

DIGESTIVE ASSOCIATIONS BETWEEN MARINE DETRITIVORES AND BACTERIA

Craig J. Plante, Peter A. Jumars and John A. Baross

School of Oceanography, WB-10, University of Washington, Seattle, Washington
98195

KEY WORDS: bacteria, detritivore, digestive associations, marine

INTRODUCTION

Although bacteria can be associated with animals in a wide variety of ways, nutritional interactions are by far the most ubiquitous. We define them simply and inclusively as interactions in which proximity allows nutrient transfer in one or both directions, with the most obvious associations involving the alimentary tract and feces, and food just prior to ingestion. Transient or indigenous, attached or free-living bacteria may be obligately or facultatively associated with their animal counterparts.

Obligate interactions of economic importance, e.g. in ruminant and termite guts, are clearly the best studied. A few other strong interactions, such as competition for food between bacteria and carnivores, are reasonably well understood intuitively. We purposely choose here a system—marine detritivory—in which intuition is a less adequate guide, and mutualism, competition, and predation all are suggested interactions. Because marine detritivores ingest bacteria-covered particles, interactions are virtually assured; we look for some methodical approach by which their existence and importance can be predicted and analyzed. The one we adopt for this review is a cost-benefit analysis that adapts and integrates disparate approaches developed for other applications. We evaluate its predictions through literature review. Then we evaluate the ecosystem consequences of our tentatively concluded interactions

and discuss discrepancies and gaps that require future research. Our focus is limited by space to be marine. We draw a few contrasts with terrestrial and freshwater detritivory to emphasize the differences and the reasons for them. Where we suspect that our analyses and conclusions could be extended to broader taxonomic groups more prevalent in these other environments (e.g. fungi), we broaden and loosen terminology (e.g. using “microbes” instead of “bacteria”).

Defining Detritivory

Detritus is usually defined from an ecosystems perspective rather than from the perspective of a species that is a gourmet or gourmand of detritus. Most often it is defined as nonliving, particulate organic matter without regard for the fact that within the biosphere nonliving detritus and living decomposers are associated intimately. Its definition nearly always includes, either implicitly or explicitly, the observation that some kinds of organic matter degrade slowly by the totality of ecosystem processes and therefore show high standing stocks. It often includes the historically easy and gross equation of low food quality with high organic carbon content relative to components that are potentially in much shorter supply, such as biochemically available nitrogen or calories of chemical energy.

The glib definition of detritivory, then, is feeding on detritus. On closer inspection, however, the ecosystem perspective from which the definition of detritus stems is inadequate to distinguish between two radically different feeding strategies. One, a “gourmet” strategy, is ingestion of only the most digestible components of the decomposer system, especially the microbes involved in decomposition. Because of the intimate association of decomposers and the detritus they inhabit, gross inspection of gut contents is unlikely to reveal immediate distinctions between such animals and less discriminating animals that ingest detritus and its associated decomposers in bulk.

A useful distinction is Yonge’s (130) idea of macrophages and microphages, the latter handling food material in bulk rather than one item at a time. The small organism searching through the detrital community and ingesting primarily relatively rich microbial biomass, then, is excluded even from the very general definition of detritivores on two counts. It feeds primarily on living matter and primarily on material that is of high bulk food value by either gross C:N indices or finer measures. We suggest that this exclusion of “gourmets” applies in general to marine meiofauna and to their terrestrial and freshwater counterparts (e.g. collembolans and free-living soil nematodes). An analogous gradation occurs among browsing herbivores. Small browsers apparently are able to be highly selective, compared to large browsers (112). Large detritivores and large browsers, then, appear to have many problems in common.

Animal size and bulk composition of ingested material clearly are easier features to identify and measure than are the constituents of ingested material that are digested and absorbed. In recognition of what was known or could be learned easily about most detritivores, a diverse group of marine scientists grappling with a useful operational definition explicitly used Sibly's (112) insightful study of browsing herbivores to redefine detritivory toward the microphagous end of the spectrum as "frequent feeding on material of low bulk food quality" (71). It should not be equated with a lack of selectivity; rather it appears that these "gourmands" of detritus that ingest up to 300 times their body dry weight per day (118) must rely on mechanical selectivity to maintain their rapid feeding rates (111). While this definition of detritivory appears to do little violence to earlier connotations based on an ecosystems perspective, there are important distinctions. Namely, there are many animals for which the bulk of ingested mass and volume is sand. It is clearly of low bulk food value by many definitions, but not by others. Near-surface, shallow-water sand, for example, may have a low C:N ratio due to the presence of phytobenthos and other colonizing microbes. In hindsight, this definition covers another area of ignorance in marine detritivory. Namely, while terrestrial and freshwater detritus originates in large measure from cellulose-rich, large, refractory packets, the origin and identity of refractory marine organic material is in serious question. Even under the open ocean, the possibility that much of the organic matter that is eventually buried in the sedimentary record comes from terrestrial sources cannot be excluded (101).

MODEL SELECTION AND DEVELOPMENT

Our modeling approach derives from the qualitative scheme developed by Hungate. He (61) predicted the type of microbe-animal association, competition or cooperation, that should exist in the guts of vertebrates based on the "kind" or quality of food being consumed. He later (62) distinguished the combined competition-cooperation model. Cooperation is predicted if a high-carbohydrate, fibrous food is consumed whereas a competitive interaction should be found if fruit or animal food—resources rich in protein or easily digested carbohydrates—is eaten. In the former case, the animal cannot efficiently digest its food and so harbors a microbial consortium to break down ingested material. The animal lives off the metabolites and (in foregut fermenters) cellular growth of these microbes. Herbivores utilizing a rumen comprise the best examples of this strategy. This foregut fermentation chamber allows first access of ingested food to gut microbes, which are then digested by the host.

In the competition case, both animal and bacteria can efficiently digest the ingested food, and so preventive measures are required to avoid significant

competition. They are especially necessary given the potential for extremely rapid growth of microorganisms. Elimination of most bacteria is accomplished by stomach acidity in many mammals. The combined competition-cooperation model is seen in hindgut fermenters. In this case the animal has first access to consumed food. Microbes in an enlarged hindgut cecum ferment undigested materials as well as sloughed cells and secretions from the animal. The apparent disadvantage of this system, especially if nitrogen is a limiting nutrient, is the inability to digest the microbial biomass. This disadvantage can be ameliorated via reingestion of feces (e.g. coprophagy in some rodents and caecotrophy in lagomorphs).

Although Hungate's ideas have been inspirational and underlie some portions of our own modeling efforts, unaltered they are insufficient for our purpose of predicting detritivore-bacteria associations. These ideas remain useful for qualitative understanding of the associations for which they are intended, but a single example shows some of their shortcomings. We have seen nonresident bacterial strains efficiently digested in the fore- and midgut of a deposit feeder, with surviving members growing at dramatic rates in the hindgut (99). It would be possible to elaborate Hungate's models to accommodate this pattern of death and growth, but we hesitate to do so. Recent experience with loop analysis (80) confirms the general problem with complex, qualitative, graph-theoretic approaches and their matrix equivalents—the outcome of perturbation and other qualitative network analyses usually are equivocal. These ambiguities cannot be removed without quantitative information (108), so we find it advantageous to bypass complex qualitative models altogether in favor of simple quantitative ones.

The obvious place to look for quantitative help is to the Lotka-Volterra equations, but the scale disparity between bacteria and detritivores makes their value dubious. These models were designed for population-population interactions and, by analogy with chemical mass action, work best where individuals of one population interact with individuals of another with a strength of interaction proportional to local abundances. Animal guts by contrast represent, in the current vernacular, a landscape (cf 47) for whole populations and communities of bacteria. More insidiously, the currency of interaction in the Lotka-Volterra equations is hidden in coefficients rather than made explicit; hence, despite their long history and abundant heuristic applications, they have not proved useful predictively with respect to kinds and intensities of interaction.

Cost-benefit analysis has the decided benefit of being explicitly predictive. We couple two of its many variants in our two-step approach. We first apply a crude level of "optimal digestion theory" (where digestion is interpreted to include absorption as well) to the separate members of the potential interaction, i.e. to detritivores and to heterotrophic microbes feeding on detritus. We

note that this approach explicitly follows Wimpenny's (128) advice to make spatial and temporal variations a part of general analytic schemes involving bacterial performance. We then embark on an analysis of costs and benefits of potential associations in terms of the digestive model variables and other landscape variables identified a priori as important to bacteria.

Optimal Digestion Theory for Detritivores

Optimal digestion theory (29, 97) provides a very general mass-balance and mass-flow framework in which to set the functioning of guts. The simplest gut structure and digestively the most effective one when internal fermentation is not important is tubular. Plug flow or a series of mixing cells in such a gut yields digestive products at high rates that can be sustained as long as feeding continues (cf 97). In the simplest such arrangement, the gut is not differentiated into regions, and both secretion of digestive enzymes and absorption of digestive products occur over its full length. Most generally, however, the gut can be divided into three regions on the basis of function. The first is digestive, while the second is digestive and actively absorptive. Digestion can continue in the third, but absorption is usually passive when present; the hindgut stores fecal material and thus allows feeding and digestion to be continuous while defecation can be discontinuous. We take this arrangement as primitive in the metazoan detritivore, although the very existence of hindguts may be related to microbial associations. This potential problem does not jeopardize our general conclusions, which would hold also for an animal with only fore- and midgut. Because digesta in an animal without a nonabsorptive hindgut should leave the absorptive sites when the marginal gain from them falls to the average for the whole gut (29), and because disappearance (via microbial uptake) of digestive products upstream decreases absorption rate everywhere downstream (because concentration of products drives absorption rate), the posteriormost absorptive portions are the least critical ones to protect from microbial invasion. The skeptic thus may substitute for what we call hindgut a hind section of still-absorptive midgut in the primitive detritivore.

In plug flow, there is a fixed relationship between the fractional extent of digestive conversion (X in Figure 1) and gut residence time (τ) (97)

$$\tau = \frac{V}{\nu} = C_{A0} \int_0^{X_{Af}} \frac{dX_A}{-r_A} \quad 1.$$

Here the subscripts A refer to a particular chemical constituent and 0 to (initial, time 0) concentration in ingested material. V is gut volume, ν is volumetric throughput rate (volume time⁻¹) and r is digestive reaction rate (moles volume⁻¹ time⁻¹).

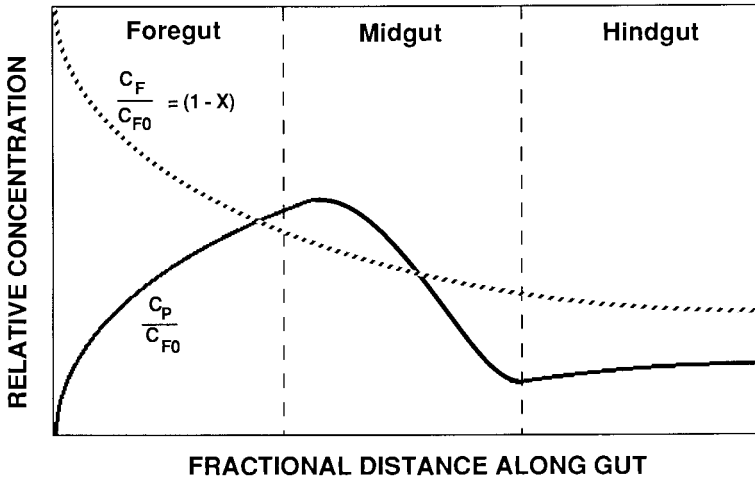


Figure 1 Schematic pattern of particulate food concentration (C_F , mol vol⁻¹) and concentration of dissolved digestive product (C_P) that would be expected along the gut of a detritivore operating in plug flow to maximize its own rate of digestive absorption (after 29, 1990). Absorption is assumed to occur only in the midgut, while digestion is assumed to occur throughout the gut; both follow Michaelis-Menten kinetics. X is the extent of digestive conversion (a fraction) while C_{F0} is the ingested food concentration. C_P in the feces of an aquatic detritivore would diffuse out within minutes from pellets smaller than 1 mm in diameter due to the small volume and sharp gradients involved (72).

