, although mixing can benefit some metazoans (e.g., subsurface deposit feeders). Initial dilution may increase bioturbation rates as bulk feeding increases in response to lowered concentration (Taghon & Greene 1990), while continued dilution may bring food levels to a threshold value below which prokaryotes dominate. Animal feeding has long been thought to stimulate microbial activity (cf. Yingst & Rhoads 1980), but here this stimulation is provided a different rationale. A coherent understanding of the relationship between food inputs and sediment mixing, important for paleoceanography, will benefit from a systematic examination of how dilution versus enrichment of food particles facilitate the partitioning of mass fluxes between bacteria and animals.

Biomass itself is concentrated labile organic matter, and its consumption (carnivory, herbivory, and bacterivory) is therefore best achieved by metazoans. Bacterivory as a principal source of nutrition, however, can only be achieved by smaller animals which can select particles at very small scales; at larger size scales the concentration of nutrition is too dilute (Cammen 1980). Carnivory, herbivory, and bacterivory are not known as bacterial feeding strategies in the sea, perhaps due in part to their low {DA} capabilities. Terrestrial myxobacteria, with higher {DA}, are bacterivorous.

Conclusions and Analogies

In the context of Eq. 1, animals are designed for relatively high {DA}, which relies on higher concentrations and mobility of digestive agents. They also appear to be adapted to higher $\Sigma^{\circ}k_{\text{O}}S_{\text{O}}$, which can be due to enriched concentrations and/or greater lability of polymer substrate.

Applying a military analogy, dispersed bacterial cells resemble guerilla warfare while animals are structured "armies" of cells. Armies, as a form of warfare, are effective against concentrated targets, and developed with the rise of agriculture and towns. They do not do well in regions of dilute resources unless connected by supply lines to a concentrated resource base (hence scorched earth tactics in military defense).

Returning to the battery analogy, food resource utilization by organisms can be parameterized in terms of wattage (W; Peters 1983), which can be decomposed

$$W = EI = \text{potential} \times \text{current} \quad (3)$$

where the potential (E) is the difference between oxidant and reductant redox states and current (I) is the mass flow of metabolized food ($\Sigma^{\circ}k_{\text{O}}S_{\text{O}}$). Oxygen-requiring animals are high-voltage consumers. Sedimentary animals seem to be tuned also for high current, requiring high food concentration and/or lability, so that animals are high-wattage consumers. In areas of low food concentration or lability (hence low I), or poor oxidants at depth in sediments (hence low E), the battery discharge is carried out primarily by low-wattage bacterial communities. The digestive approach of the metazoan "washing machine" is suited to its high wattage requirements. Thus metazoans emerge or arrive to discharge food enrichments, in space and in time, where oxygen is also available. It is intriguing to consider how metazoan evolution in the Proterozoic–Paleozoic might have been guided by current versus voltage.

Acknowledgments

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