In general, digestion and the animal absorption to which it is coupled will produce a steadily decreasing concentration of the starting food material and an intermediate (in the along-gut direction) peak in digestive products. More surprisingly, an animal acting to maximize its gross rate of absorption will have an optimal retention time and will egest substantial portions of ingested food undigested and digestive products unabsorbed (29; see also Figure 1). Because it requires added gut residence time and thus necessarily a slower rate of digestive production (Equation 1 with Michaelis-Menten kinetics for digestion) more efficient absorption when food is not limiting will decrease the rates of both digestion and absorptive gain. We assume that the ingested food characterized in volumetric concentration by C_{A0} for a detritivore is particulate and that the digestive product characterized by C_P is dissolved.

Digestion by Microbes

We know of no comparable, explicit optimal foraging models for an individual bacterium. Hence, we rely on a rough analysis for end-member cases (Figure 2) to place bacteria in the context of digestive strategies. We do not restrict ourselves to the case of bacteria attached to detritus because the possibilities for association with animal detritivores are not so restricted.

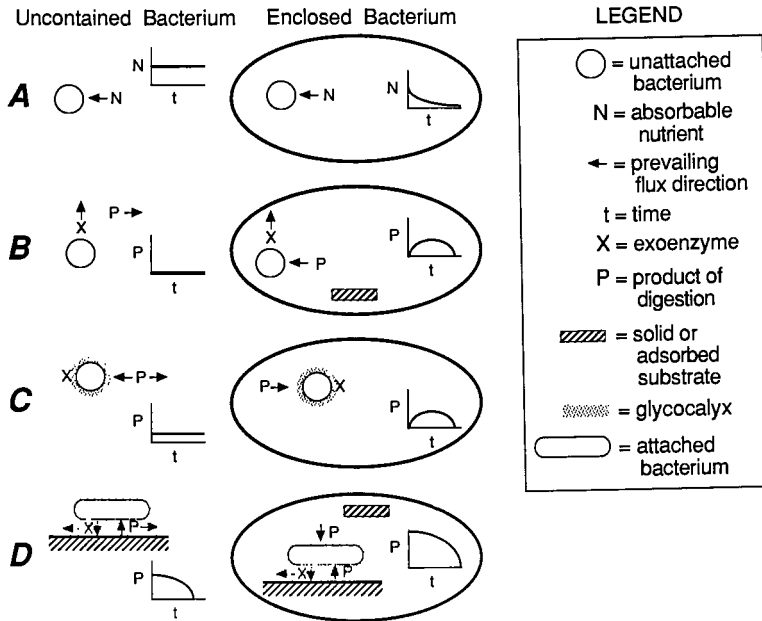


Figure 2 Effects of enclosure on microbial digestion (via exoenzymes) and absorption across the outer membrane of the cell. Enclosure in the gut lumen occurs upon ingestion and ends upon defecation. Foraging activities of detritivores also rearrange ambient sedimentary particles and thereby both create and destroy enclosures. A: An unattached bacterium without exoenzymes depends on nutrients that can be absorbed directly; enclosure cuts off its supply. B: An unattached bacterium with freely released exoenzymes benefits from them only under enclosure. C: An unattached bacterium with exoenzymes immobilized in a glycocalyx experiences some gain in both situations. D: An attached bacterium that channels diffusion by means of its glycocalyx also gains in both cases. In cases B and D the bacterium has access to remote particulate substrates as well as dissolved substrates. Note that in these two cases, per the models of (75), enclosure of two microbial strains with different digestive products and with abilities to absorb each others' would lead readily to mutualism. It also must lead toward anoxia, thus explaining the prevalence of anaerobic consortia. Members of such consortia are likely to be ingested simultaneously by detritivores.

To place bacteria in the same digestive context as metazoans, we consider digestion via exoenzymes and absorption by active transport across the cell wall. The simplest case (Figure 2) is absorption without digestion—food acquisition without the aid of exoenzyme secretion. It is clearly the most energetically profitable, since the costs of digestion are absent. Taking an unattached bacterium as a sphere of roughly $1 \mu\text{m}$ in diameter, one can apply the diffusion equation in spherical coordinates to get some idea of constraints. Solving that equation in spherical coordinates and then integrating over the

surface of the sphere, one finds that the flux of dissolved constituents to the cell surface of an individual at steady state is given as

$$4 \pi r_0 D (C_\infty - C_0), \quad 2.$$

where r_0 is the cell radius, D is the diffusion coefficient [L^2T^{-1}] for the substance of interest, C_∞ is its ambient concentration, and C_0 is the solute concentration at the cell surface. With natural turbulence levels, this flux is virtually unaffected by the flow regime (95) for the simple reason that particles of the size and specific gravity of bacteria track flow perfectly and are too small to experience much turbulence-induced but laminar shear across their cell surfaces. The only freedom that the cell has in maximizing net uptake rate, then, is in altering cell size and uptake kinetics (the latter determining C_0). An expanded form of Equation 2 that incorporates uptake kinetics explicitly is given by Pasciak & Gavis (95), but for brevity we do not include it here. We simply note that for this small and unattached cell, the ensuing balance that sets C_0 will be of molecular diffusion of solute to the cell surface with (Michaelis-Menten) uptake kinetics. Assuming invariant uptake kinetics, the uptake-vs-time plots of Figure 2 are set, then, by the pattern of C_∞ vs time.

If one considers the possibility of exoenzymatic digestion by bacteria, in an unattached state, diffusion becomes a two-edged sword. It is easy to demonstrate with three-dimensional random-walk models (39) that there is a small probability of return of a product molecule from the sending out of an exoenzyme molecule. The effective dimensionality of connected pore spaces in detritus or sediments falls below three (116), so the return probability rises. Here, time enters into the difficulties as well. If l_f is the distance to a substrate molecule, the fact that diffusion times vary as distance squared gives return time a $2l_f^2$ dependence. If a released enzyme is inactivated after some time (t_i), particulate substrates beyond a given distance ($\propto \sqrt{At_i}$) are unavailable. Complete enclosure in a small space (or the filling of a larger enclosure with clone members) is apparently necessary to provide strong selective pressure for such free release of exoenzymes.

Exoenzymes may be immobilized in a glycocalyx. For an unattached bacterium this situation is much improved over letting enzymes diffuse freely away, but diffusion will carry more than half of the products away from the cell rather than toward it. Bacteria attached to particles can further constrain, via the glycocalyx and the particle, diffusion geometry (Figure 2). To the degree that enzymes are prevented from diffusing away and diffusion of products can be channeled by exopolymer strands toward the microbe, exoenzymes can yield net gain. In the case of attachment to an organic particle and in the absence of enzymatic poisoning, digestion would continue until a surface inert to the enzyme complement were reached.

Attached bacteria also may benefit in enhanced solute flux—without exoenzymes—from relative motion through the surrounding fluid of the particle to which they are attached. In the extreme case of a flat object with a microbial film, boundary-layer depletion can be reduced by fluid motion. Details of cost and benefit to the bacterium depend very heavily on large and small-scale geometry (105), and thus quantitative generalizations are difficult.

Effective enclosure thus appears crucial to the success of exoenzymes. At a critical particle (volumetric) density (116), sediments become dramatically less permeable to diffusion and pore spaces become unconnected to each other. Similarly on a much more local level, natural detrital and mineral grains easily can form enclosures (e.g. Figure 25 in 2). In this case return of products resulting from diffusion of an exoenzyme can become much more likely. Significant early returns are thus more likely in small spaces until substrate concentration becomes limiting (or metabolite build-up becomes inhibiting). Further generalization again will be highly dependent upon geometry.

Environmental Covariables

The stage for association is not well set by digestion of detritus alone; it requires inclusion of environmental covariables. Strong covariation exists, for example, between availability of O_2 and the aforementioned diffusion geometry. This difference in oxygen environments carries over to animal respiration. External surfaces of aerobic metazoans must be exposed to oxygenated fluid. Burrow- or tube-constructing animals that are large or that penetrate anoxic sediments must pump in oxygenated water to supply their respiratory needs, with numerous consequences to the surrounding sediments (2, 3). Respiratory as well as feeding currents of both benthic and planktonic animals entrain suspended microbes and expose them to solutes emanating from the animals and their feces.

Some features of the gut itself are nearly universal across environments. One is temporary freedom of microbes from a panoply of predators during gut passage or attachment to gut linings. Many chemical variables in the gut appear to covary with osmotic and water stresses across the range of terrestrial, marine, and freshwater environments and to account for variable linking of the treatment of nitrogenous wastes to the gut environment. Not only the gut environments per se, but in particular the degrees to which the gut and ambient detrital environments should differ change sharply across terrestrial, freshwater, and marine environments (Figure 3). The contrasts are most marked between marine and terrestrial systems. Decomposition of terrestrial detritus often is limited by the availability of water. Nitrogen in any form assimilable by bacteria is scarce in most terrestrial detrital systems. Guts of terrestrial detritivores guarantee water availability to resident or transient

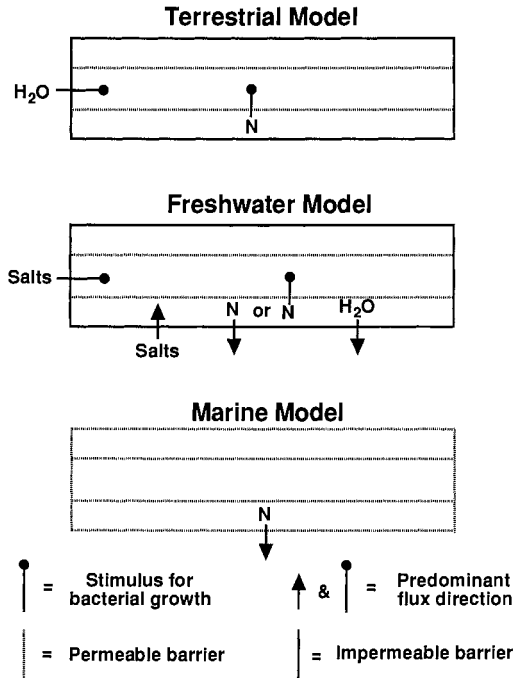


Figure 3 Contrasts among environments of osmotic balance and nitrogenous waste excretion in detritivores. The inner "tube" (in longitudinal section) represents the gut lumen, and the oral opening is on the left. The diagram thus summarizes salient nondigestive features of the gut landscape experienced by microbes. Duration of exposure to these features is set by gut residence time (τ).

microflora. Water stress in many microenvironments is so severe that detritivores control water loss not only through being relatively impermeable externally, but also through reabsorbing fluids associated with nitrogenous waste excretion; nitrogenous wastes often are excreted into the gut. While fluids are precious, recycling allows them to be used lavishly internally in terrestrial animals. Humans, for example, characteristically eat about 1 liter of solids per day, but they secrete about 7 liters of fluids into those gut contents and resorb them. The consequences for bacteria that grow in the gut are enormous. Eighty percent of the wet weight of human feces is bacterial (35).

Limited exposure of terrestrial animal guts to ambient conditions allows radical chemical departures that optimize pH for specific animal digestive enzymes and may act either as general antibacterial treatments or culture media for specialized microbes. The human "acid wash" of food in the stomach, for example, is thought to be a general antibacterial, and anaerobic

conditions in the human hindgut may be an evolutionary compromise that allows containment of bacterial growth while water is resorbed, adds little respiratory demand, and can return some modest benefits as volatile fatty acids (VFAs).

The general picture in terrestrial guts, then, is of very large benefits and costs to most bacterial strains. There is little likelihood, then (since large costs and benefits rarely will sum to zero), of casual associations of bacteria with animal guts, either as residents or transients. To overgeneralize, it should be an evolutionary “love-hate” relationship.

Marine animals, in stark contrast, are highly open systems. Non-enzymatic variables, such as water availability, pH, Eh, and O₂ tension would be expected in the absence of microbial associations to change very little upon ingestion and during transit (Table 1), as opposed to the marked deviations from ambient values reported in some terrestrial (14) and freshwater (85) detritivore guts. Animal nitrogenous wastes rarely are excreted into the gut lumen but often are excreted through widely distributed, externally opening ducts or respiratory surfaces (with the proviso that NH₄⁺ may still diffuse in substantial quantity into the gut). Thus, the respiratory and feeding currents of marine animals double in a nitrogen-flushing capacity. Further, in many marine systems nitrogen is available in the form of NO₃⁻ to bacteria on detritus. Casual associations of bacteria with detritivore guts thus appear to be far more likely than in terrestrial systems.

Freshwater systems appear to be intermediate. More precisely they appear to be derived with relatively little modification from one of the other two systems, despite the obviously different osmotic problems in fresh water. The ions needed to balance the osmotic flow of water into freshwater detritivores generally are obtained both from food and from active ion transport over respiratory surfaces. As in terrestrial organisms (but for the opposite reasons), the rest of the external surfaces are often relatively impermeable. Unlike either terrestrial or marine organisms, freshwater detritivores minimize their ingestion of water. Ingestion certainly occurs, however, as does the repeatedly noted but still poorly explained phenomenon of anal intake of water (e.g. 49). Nitrogenous waste excretion is focused into the gut in some freshwater animals (notably the larval stages of insects) but not in others (e.g. crustaceans), with the difference seemingly based more on evolutionary history (terrestrial versus marine) than on present environment. Nitrogen can often be available as NO₃⁻ in ambient water, since PO₄³⁻ is more often the limiting nutrient.

Models of Association

There should evolve non-chance associations (including “avoidances”) between microbes and marine detritivores whenever the risks and benefits to

Table 1 Physico-chemical conditions of marine detritivore guts^{a,b}

Animal	N	Niche	Ingested sediment	FG	MG	HG
ECHINODERMATA						
<i>Molpadia intermedia</i>						
Eh	7	shallow	+122	+322	+189	+232
pH	7	subtidal,	7.2	7.6	7.5	7.5
[O ₂] ^c	8	SSDF ^d	0 ^e	0	0	0
<i>Brisaster latifrons</i>						
Eh	4	shallow	+378	+310	+249	+273
pH	3	subtidal,	7.5	7.3	7.4	7.4
[O ₂]	4	SSDF?	0	0	0	0
<i>Pannychia</i> sp.						
Eh	3	bathyal,	+466	+359	+386	+404
pH	—	SDF ^d	—	—	—	—
[O ₂]	3		49	26	26	30
<i>Scotoplanes</i> sp.						
Eh	4	bathyal,	+466	+360	+375	+377
pH	—	SDF	—	—	—	—
[O ₂]	4		49	8	3	4
ANNELIDA						
<i>Abarenicola pacifica</i>						
Eh	2	sandy	+248	+278	+95	+162
pH	2	intertidal,	7.1	7.1	7.1	6.9
[O ₂]	4	SSDF	0	0	0	0
<i>Travisia foetida</i>						
Eh	2	shallow	+86	+65	+36	+90
pH	3	subtidal,	7.7	6.9	7.2	7.7
[O ₂]	2	SSDF	0	0	0	0
<i>Eupolymnia heterobranchia</i>						
Eh	2	muddy	-65	-144	-37	-7
pH	1	intertidal,	6.9	6.8	7.6	7.2
[O ₂]	1	SSDF?	0	0	0	0

^a Measured with mini- (pH) or microelectrodes (O₂, Eh)^b Mean values^c Concentration in mM^d SDF = surface deposit feeder, SSDF = subsurface deposit feeder^e Below detection limit (ca. 1% sat.)

either party are unequal. Note that this fitness-based analysis focuses on one, single-species population each of detritivore and microbe. What makes the detritivore-microbe system particularly interesting is that frequency of encounter of diverse microbes by a detritivore is likely to be high relative to organisms that ingest living tissues (herbivores and carnivores); decomposer

microbes inhabit detritus and detritivores forage for it and them. As the ground state from which to analyze whether a mutualism or parasitism will evolve, we envisage a situation where most predation pressure and other mortality terms on the microbe population come from factors other than simple predation by the detritivore population in question. We suggest that for any marine detritus-associated microbe population, then, predation by the combination of other species of detritivores, and in particular by a diversity of smaller "gourmets" (i.e. protozoans and metazoan meiofauna), will overwhelm the negative effects of the particular detritivore population on the particular microbe population being analyzed. Thus, only two kinds of two-way association are to be contrasted explicitly, namely, mutualism and parasitism, together with their gradations into commensalisms with little effect in one direction.

To look at associations in animal guts, we follow Keeler's (75) general approach to the analysis of mycorrhizal fungi. Specifically, we define

$$w_{um} = pw_u + qw_n, \quad 3.$$

where w is fitness, the subscript m denotes microbes, u refers to the population fraction (p) that is mutualistic, and n to the fraction (q) that may be ingested occasionally but is not mutualistic. Take $w_u = g_0 + g_u$ and $w_n = g_0$ such that g_0 is the net population growth for the nonmutualist, background population and g_u is the incremental gain from mutualism. Hence,

$$w_{um} = g_0 + pg_u. \quad 4.$$

We suggest that due to the foraging of the detritivore, encounter is likely to be less limiting in evolution of the gut-microbe association than in the development of the mycorrhizal one (allaying some of Keeler's concerns about the appropriateness of the model as applied to mycorrhizae). Hence, development of the mutualism will depend more exclusively on

$$g_u = b_u - c_u + f_u p, \quad 5.$$

where b is the benefit and c the cost of the mutualism to the microbe. The term f quantifies the feedback to the microbe from the association, since microbial gain via the mutualism drives up the abundance of the detritivore and will alter p . Exactly the same model (with alteration of the subscript m in Equation 3) applies to the detritivore. A first step in analyzing the potential for mutualism, then, is to find benefits to both parties.

Two apparently universal benefits to ingested microbes are relief from predation by other predators and exposure both to the mechanical energy (removal of diffusive limitation for particle-associated microbes) and to a

reliable stream of the detritivore's food—usually higher in dissolved and particulate organic value than is the ambient medium. Costs will universally include defense from animal digestive enzymes, while terrestrial and to some extent freshwater animal guts will have added costs due to greater changes in other chemical variables (e.g. pH and Eh). The act of enclosure upon ingestion is universal, but returns to the microbe of materials digested by its exoenzymes will depend upon whether it is attached, upon whether the substrate for digestion is dissolved or particulate, on gut (enclosure) size, and upon residence time of material in the gut, as well as on the kinetics of microbial digestion. In the case of transient microbes, the time to induce exoenzyme secretion must be considered as well.

We suggest that the currency of transaction and the magnitudes of the terms can differ radically between attached and unattached (to the gut) bacteria, and thus we distinguish these two cases. We begin with the former and subdivide it further into regions of attachment, i.e. fore- mid- and hindgut. We suggest that (cf Figure 1) potential gains from dissolved products of detritivore digestion are modest in the foregut but in marine detritivores constitute the most obvious gain to microbes. Whether particulate food is available at all to gut-attached microbes via their own exoenzymes will depend critically upon the along-gut velocity of particulate food (v /local cross-sectional area of the gut). Since we have defined the situation as a mutualism, we must find something for the microbe to donate, and the most likely donation appears to be a digestive enzyme. Further, the costs to the detritivore may be substantial as lost potential for absorption of its own digestive products (29), escalating microbial c_u via defenses against microbial attachment.

While potential gains in terms of concentrations of detritivore digestive products are greater in the midgut (Figure 1), so are the obvious costs to the detritivore. We suggest that the costs of occlusion of the detritivore's own absorptive system are so great that detritivore defenses will in general make c_u insurmountable, precluding mutualism. A gift of enzymes is not as useful here, since there is less gut area remaining over which absorption can occur. Production of energy-rich products, like volatile fatty acids (VFAs), from the animal's digestive products would again (as in the foregut) appear to be at the expense of the inherent inefficiency of microbial growth (22). Hence there appears to be good reason to find the midgut relatively free of attached mutualists.

The situation in the hindgut is entirely different. There is little obvious cost to the detritivore of allowing attachment. There is substantial gain to the microbe of dissolved digestive products. The obvious microbial contribution is as VFAs that can be absorbed directly by the detritivore without an active transport system. Besides digesta, the hindgut contains the products of gut tissue ablation (that we would argue is at least in part an evolved defense

against microbial fouling of the midgut), and hindgut fermentation allows partial recovery of these sloughed gut materials as VFAs.

For unattached (to the gut) microbes transiting a gut, one must take the mean of these conditions. Rather than sitting at one point in Figure 1, then, the transiting microbe follows the curves drawn in that figure. The microbe's cost of attachment to the gut wall disappears. The total time of transit may be long enough in this Lagrangian reference frame for the microbe to take local digestive advantage of the particles with which it transits. Detritivore defenses in the fore- and midgut must change in character to be effective against microbes in transit. We suggest that they will be more expensive for marine detritivores than for terrestrial and freshwater ones whose isolation of the gut from ambient conditions—by reason of both water balance and longer gut residence times than normally seen in marine detritivores without mutualists—allows radical pH and redox changes (e.g. the termite gut). It does not appear, however, that under rapid transit unattached microbes would impose any serious problem, for they would have difficulty equalling the absorptive surface area of the gut in any but the largest detritivores. Assume, for example, a cylindrical gut, spherical bacteria $1\ \mu\text{m}$ in diameter, and 5×10^8 bacteria/cc of ingested detritus. We used the 10% figure of Novitsky (93a) for the proportion of bacteria in sediments that are metabolically active. For a deposit feeder of gut diameter, 1 mm, over 10^{10} bacteria/cc would be needed to provide equal area. At typical ambient standing stocks of bacteria, significant absorptive competition (at 10% absorptive area) would occur in guts of over 2.5 mm diam., assuming a perfectly smooth gut wall. Thus, there may be neither ready means nor reasons for general detritivore defenses. The question then becomes whether the costs of running the enzymatic gantlet are balanced by the gains in digestive products from the detritivore—in concentration of particulate organic material via selection on the part of the animal or in protection from, say, protozoan bacterivores. The cost-benefit model of Lehman (79), although developed for external encounters, is directly applicable to this analysis.

The situation grades into a one-sided mutualism or simpler commensalism (hindgut) and then into parasitism (foregut and midgut) to the extent that digestive products lost to the microbe are not recovered as VFAs. In order to save space, we forego the formal analysis of parasitism given by Keeler. The critical question clearly is whether b_u for a microorganism in transit is large, and the cost in its fitness from decreased detritivore stocks (making f_u negative) is smaller. It thus seems as though a one-sided benefit or a very benign form of parasitism will be common in microbes transiting detritivore guts. In terms of attached parasites, the midgut clearly is the place with the biggest benefit and cost terms.

While this form of analysis is most often applied to incipient associations, it

is applicable in slightly modified form to subsequent evolution of those associations. Namely, if one takes as the ground state the present form of the association, then one can examine the effects of subsequent evolutionary perturbations (mutations) from it. Consider, for example, a simple, tubular gut of uniform diameter and an incipient hindgut mutualism, and take the animal's point of view. If the net return to the animal is limited by time for microbial growth, then evolution should cause the hindgut to lengthen or widen, with the latter being cheaper in gut-lining materials but less advantageous if diffusion of products to the gut wall is rate limiting. (Continuity demands that an increase in pipe diameter be associated with local reduction in flow velocity.) If, on the other hand, net return is limited instead or in addition by surface area for absorption of VFAs, then invagination of the gut lining may be a cheaper solution (i.e. one producing higher net gain). One can envision a chain of escalating mutualism wherein each change is repaid by added gain: The invagination eventually acquires ciliary transport that moves especially fermentable material into it. In terms of flow of material (97), such an invagination not only increases mean residence time, it also adds greatly to variance in residence time. Thus, to shift briefly to the microbe's point of view, invagination affords statistical protection from washout as would dead space in a chemostat. The marginal value theorem in turn dictates that this escalation of gut size or ramification will continue until the net gain from further expansion is not repaid.

Hindgut diverticula in turn would appear to be ideal sites for development of microbial consortia, but the animal, and hence the mutualism, might suffer from S^{2-} toxicity under anaerobic conditions. Here an especially valuable donation from the microbial side would be a mechanism of detoxification (i.e. via microbial chemoautotrophy). Similar but probably weaker arguments might be made for NH_4^+ . Any chemoautotrophy (e.g. one based on CH_4), in turn, might directly or indirectly provide a new source of nutrients to the detritivore. If the mutualism reached the point of cellular contact (or by diffusion even before), we suggest that f_u could skyrocket from access of the bacterial consortium to oxygen provided by the detritivore to its tissues and access of the detritivore to the organic products of chemoautotrophy. If the environment, in turn, were rich in reduced solutes but poor in detrital food value, it is relatively easy to construct an apparently viable chain of events from detritivory to hindgut fermentation, to atrophy of the normal gut, to obligate mutualism. The Pogonophora appear to be likely end products of such a chain of hindgut evolutionary events, starting with a detritivore.

One can also anticipate mechanisms for reducing costs of association to the detritivore. Microbial growth requires oxidants. Where anoxia of tissues might otherwise present a problem or where provision of strong oxidants

results in greater rate of gain, there appears to be no theoretical barrier to evolution of respiratory and circulatory features surrounding the region of greatest microbial activity. One can expect respiratory structures or behaviors associated with particularly active hindgut mutualisms.

This exercise thus makes it clear how radical hindgut expansions and hindgut diverticula may evolve in detritivores. Because such past chains of events are difficult to test, however, it may be more instructive to look for cases where a conceivable end product of evolution would be highly successful, but no chain of events can be found to it. For example, a termite with a foregut fermentation chamber instead of a hindgut "paunch" would appear formidable. Similarly, it is plain that hindgut fermenters are far more polyphyletic than foregut fermenters (132). Foregut fermentation, i.e. turning of particulate ingesta into dissolved products by microbial digestion before entry into the midgut, requires substantial residence time (97). Thus, an incipient mutualism of this sort requires for its development an animal with a long gut residence time—a large animal or one that specializes on especially slowly digestible material or both. An animal meeting this requirement stands, by means of the mutualism, to gain access to ingested particulate material as easily absorbed fermentation products, making its benefits transparent. The microbes, in turn, benefit from an enclosure for their exoenzymes (Figure 2). In addition, such enclosures where rapid, obligate metabolite exchanges are possible in the absence of diffusive losses, are ideal for the evolution of microbial consortia. Arguments for subsequent evolution of foregut expansions and diverticula follow those for the hindgut.

External nutritional associations can be diverse. The first dichotomy is having the microbes attached (to the detritivore body) versus unattached. Microbes associating with the external surfaces of animals, particularly with the respiratory surfaces of animals, obtain certain access to O_2 as one contribution to b_u . Defense against external attachment should result unless the return to the animal, e.g. detoxification, exceeds the tax on its respiration. It would appear that f_u would be particularly large in systems where this detoxification in turn allowed the detritivore access to rich resources, e.g. chemolithotrophic products of hydrothermal vents. In this setting the feedback is intense, as the bacterial need for the attachment includes both a growing requirement for access to oxygen and a means to avoid expatriation. The likelihood of donation of chemoautotrophic production by the attached bacteria to the invertebrates is not clear, however, because the relative magnitude of its effect on c_u versus f_u is not obvious a priori.

Commensalism of aerobic microbes with respiratory streams of bottom-dwelling invertebrates is well established (2). It is obvious, even to the casual observer, as an oxic, reddish (from Fe^{3+}) halo about the tubes and burrows that penetrate anoxic sediments. The obvious benefit of such association to

functionally aerobic bacteria is a stronger oxidant that provides more ATP per mole of organic matter respired than would residence in the surrounding sediment, and the scale disparity of the two associates suggests that the added water movement needed to support the oxygen demands of any one microbial population results in little cost to the invertebrate. The cost to the detritivore from O₂ demand distributed across all aerobic microbes may be substantial, however.

Miller et al (88) suggest that a necessary but insufficient condition for external mutualisms is that geophysical sediment movement is infrequent relative to microbial growth rate. Digestion theory coupled with Keeler's variety of cost-benefit analysis provides additional insight by taking the microbe's perspective first and then looking for positive feedbacks. For lack of space, we do not reproduce her derivations (75, pp. 113–17) for fungus-gardening ants, for they can be adopted without modification. Particularly following our suggestion of rapid microbial growth in the hindgut, microbial growth on feces is the likely beginning of such an association. One positive feedback to the detritivore from subsequent coprophagy is access to food particles with long digestive reaction times as per the arguments of Penry & Jumars (97). An added benefit underscored by Keeler is the reduced cost of foraging both in search costs and risks of predation. We have argued previously (70) that the most likely place to look for such associations among marine detritivores is in the deep sea. Keeler's analysis supports our contention that two sorts of mutualisms are likely. One is based on highly episodic inputs of labile material (phytoplanktonic detritus); Keeler's analysis shows how the caching of such material can benefit the detritivore by smoothing out the valleys between infrequent peaks of inputs at the same time that it—somewhat paradoxically—benefits the associating microbe in terms of population growth rate. The other sort is based on caching of refractory (to detritivore digestion) but energy-rich materials such as cellulose (imported plant debris) and chitin (cast exoskeletons of zooplankton). The situation here is the classic one of renewable resources (81, 83), but the gatherer of energy-rich particles in an otherwise food-poor environment fuels this microbial growth and gets its benefits. Donation of reduced nitrogenous wastes by the detritivore specifically to the microbes might be expected in a tight mutualism.

We suggest that free-living, unattached bacteria will benefit from the excretions of detritivores as sources of reduced nitrogen and from diffusion out of fecal pellets (72) as major sources of labile, dissolved organic carbon. They are entrained in feeding and respiratory streams but, because of the mechanics of particle capture, fall in a size category that runs almost no risk of being eaten by metazoans (41). Thus the quantitative risk-benefit model of Lehman (79) again can be adopted directly.

LITERATURE-BASED EVALUATION

The intent of our modeling effort is to make predictions and guide future experimentation to test these predictions. Since very little testing of the theory presented has been completed to date, however, we are forced to use extant data, largely obtained with unrelated goals in mind, to evaluate our efforts. They constitute more a consistency check than a rigorous test.

Returns from association rest clearly on the coupled kinetics of gut passage (Equation 1) and microbial growth (Eq. 5). Of particular interest are typical detritivore gut residence times—gut residence times in detritivores not suspected to be obligate mutualists as well as in those known to harbor microbial mutualisms—and maximal bacterial growth rates. To get an idea of τ in the absence of known mutualisms, we combine characterization of median gut volume (98) and ingestion rates (23, 24) of deposit feeders to give a crude estimate of residence time of material in animal guts operating on shallow-water organic detritus (at 15°C for Cammen's results). Calculated values of order 1 hr for both *Abarenicola pacifica*, a large marine deposit feeder, and for a 20 mm³ *Capitella capitata*, near the hypothetical lower size limit for a true deposit feeder (70), agree reasonably well with published values (45, 60, 99). Because there is a roughly linear relation between body size and proportion of body volume occupied by gut among deposit feeders (98) and ingestion rate scales as weight^{0.7} (23, 24), there is a tendency toward longer residence time for larger animals and individuals, but it is not especially strong. For shallow-water deposit feeders a range of 0.5 hr to 2 hr encompasses most reported observations of τ .

This approach is rough for a number of related reasons. The variance is large in Cammen's (23) study, with ± 1 SD spanning an order of magnitude. At least part of the reason for this spread is that residence time varies about the species mean as a function of ingested food quality (e.g. 118). The approach has the added problem that it includes whatever undefined microbial relationships already are present in the detritivores. Termites and wood-boring isopods, known with the help of microbial associates to digest extremely resistant materials, have gut residence times on the order of days (19, 58). Thus, it does not appear that the detritivores we characterize with gut residence times an order of magnitude shorter are likely to reflect comparably obligate associations. The values obtained for marine detritivores underscore the difficulty of being a bona fide detritivore at small body size; limited volume and short residence time conspire to restrict small animals to labile material. One does not know, however, whether the longer residence times characteristic of larger species provide significant access to material with slow digestive kinetics or simply allow greater efficiency of absorption of the same rapidly digested constituents that small animals must use.

The potential for association depends on the ratio of τ to microbial doubling time. Under optimal conditions with unlimited levels of dissolved carbon substrate and an assimilable source of nitrogen, bacterial growth rates can be explosive. Doubling times of under 15 min have been achieved for marine bacteria in pure cultures (122). In natural settings such as in aquatic sediments or in open-ocean and coastal waters “bulk” growth rates are considerably slower and can range from hours to days (76, 90, 91). Sedimentary bacteria can show, however, a rapid growth response to substrate manipulation or physical mixing (e.g. 91). Growth rates approaching those observed under optimal conditions in laboratory cultures have been measured in the guts of some marine detritivores (30). For example, Plante et al (99) recorded doubling times of approximately 1 hr for sedimentary bacteria both under optimal laboratory conditions (at *in situ* temperature) and within deposit-feeder guts.

A further restriction on mutualisms dependent upon provision of exoenzymes by microbes transiting guts would be the time needed to induce their secretion if they are not already present. In accord with our theoretical arguments (Figure 2), in water-column environments bacterial exoenzymes are scarce (26). Diffusive losses of exoenzymes in general are large in aerobic environments—they must be large to keep those environments aerobic—so exoenzymes are scarce in aerobic pore waters as well (86).

The environmental constancy offered by the gut relative to ambient detrital environments might suggest that large populations of bacteria should be found attached to the gut wall. Our cost-benefit analysis, however, points out that in the foregut—especially in view of the short residence times noted—benefits may not be sufficient to foster association, and in the midgut costs to the animal will be so great that defense mechanisms should overwhelm potentially great gains. Foreguts are, indeed, poorly utilized by microorganisms (14 and references within), and mechanisms such as harsh chemistry (14–16, 36), continuous sloughing (121), and peritrophic membranes (8, 14) are common to terrestrial, freshwater, and marine detritivore midguts and are effective in keeping tissues devoid of association (17–19, 78). Bacterial attachment to hindguts of terrestrial and freshwater detritivores is ubiquitous (8, 10, 19, 27, 28, 78, 87). Insufficiency of data precludes the same conclusion for marine detritivores, but available data do reveal hindgut associates and anterior regions free of attached bacteria (e.g. 30, 113). Net gain or loss in fitness to marine invertebrates through such interaction is currently unknown.

In terrestrial systems pH and Eh of gut compartments of both invertebrates and vertebrates often are such that microbial growth or viability is precluded within transiting material (e.g. 61). In marine detritivores direct and viable counts of ingested versus defecated material show that bacteria are indeed removed by some mechanism in the gut (8, 9, 30, 113). When counts among

the gut sections have been performed, numerical reduction has been shown to occur in the foregut or anterior midgut (8, 30, 99, 113, 131). Efficiency of digestion of bacteria by detritivores, often inadvertently referred to as "assimilation efficiency," is normally quite high, often over 90% (9, 12, 56, 99). In some cases these values are underestimates since selective feeding (73, 111) or regrowth in the posterior of the gut (99) has been neglected in experimental design. The most likely explanation for bacterial removal is that cells are enzymatically digested by the animal: Appropriate enzymes are available, cell numbers and not just viabilities decrease, and bacterial carbon is assimilated. In marine deposit feeders, true assimilation efficiency has been estimated to be up to 70% via radiolabelling (57, 82). Uptake and incorporation of bacterial cell constituents indicate some benefit to the animal. The debate of direct quantitative importance of microbes to detritivore nutrition, however, will continue until limiting factors are better established.

Our cost-benefit analyses, based on predicted digestive product distributions and regional gut functions, suggest that most transient bacterial growth should be within and posterior to the midgut and that it likely continues within defecated material (albeit with the rapid loss of dissolved digestive products from pellets). Efficient digestion of protozoans and meiofauna, likely predators of bacteria, has been documented (64, 65). Experiments designed explicitly to test the predictions of digestive product distribution in the gut have yet to be performed, but the profiles of soluble proteins and carbohydrates in the guts of abyssal holothurians obtained by Sibuet et al (113) resemble those of digestive products in Figure 1. Numerous studies have shown growth, sometimes remarkably rapid, in the guts and feces of detritivores (5, 30, 74, 78, 87, 92, 94, 99, 103, 119). Once again, only a subset of these studies allows assignment of growth to sections within the gut; when done in such a manner the posterior gut regions indeed exhibit most of the growth (30, 78, 94, 99, 113).

In some instances, numbers in feces or in the hindgut are lower than in ingested materials. Attention to Keeler's models, however, shows that this observation is not sufficient to demonstrate a net loss to bacterial fitness. Numbers may initially be reduced to such an extent in the foregut (e.g. 99, 131) that growth in the hindgut, especially if transit is rapid, may not bring numbers up to original levels. Stimulated growth, however, may continue within the feces and even after disaggregation (100). Overall microbial fitness—i.e. net loss or gain to integrated population growth rates rather than short-term abundance change—needs to be estimated and may be influenced long after bacteria leave the gut. Few studies have followed the microbial response through fecal pellet production and decay. Hargrave (55), however, has demonstrated increasing metabolic activity in fecal pellets up to two days after defecation. Loss of dissolved substrates from pellets may be rapid (72),

but digestion and mechanical disruption of the constituent particles clear new surfaces for microbial growth. The net benefits over time to bacteria contained in the pellets as compared to those freely suspended in fluids to which dissolved digestive products diffuse require experimental evaluation.

Bacterial growth rates in the presence of particles such as sediment grains and detritus currently cannot be measured easily or with high confidence. The reliability of the common methods (increase in abundance over time, frequency of dividing cells, and incorporation of tritiated nucleic acid precursors) has been brought into question repeatedly (e.g. 25, 89, 90, 93, 107). The few attempts to measure growth rates in detritivore guts or egesta nonetheless indicate rates that are orders of magnitude faster than in ambient detrital environments—near laboratory maxima for in situ pressures and temperatures (30, 99).

We caution that measurements of numbers, growth rates, and activities of total bacterial communities mask interactions of major biological or geochemical importance involving single strains of bacteria and detritivores. The differential effects of consumption and gut passage on various populations of microbes have been demonstrated in terrestrial (103, 117), freshwater (20, 124), and marine (32) environments. Beyond the demonstration of community changes with gut transit, little can be said about which microbes should fare best under specific circumstances. Mechanisms responsible for such community shifts remain undetermined but are likely related both to differential digestion and to varying abilities to take advantage of the benefits of gut passage. What can be said, however, is that the degree to which sediment reworking determines microbial community composition must depend heavily on the frequency of gut passage. If we equate the "rest interval" of sedimentary particles calculated by Wheatcroft et al (127) with the average period between ingestion of sedimentary bacteria by a deposit feeder, 1 to 1500 days may elapse between ingestion in various environments. It therefore appears that the effects of detritivore gut passage can be important in determining microbial community structure in at least some benthic settings.

Thus our predictions regarding incipient mutualism and commensalism within guts are supported by available data. The next question is whether the scenarios regarding further coevolution of mutualists are well met. Again, residence-time data and documentations of microbial associations are sparse, so observations of ceca or diverticula or prominent local expansions are noted as circumstantial evidence. Such information can be ambiguous, however, since structures that appear to have one function (e.g. mixing) may (also) serve another (e.g. sorting and bypass of indigestible material) (96). We also note the bias of an apparent social tabu. Structures of the foregut are drawn more frequently and in far more detail than structures near the anus.

Numerous taxa (e.g. most crustaceans, cf 14) possess midgut diverticula

that sometimes have been suggested (without evidence) to harbor microbial associates. We know of no direct evidence that any such suggestion is true. On the contrary, deliberate examinations of midgut diverticula invariably have revealed them to be sites of enzyme secretion and absorption of digestive products (e.g. 17, 21) and to lack enclosed microbial associates. Thus, their enhancement of residence time and surface area for absorption and their selective entrainment of particularly digestible material appear, in accord with our theoretical suggestion of a microbially "inviolable" midgut, to be adaptations enhancing digestion by the animals' own means.

Also in accord with our predictions, the majority of ceca or other such enlargements that prolong retention are located in the hindgut, e.g. in the termite (19), crane fly larvae (78, 87), millipedes (5), mayfly larvae (28), cockroaches (27), isopods (58), and in certain holothuroids (43), irregular urchins (31) and deep-sea molluscs (1). Microbial symbiosis and fermentation have indeed been observed in the hindgut ceca of terrestrial (10, 11, 13, 119) and freshwater detritivores (77, 114), but unequivocal evidence for microbial fermentation in the guts of marine detritivores does not exist. The demonstration of fermentative mutualisms in marine herbivores (44) is, however, highly suggestive.

Prominent foregut diverticula are rare among detritivores. Models of cooperative digestive associations general to all animals would predict both foregut and hindgut diverticula for such purposes. Foregut associations of this type are not documented in detritivores, however, in accord with our suggestions regarding residence time. While such a development would appear highly adaptive (there being no obvious reason why, for example, termite equivalents with foregut fermentation should not do better than extant termites), there appears from our theoretical considerations to be no ready way to initiate it. We suggest that long residence time would be required for initiation (to allow absorptive midgut gain from microbial digestion in the fore- and midgut), perhaps accounting for the rarity of evolution of foregut fermenters. The only suggestion that we can find of foregut diverticula among detritivores is by Penry & Jumars (98) for the deep-burrowing, large deposit feeder, *Travisia foetida*. Direct examinations of microbial associates in it and of its gut residence time and the residence times of related species (including some without diverticula) are needed to evaluate the possibility of mutualism. Decapod crustaceans would appear a likely place for foregut associations to evolve for the simple reason that gastric mills evolved for grinding large food items could serve as preadaptations adding residence time and escape from microbial washout. The crystalline style of bivalves may offer the same (110).

Experimental evidence for microbial aid in digestion among invertebrate detritivores is limited largely to the digestion of cellulose (77, 85, 114). Uptake of product from cellulose breakdown has been demonstrated in the

hindgut of host detritivores (77, 85). Furthermore, these associations are reflected in hindgut expansions or diverticula. Thus, our theoretical predictions appear well met.

The strongest evidence of their contradiction, however, comes from similar tracer studies of other stream detritivore species (114) and of marine or estuarine mysid shrimp (48, 123). The stream detritivore, *Pteronarcys*, assimilates carbon from cellulose (114) but shows no obvious gut expansions or attached associates (28). Further, Sinsabaugh et al (114) have shown that absorption of the radioactive label is primarily as sugars in the midgut. Sinsabaugh et al invoke "acquired enzymes," i.e. utilization by the detritivore of enzymes acquired from ingested microbes. This interpretation contradicts our prediction that foregut associations would be rare due to kinetic constraints. It requires significant production of microbial exoenzymes and digestion of cellulose during food passage from the point of ingestion to the midgut absorptive sites (i.e. during roughly two thirds of the gut residence time). If their interpretation is correct, then we would anticipate that this captivation of enzymes resulted from the preassociation condition of detritivores specializing on refractory detritus, thereby having relatively long gut residence times compared to those we presented for marine deposit feeders. An alternative possibility cannot be ruled out, however, by the data presented. Namely, the detritivore species involved may be a "gourmet" of microbial species that are digestive specialists on the low-molecular-weight, labile sugars taken up and manufactured by cellulose-digesting bacteria. Nothing in the experimental protocol precludes the possibility that most of the cellulose digestion indicated by the presence of radioactivity in sugars absorbed by the detritivores occurs prior to ingestion. Both interpretations beg the other interesting question of what might be the source of nitrogen.

Mysids efficiently digest and assimilate cellulose with a reported gut residence time of 30 min (48). Microscopy reveals no attached associates (51), but antibiotics do inhibit the assimilation (123). One interpretation of these findings is that acquired enzymes must be responsible for cellulose breakdown. The earlier data of Foulds & Mann (48), however, appear to exclude this possibility since initially sterile cellulose is digested and assimilated. Friesan et al (50) conclude that enzymes endogenous to the animal must be digesting cellulose and that the antimicrobials employed by Wainwright et al must have inhibited the mysid's ability to produce cellulolytic enzymes. The short residence times are still troubling, but the numerous midgut pouches (51) may allow selective retention. Endogenous cellulases in invertebrates are not extremely rare and, strangely, appear to be more common in marine than in freshwater or terrestrial detritivores (129). Perhaps the openness of marine detritivore guts has provided greater opportunity for cellulase-sharing associations to develop—which have been mistaken for endogenous production.

With respect to external associations, we do not discount the potential importance of “gardening” as originally proposed by Hylleberg (64), i.e. the stimulation of microbes by pumping in oxygen and mechanical agitation for subsequent ingestion, but we know of no published evidence that the obvious and measurable effects on the microbial community affect fitness of the supposed gardener. Hylleberg (64) studied the lugworm *Abarenicola pacifica* and speculated that its tail-toward-head pumping of water into its burrow enhances the growth of microbes in the sediments it swallows. He presented no bacterial counts or growth estimates to document the feasibility of this mechanism in enhancing food supply. A necessary and also untested corollary is that the bulk of bacterial growth that is stimulated occurs on substrates that are not available directly to the worm’s digestive system. Dobbs & Whitlatch (33) made a concerted effort to document gardening in another subsurface deposit feeder. While they made numerous valuable observations, they produced no convincing evidence of gardening. Bacterial growth enhancement (as in gardening) would need to occur at the feeding depth between the time that the microbial community is first influenced by the deposit feeder and the time that it is ingested. Unfortunately, the geometry and timing of site (re)visitation is not known for either of these subsurface deposit feeders. The microbial effects of pumping in of oxygen and mechanical agitation certainly can be expected to be major in what otherwise is an anoxic and quiescent environment. Thus, an effect on the microbial community—stress reactions of anaerobes and incipient growth of aerobes—would result. The time history and spatial extent of these effects relative to geometries and rates of deposit feeding need investigation as direct evidence, pro or con, of gardening. To date evidence is lacking to allow discounting of two other hypotheses. Subsurface deposit feeders may depend upon nonrenewable resources slowly accumulated with gradual, often anaerobic decomposition as material arrives by sedimentation at their feeding horizons. Alternatively, they may rely upon subduction of more recently deposited and presumably more labile organic material (106).

We have argued that gut volume is a major constraint on detritivores in general and deposit feeders in particular. Another aspect of this same volumetric constraint is on residence time. One way to alleviate both these limitations would be to carry out some of the digestion externally, with reingestion some time after egestion. Evidence for this sort of behavior in detritivores is primarily circumstantial and anecdotal, but it is at least as strong as the evidence for gardening, and there is much better reason a priori to expect a two-way interaction between microbes and detritivores. Further, gross anatomy and environmental characteristics combine to suggest that it will be found in deep-sea sipunculids and echiurans (70). Echiurans have nitrogenous waste excretion into anal sacs and are known to tend and periodically move collections of their fecal pellets (115). Nitrogenous waste

excretion and egestion are closely juxtaposed in sipunculids. X-radiographs suggest smearing of burrow walls with X-ray transparent material (Figure 1 of 70), and Graf et al (53) recently have shown that bathyal sipunculids cause rapid microbial growth, presumably by subduction of newly sedimenting remains of a phytoplankton bloom, several centimeters below the sediment-water interface. Thus, there clearly is an interaction in this case between the detritivores and microbes, but its nature is still ambiguous. Jumars et al (70) have argued that if labile food arrives at the seafloor in widely separated pulses then caching should be seen, and Graf's observations appear to provide strong support of this hypothesis. The role of bacteria is unclear, however. They may be competitors for this labile material or they may be "gardened" as in fungus-ant associations (75).

Nor must caching be limited to labile material. If calories as well as available nitrogen become scarce in deep-sea sediments, then caching of structural carbohydrates and chitin would be expected. The terrestrial analogue of this sort of association would again be fungal gardening ants. While macrophytic debris apparently subducted by deposit feeders has been seen in both shallow water (106) and the deep sea (102), there is no strong evidence linking it to caching behavior or indicating particular microbial associates that might make the calories available to detritivores.

Geochemical Consequences

Microbes are the primary decomposers of organic matter in nature. It has become abundantly clear, however, that the actions of detritivores accelerate decomposition in both terrestrial (6, 54, 94, 104) and aquatic (40, 42, 66) ecosystems. Mesocosm experiments reveal that benthos, chiefly deposit feeders, within shallow marine sediments in concert with microbes play a major role in enhancing primary production in the water column above by regenerating up to 100% of nutrients immobilized in deposited materials (34 and references within).

Among possible effects accelerating breakdown and mineralization are distribution of cells to sites more favorable to growth, removal of bacterial competitors and predators, enrichment by excretions or digestive products, and increase in surface area via fragmentation. In terrestrial and freshwater ecosystems detritivore fragmentation is likely the predominant factor, especially where vascular plant debris is substantial (125). Mechanical disruption is important in increasing surface area for microbial colonization and in breaking microbial barriers such as tough cell walls. The same stimulation of remineralization by mechanical disturbance has not always been observed in marine detritus (4). A high degree of autolysis is characteristic of the producers of marine detritus (chiefly algae and seaweed) relative to vascular plants

(109). In addition, phytodetritus will present high surface area without physical disruption, and seaweed, lacking the structural polymers of vascular plant cell walls, is much more prone to fragmentation by abiotic factors. Rapid decomposition of typical marine detritus is probably less dependent on invertebrate comminution. The paucity of marine shredders supports this assertion. In two situations fragmentation should be important in the marine setting, in nearshore areas where vascular plant and seaweed input is high and in places where living phytobenthos contribute significantly to the diet. The latter appear to be unavailable to bacterial colonization prior to mechanical cell rupture or autolysis (52). The lower content of available calories and nitrogen characteristic of terrestrial detritus (120) also means that a supplement food source, possibly fungi or bacteria, should be an absolute requirement.

In considering animal-microbe interactions we have focused on circumstances within the gut. In terms of geochemical importance, however, the feces may be of greater interest both because gut residence times are short relative to the lifetime of fecal materials, and chemical exchange with overlying water and sediments will occur in feces. Digestion theory predicts that substantial amounts of dissolved digestive products should be ejected in the feces, especially when food is abundant. The large concentration gradients and small size of fecal pellets should result in extremely rapid flux of solutes to surrounding waters (72). This condition, coupled with the observed enhanced mineralization in guts and feces, indicates that feces are understudied sites of major "sediment"-water exchange of dissolved organic substances and inorganic trace elements. The peritrophic membrane covering fecal pellets of some detritivores will likely affect these fluxes much as do the tube membranes of certain deposit feeders (3).

Stimulated bacterial growth and decomposition due to these dissolved products in the gut and feces will deplete oxygen and may create reducing conditions. Metabolic reactions resembling those in anaerobic sediments, e.g. sulfate reductions (67), can come to dominate in fecal pellets. Oxygen consumption by bacteria and their metabolic products, e.g. H_2S , will continue to remove oxygen from ambient waters. Qualitatively, the effects of a switch from aerobic to anaerobic microbial metabolism, or vice versa, are fairly well understood. In the presence of oxygen, aerobic respiration, characterized by the ability of single species to completely mineralize organic matter, will predominate. With anaerobiosis, fermentation and various types of anaerobic respiration, utilizing $(NO_3)^-$, Mn^{4+} , Fe^{3+} , $(SO_4)^{2-}$, or CO_2 as terminal electron acceptors, will occur together. Anaerobic processes are characterized by incomplete mineralization by any one group of microbes, so that a complex consortium is needed to achieve complete mineralization.

The quantitative aspects, i.e. rate and extent of conversion, of aerobic

versus anaerobic decomposition have been debated. It is well known that aerobic growth is more efficient in terms of ATP produced per mole of substrate and that bacterial biomass production is higher in the presence of oxygen (63). Confusion between efficiency and reaction kinetics has led to the mistaken assumption that aerobic decomposition rates must exceed anaerobic ones. Additionally, numerous field studies which demonstrate that aerobic decomposition proceeds much more rapidly than does anaerobic breakdown (67, 69) have reinforced the idea that aerobic breakdown is inherently faster than anaerobic breakdown; that is, under identical conditions save for the presence or absence of oxygen, organic matter will decompose more quickly if oxygen is available. Laboratory studies, on the other hand, usually reveal that there is essentially no difference in rates (46, 126). We hold the opinion that it is not the presence of oxygen per se that seems to accelerate degradation over relevant time scales, but rather factors largely restricted to oxygenated regimes such as mechanical mixing from currents and animals. Agitation, whether due to fluid dynamic processes or bioturbation, will stimulate bacteria even without the addition of oxygen (37, 46, 48). All other things being equal, anoxic decomposition of fresh organic matter may be faster or slower than oxic decomposition depending on the nature of the substrate (59). An environment of fluctuating oxygen status, then, may show decomposition rates higher than either purely aerobic or anaerobic systems. Additionally, inhibitory end-products of anaerobic metabolism will be removed when oxygenated. This hypothesis may explain the disparate results found in field versus laboratory comparisons of aerobic and anaerobic decomposition rates since strictly aerobic detrital environments are rare in nature. Where deposit feeding is intense, fluctuating oxygen conditions will be especially prevalent due either to ingestion and defecation at different depths or oxygen consuming processes in the gut or feces.

The guts of detritivores provide a unique environment where both mechanical agitation and anaerobiosis are found. We therefore expect to find rapid decomposition comparable to rates in oxic zones yet with all the characteristics of anoxic degradation—the end-products of anaerobic respiration such as NH_3 , H_2 , H_2S , and CH_4 , incomplete mineralization, and free fermentation products. Thus, an animal using the anaerobic degradation of its associated microbes may garner a rapid rate of gain, as do ruminants. Beyond mutualistic situations, the environmental consequences of this unique situation should motivate interest. Guts will surely be sites of high rates of anaerobic biogeochemical conversions—possibly among the highest in nature, adding credence to the speculation that the missing marine source of CH_4 and other end-products of anaerobic metabolism may be found in animal guts (63).

Conversely, oxygen may be supplied to the gut lumen through the ill-studied mechanisms of anal swallowing (e.g. 49), the diffusion of oxygen

through the gut wall (62; C. Plante, unpublished), and possibly from the close spatial association of the respiratory trees and gut in holothuroids. Oxidation of gut contents may simply be incidental to physiological requirements unrelated to digestion, but the oxidation will affect microbial production. Deposit feeding, including events before ingestion and after defecation, may be particularly influential in geochemical cycling. The results of this sort of unsteadiness have been little explored.

CONCLUSIONS

We conclude that the opportunity for facultative and relatively weak microbe-detrivore associations is far greater in marine than it is in terrestrial or freshwater environments. The reason is that the costs and benefits to microbial populations of association in general are both smaller. Marine animal guts on average will differ less from the detrital microbial environment in such leading chemical environmental parameters as water availability, pH, oxygen tension, Eh, and supply of inorganic but reduced nitrogen. The underlying reasons appear related to weaker or nonexistent evolutionary linkage between osmotic and digestive control in marine animals. The microbial environment of marine detritivore guts for these reasons appears well characterized spatially and temporally by digestion-absorption models based on chemical reactor theory. The major costs and benefits to microbes thus can be formulated, respectively, as risks of enzymatic digestion and local rates of supply of the products of animal digestion. Predictions can be made more precise when those products are better identified and their concentrations measured. For these same reasons of general openness to the external environment, the opportunities for invasion of detritivore guts by microbes are far more frequent than in terrestrial or even freshwater settings. Hence we anticipate that enzymatic and mechanical means of avoiding microbial attachment to the midgut will be found to be far more prevalent in the guts of marine detritivores—which do not have the general antibiotic benefits of radical pH and Eh changes. These mechanical means include encasement of gut contents in peritrophic membranes as well as frequent ablation and replacement of gut linings. On the other hand, transiting bacteria may not be important competitors, given our comparisons of absorptive area for ingested bacteria versus detritivore guts. These calculations, however, are heavily dependent on the validity of the numerous explicit assumptions. Especially important is the use of the value of 10% for proportion of active cells in ingested detritus. This number comes from one study of bacterial activity in marine sediments (93a) and may be quite different within a gut.

Once the “war of absorption” is over, the hindguts and feces of marine detritivores are excellent environments for microbial growth and may be major

unstudied sites of geochemical transformation. In many detritivores they have the unusual combination of the (albeit limited) mechanical mixing of gut passage and low Eh. Digestion theory predicts that the hindguts and feces of animals operating to maximize their own rates of absorptive gain will be sites of high availability of digestive products to microbes. Micrography of crustacean hindguts and our own experiments support this idea.

Our review also highlights obvious places to look for exceptions to these generalizations. Where supplies of structural carbohydrates and proteins of relatively uniform composition are available, the strong benefits of mutualism suggest greater association. Specific substrates are cellulose from terrigenous inputs and seagrasses, various structural carbohydrates from macroalgae and chitin from crustacean molts. Conversely, we strongly doubt that the heterogeneous substrates lumped under such chemically uninformative labels as "humic substances" are amenable to rapid digestion by microbial fermentation in digestive associations. Unlike terrestrial and freshwater environments, then, there is much less apparent improvement of food quality of the dominant inputs (phytoplankton detritus) with microbial aging or animal trituration. Away from local concentrations of macrophytes, shredders constitute a much less important guild in the sea than they do in fresh water and on land.

The case for and against acquired enzymes needs particularly close scrutiny. Similarly, gain to microbes from exoenzyme release needs examination as a function of enclosure size, geometry and residence time.

Our models explicitly deal with the interactions of individual microbial populations with animals while empirical studies largely remain at the community level. With bulk measurements of bacterial standing stocks or growth rates, differential effects of gut transit on distinct populations, each playing unique biological and geochemical roles, are hidden. More specific methodologies, such as immunofluorescence techniques and molecular probes, are required.

Likely invertebrate detritivore targets for studies of associations also can be pinpointed. Obvious associations to look for are fermenters in guts of animals in or near marshes, seagrass beds, kelp beds, and river deposits. In deep water one can expect caching by detritivores of energy-rich materials. In cases where these caches are of diatom detritus one can expect associations with specific bacteria and antibiotic protection from invasion by others. In caching of chitin or cellulose, the utility of fermentative associations is clear. Sipunculids and echiurans are particularly promising for studies of close external associations because of their unique (for marine invertebrates) potential for provision of reduced inorganic nitrogen to their associates. Documented cases of associations support these ideas but are too scarce to provide much confidence. We suggest, however, that cost-benefit theory can now provide the basis for an efficient attack on the mechanisms and consequences of digestive associations of marine microbes and detritivores.

ACKNOWLEDGMENTS

We are grateful to Deborah Penry, Jody Deming, and Jim Staley for critical evaluations of the manuscript. This work was supported by NSF grant OCE 86-08157 and ONR grant N 00014-87-K0126.

Literature Cited

- Allen, J. A., Sanders, H. L. 1966. Adaptations to abyssal life as shown by the bivalve *Abra profundorum* (Smith). *Deep-Sea Res.* 13:1175-84
- Aller, R. C. 1982. The effects of macrobenthos on chemical properties of marine sediment and overlying water. In *Animal-Sediment Relations*, ed. P. L. McCall, T. J. S. Tevesz, pp. 53-102. New York: Plenum
- Aller, R. C., Yingst, J. Y. 1978. Biogeochemistry of tube dwellings: A study of the sedentary polychaete *Amphitrite ornata* (Leidy). *J. Mar. Res.* 36:201-54
- Alongi, D. M. 1985. Effect of physical disturbance on population dynamics and trophic interactions among microbes and meiofauna. *J. Mar. Res.* 43:351-64
- Anderson, J. M., Bignell, D. E. 1980. Bacteria in the food, gut contents and faeces of the litter-feeding millipede *Glomeris marginata*. *Soil Biol. Biochem.* 12:251-54
- Anderson, J. M., Ineson, P., Huish, S. A. 1983. Nitrogen and cation mobilization by soil fauna feeding on leaf litter and soil organic matter from deciduous woodlands. *Soil Biol. Biochem.* 15:463-67
- Anderson, J. M., Macfadyen, A., ed. 1976. *The Role of Terrestrial and Aquatic Organisms in Decomposition Processes* (17th Symp. of Brit. Ecol. Soc.). Oxford: Blackwell. 474 pp.
- Austin, D. A., Baker, H. J. 1988. Fate of bacteria ingested by larvae of the freshwater Mayfly *Ephemera danica*. *Microb. Ecol.* 15:323-32
- Baker, J. H., Bradnam, L. A. 1976. The role of bacteria in the nutrition of aquatic detritivores. *Oecologia* 24:94-105
- Bayon, C. 1980. Volatile fatty acid and methane production in relation to anaerobic carbohydrate fermentation in *Oryctes nasicornis* (Coleoptera: Scarabaeidae). *J. Insect Physiol.* 26:819-28
- Bayon, C., Mathelin, J. 1980. Carbohydrate fermentation and by-product absorption studied with labelled cellulose in *Oryctes nasicornis* larvae (Coleoptera: Scarabaeidae). *J. Insect Physiol.* 26:833-40
- Berrie, A. D. 1976. See Ref. 7, pp. 323-38
- Bignell, D. E. 1977. Some observations on the distribution of gut flora in the American cockroach (*Periplaneta americana*). *J. Invert. Pathol.* 29:338-43
- Bignell, D. E. 1984. The arthropod gut as an environment for microorganisms. In *Invertebrate-Microbial Interactions*, ed. J. M., Anderson, A. D. M. Rayner, D. W. H. Walton, pp. 205-27. Cambridge: Cambridge Univ. Press
- Bignell, D. E. 1984. Direct potentiometric determination of redox potentials of the gut content in termites *Zootermopsis nevadensis* and *Cubitermes severus* and in three other arthropods. *J. Insect Physiol.* 30:169-74
- Bignell, D. E., Anderson, J. M. 1980. Determination of pH and oxygen status in the guts of lower and higher termites. *J. Insect Physiol.* 26:183-88
- Bignell, D. E., Oskarsson, H., Anderson, J. M. 1980. Distribution and abundance of bacteria in the gut of a soil-feeding termite. *J. Gen. Microbiol.* 117:393-403
- Boyle, P. J., Mitchell, R. 1978. Absence of micro-organisms in crustacean digestive tracts. *Science* 200:1157-59
- Breznak, J. A. 1982. Intestinal microbiota of termites and other xylophagous insects. *Annu. Rev. Microbiol.* 36:323-43
- Brinkhurst, R. O., Chua, K. E. 1969. Preliminary investigations of the exploitation of some potential nutritional resources by three sympatric tubificid oligochaetes. *J. Fish. Res. Bd. Can.* 26:2659-68
- Buddington, R. K., Diamond, J. M. 1987. Pyloric ceca of fish: a 'new' absorptive organ. *Am. J. Physiol.* 252:665-76
- Calow, P. 1977. Conversion efficiencies in heterotrophic organisms. *Biol. Rev.* 52:385-409
- Cammen, L. M. 1980. Ingestion rate: an empirical model for aquatic deposit feeders and detritivores. *Oecologia* (Berlin) 44:303-10
- Cammen, L. M. 1987. Polychaetes. In *Animal Energetics*, ed. T. J. Pandian, F.

- J. Vernberg, pp. 217-60. New York: Academic
25. Carman, K. R., Dobbs, F. C., Guckert, J. B. 1988. Consequences of thymidine catabolism for estimates of bacterial production: An example from a coastal marine sediment. *Limnol. Oceanogr.* 33:1595-1606
 26. Chrost, R. J. 1989. Characterization and significance of β -glucosidase activity in lake water. *Limnol. Oceanogr.* 34:660-72
 27. Cruden, D. C., Markovetz, A. J. 1987. Microbial ecology of cockroach gut. *Annu. Rev. Microbiol.* 41:617-43
 28. Cummins, K. W., Klug, M. J. 1979. Feeding ecology of stream invertebrates. *Annu. Rev. Ecol. Syst.* 10:147-72
 29. Dade, W. B., Jumars, P. A., Penry, D. L. 1989. Supply-side optimization: maximizing absorptive rates. In *Behavioral Mechanisms of Food Selection*, ed. R. N. Hughes, pp. 531-56. London: Springer-Verlag
 30. Deming, J. W., Colwell, R. R. 1982. Barophilic growth of bacteria from intestinal tracts of deep-sea invertebrates. *Microb. Ecol.* 7:85-94
 31. DeRidder, C., Jangoux, M. 1982. Digestive systems: Echinoidea. In *Echinoderm Nutrition*, ed. M. Jangoux, J. M. Lawrence, pp. 213-34. Rotterdam: Balkema
 32. Dobbs, F. C., Guckert, J. B. 1988. Microbial food resources of the macrofaunal-deposit feeder *Psychodera bahamensis* (Hemichordata: Enteropneusta). *Mar. Ecol. Prog. Ser.* 45:127-36
 33. Dobbs, F. C., Whitlach, R. B. 1982. Aspects of deposit-feeding by the polychaete *Chlymenella torquata*. *Ophelia* 21:159-66
 34. Doering, P. H. 1989. On the contribution of the benthos to pelagic production. *J. Mar. Res.* 47:371-83
 35. Drasar, B. S., Barrow, P. A. 1985. *Intestinal Microbiology*. Washington, DC: Am. Soc. Microbiol. 80 pp.
 36. Drew, R. A. I., Courtice, A. C., Teakle, D. S. 1983. Bacteria as a natural source of food for adult fruit flies (Diptera: Tephritidae). *Oecologia* 60:279-84
 37. Fallon, R. D., Brock, T. D. 1979. Decomposition of blue-green algal (cyanobacteria) blooms in Lake Mendota, Wisconsin. *Appl. Environ. Microbiol.* 37:820-30
 38. Fasham, M. J., ed. 1984. *Flows of Energy in Marine Ecosystems: Theory and Practice*. New York: Plenum. 733 pp.
 39. Feller, W. 1968. *An Introduction to Probability Theory and Its Applications*. New York: Wiley. 360 pp.
 40. Fenchel, T. 1970. Studies on the decomposition of organic detritus from the turtle grass *Thalassia testudinum*. *Limnol. Oceanogr.* 15:14-20
 41. Fenchel, T. 1984. See Ref. 38, pp. 301-15
 42. Fenchel, T. M., Jørgensen, B. B. 1977. Detritus food chains of aquatic ecosystems: the role of bacteria. *Adv. Microb. Ecol.* 1:1-58
 43. Feral, J-P., Massin, C. 1982. Digestive systems: Holothuroidea. In *Echinoderm Nutrition*, ed. M. Jangoux, J. M. Lawrence, pp. 191-212. Rotterdam: Balkema
 44. Fong, J. B., Mann K. H. 1980. Role of gut flora in the transfer of amino acids through a marine food chain. *Can. J. Fish. Aquat. Sci.* 37:88-96
 45. Forbes, T. L. 1989. See Ref. 84, pp. 171-200
 46. Foree, E. G., McCarthy, P. D. 1970. Anaerobic decomposition of algae. *Environ. Sci. Technol.* 4:842-49
 47. Forman, R. T. T., Godron, M. 1986. *Landscape Ecology*. New York: Wiley
 48. Foulds, J. B., Mann, K. H. 1978. Cellulose digestion in *Mysis stenolepis* and its ecological implications. *Limnol. Oceanogr.* 23:760-66
 49. Fox, H. M. 1952. Anal and oral intake of water by crustacea. *J. Exp. Biol.* 29:583-99
 50. Friesan, J. A., Mann, K. H., Novitsky, J. A. 1986. *Mysis* digests cellulose in the absence of a gut microflora. *Can. J. Zool.* 64:442-46
 51. Friesan, J. A., Mann, K. H., Willison, J. H. M. 1986. Gross anatomy and fine structure of the gut of the marine mysid shrimp *Mysis stenolepis* Smith. *Can. J. Zool.* 64:431-41
 52. Golterman, H. L. 1972. The role of phytoplankton in detritus formation. *Mem. Ist. Ital. Idrobiol.* (Suppl.)29:89-103
 53. Graf, G. 1989. Benthic-pelagic coupling in a deep-sea benthic community. *Nature* 341:437-39
 54. Hanlon, R. D. G., Anderson, J. M. 1979. The effects of collembola grazing on microbial activity in decomposing leaf litter. *Oecologia* 38:93-99
 55. Hargrave, B. T. 1976. See Ref. 7, pp. 301-21
 56. Harper, R. M., Fry, J. C., Learner, M. A. 1981. A bacteriological investigation to elucidate the feeding biology of *Nais variabilis* (Oligochaeta: Naididae). *Freshwater Biol.* 11:227-36
 57. Harvey, R. W., Luoma, S. N. 1984. The role of bacterial exopolymer and

- suspended bacteria in the nutrition of the deposit-feeding clam, *Macoma balthica*. *J. Mar. Res.* 42:957-68
58. Hassall, M., Jennings, J. B. 1975. Adaptive features of gut structure and digestive physiology in the terrestrial isopod *Philoscia muscorum* (Scopoli). *Biol. Bull.* 149:348-64
 59. Henrichs, S. M., Reeburgh, W. S. 1987. Anaerobic mineralization of marine sediment organic matter: rates and the role of anaerobic processes in the oceanic carbon economy. *Geomicrobiol. J.* 5:191-237
 60. Hobson, K. D. 1967. The feeding ecology of two North Pacific *Abarenicola* species (Arenicolidae, Polychaeta). *Biol. Bull.* 133:343-54
 61. Hungate, R. E. 1975. The rumen microbial ecosystem. *Annu. Rev. Ecol. Syst.* 6:39-66
 62. Hungate, R. E. 1976. Microbial activities related to mammalian digestion and absorption of food. In *Fiber in Human Nutrition*, ed. G. Spiller, R. Amen, pp. 131-49. New York: Plenum
 63. Hungate, R. O. 1985. Anaerobic biotransformations of organic matter. In *Bacteria in Nature*, ed. E. Leadbetter, J. Poindexter, 1:39-95. New York: Plenum
 64. Hylleberg, J. 1975. Selective feeding by *Abarenicola pacifica* with notes on *Abarenicola vagabunda* and a concept of gardening in lugworms. *Ophelia* 14: 113-37
 65. Hylleberg, J., Gallucci, V. G. 1975. Selectivity in feeding by the deposit-feeding bivalve *Macoma nasuta*. *Mar. Biol.* 32:167-78
 66. Hylleberg, J., Henriksen, K. 1980. The central role of bioturbation in sediment mineralization and element recycling. *Ophelia* suppl. 1:1-16
 67. Jørgensen, B. B. 1977. Bacterial sulfate reduction within reduced microniches of oxidized marine sediments. *Mar. Biol.* 41:7-17
 68. Jørgensen, B. B. 1978. A comparison of methods for the quantification of bacterial sulfate reduction in coastal marine sediments. I. Measurements with radio-tracer techniques. *Geomicrobiol. J.* 1: 11-27
 69. Jørgensen, B. B. 1980. Mineralization and the bacterial cycling of carbon, nitrogen and sulfur in marine sediments. In *Contemporary Microbial Ecology*, ed. D. C. Ellwood, J. N. Hedger, M. J. Latham, J. M. Lynch, J. H. Slater, pp. 239-52. London: Academic
 70. Jumars, P. A., Mayer, L. M., Deming, J. D., Baross, J. A., Wheatcroft, R. A. 1990. Deep-sea deposit-feeding strategies suggested by environmental and feeding constraints. *Philos. Trans. Royal Soc. Lond.* In press
 71. Jumars, P. A., Newell, R. C., Angel M. V., Fowler, S. W., Poulet, S. A., Rowe, G. T., Smetacek, V. 1984. See Ref. 38, pp. 685-93
 72. Jumars, P. A., Penry, D. L., Baross, J. A., Perry, M. J., Frost, B. W. 1989. Closing the microbial loop: dissolved carbon pathway to heterotrophic bacteria from incomplete ingestion, digestion and absorption in animals. *Deep-Sea Res.* 36:483-95
 73. Jumars, P. A., Self, R. F. L., Nowell, A. R. M. 1982. Mechanics of particle selection by tentaculate deposit feeders. *J. Exp. Ecol. Mar. Biol.* 64: 47-70
 74. Juniper, S. K. 1981. Stimulation of bacterial activity by a deposit feeder in two New Zealand intertidal inlets. *Bull. Mar. Sci.* 31:691-701
 75. Keeler, K. H. 1985. Cost:benefit models of mutualism. In *The Biology of Mutualism*, ed. Douglas H. Boucher, pp. 100-127. London: Croom Helm
 76. Kemp, P. F. 1987. Potential impact on bacteria of grazing by a macrofaunal deposit-feeder, and the fate of bacterial production. *Mar. Ecol. Prog. Ser.* 36:151-61
 77. Lawson, D. L., Klug, M. J. 1989. Microbial fermentation in the hindguts of two stream detritivores. *J. N. Am. Benthol. Soc.* 8:85-91
 78. Klug, M. J., Kotarski, S. 1980. Ecology of the microbiota in the posterior hindgut of larval stages of the crane fly *Tipula abdominalis*. *Appl. Environ. Microbiol.* 40:408-16
 79. Lehman, J. T. 1987. Selective herbivory and its role in the evolution of phytoplankton growth strategies. In *Growth and Reproductive Strategies of Freshwater Phytoplankton*, ed. C. Sandgren, pp. 369-87. London: Cambridge Univ. Press
 80. Levins, R. 1975. Evolution in communities near equilibrium. In *Ecology and Evolution of Communities*, ed. M. L. Cody, J. M. Diamond, pp. 16-50. Cambridge, Mass: Belknap
 81. Levinton, J. S., Lopez, G. R. 1977. A model of renewable resources and limitation of deposit-feeding benthic populations. *Oecologia* 31:177-90
 82. Lopez, G. R., Cheng, I-J. 1983. Synoptic measurements of ingestion rates, ingestion selectivity, and absorption efficiency of natural foods in the deposit-feeding molluscs *Nucula annulata*

- (Bivalvia) and *Hydrobia Totteni* (Gastropoda). *Mar. Ecol. Prog. Ser.* 11:55-62
83. Lopez, G. R., Levinton, J. S. 1987. Ecology of deposit-feeding animals in marine sediments. *Q. Rev. Biol.* 62: 235-60
 84. Lopez, G. R., Taghon, G. L., Levinton, J. S. ed. 1989. *Ecology of Marine Deposit Feeders*. New York: Springer-Verlag. 322 pp.
 85. Martin, M. M., Martin, J. S., Kukor, J. J., Merritt, R. W. 1980. The digestion of protein and carbohydrate by the stream detritivore, *Tipula abdominalis* (Diptera, Tipulidae). *Oecologia* 46:360-64
 86. Mayer, L. M. 1989. Extracellular proteolytic enzyme activity in sediments of an intertidal mudflat. *Limnol. Oceanogr.* 34:973-81
 87. Meitz, A. K. 1975. *Alimentary tract microbiota of aquatic invertebrates*. MS thesis. Mich. State. Univ., East Lansing, Mich. 64 pp.
 88. Miller, D. C., Jumars, P. A., Nowell, A. R. M. 1984. Effects of sediment transport on deposit feeding: scaling arguments. *Limnol. Oceanogr.* 29: 1202-17
 89. Moriarty, D. J. W., Pollard, P. C. 1981. DNA synthesis as a measure of bacterial productivity in seagrass sediments. *Mar. Ecol. Prog. Ser.* 5:151-56
 90. Moriarty, D. J. W., Pollard, P. C. 1982. Diel variation of bacterial productivity in seagrass (*Zostera capricorni*) beds measured by rate of thymidine incorporation into DNA. *Mar. Biol.* 72:165-73
 91. Moriarty, D. J. W., Pollard, P. C., Hunt, W. G., Moriarty, C. M., Wasenberg, T. J. 1985. Productivity of bacteria and microalgae and the effect of grazing by holothurians in sediments on a coral reef flat. *Mar. Biol.* 85:293-300
 92. Newell, R. C. 1965. The role of detritus in the nutrition of two marine deposit feeders, the prosobranch *Hydrobia ulvae* and the bivalve *Macoma balthica*. *Zool. Soc. Lond. Proc.* 144:25-45
 93. Newell, R. C., Fallon, R. D. 1982. Bacterial productivity in the water column and sediments of the Georgia (USA) coastal zone: Estimates via direct counting and parallel measurement of thymidine incorporation. *Microb. Ecol.* 8:33-46
 - 93a. Novitsky, J. A. 1983. Heterotrophic activity throughout a vertical profile of seawater and sediment in Halifax Harbor, Canada. *Appl. Environ. Microbiol.* 45:1753-60
 94. Parle, J. N. 1963. Micro-organisms in the intestines of earthworms. *J. Gen. Microbiol.* 31:1-11
 95. Pasciak, W. J., Gavis, J. 1974. Transport limitation of nutrient uptake in phytoplankton. *Limnol. Oceanogr.* 19:881-88
 96. Penry, D. L. P. 1989. Tests of kinematic models for deposit-feeders' guts: patterns of sediment processing by *Parastichopus californicus* (Stimpson) (Holothuroidea) and *Amphiteis scaphobranchiata* Moore (Polychaeta). *J. Exp. Mar. Biol. Ecol.* 128:127-46
 97. Penry, D. L., Jumars, P. A. 1987. Modeling animal guts as chemical reactors. *Am. Nat.* 129:69-66
 98. Penry, D. L., Jumars, P. A. 1990. Gut architecture, digestive constraints and feeding ecology of deposit-feeding and carnivorous polychaetes. *Oecologia.* 82:1-11
 99. Plante, C. J., Jumars, P. A., Baross, J. A. 1989. Rapid bacterial growth in the hindgut of a marine deposit feeder. *Microb. Ecol.* 18:29-44
 100. Porter, K. G. 1976. Enhancement of algal growth and productivity by grazing zooplankton. *Science* 192:1332-34
 101. Prah, F. G., Muehlhausen, L.A. 1989. Lipid biomarkers as geochemical tools for paleoceanographic study. In *Productivity of the Oceans: Present and Past*. Report of the Dahlem workshop on productivity of the ocean, present and past. Berlin (1988), ed. W. H. Berger, V. S. Smetacek, G. Wefer, pp. 271-89. New York: Wiley
 102. Reichardt, W. 1987. Microbiological aspects of bioturbation. Proc. 22nd European Marine Biology Symposium (Barcelona, 1987), Investigacion Pesquera (Suppl.)
 103. Reyes, V. G., Tiedje, J. M. 1976. Ecology of gut microbiota of *Tracheoniscus rathkei* (Crustacea, Isopoda). *Pedobiologia* 16:67-74
 104. Reyes, V. G., Tiedje, J. M. 1976. Metabolism of ¹⁴C-labeled plant materials by woodlice (*Tracheoniscus rathkei* Brandt) and soil microorganisms. *Soil Biol. Biochem.* 8:103-8
 105. Riber, H. H., Wetzell, R. G., 1987. Boundary-layer and internal diffusion effects on phosphorus fluxes in lake periphyton. *Limnol. Oceanogr.* 32:1181-94
 106. Rice, D. L. 1986. Early diagenesis in bioadvective sediments: Relationships between the diagenesis of beryllium-7, sediment reworking rates, and the abundance of conveyor-belt deposit-feeders. *J. Mar. Res.* 44:149-84

107. Riemann, B., Nielson, P., Jeppeson, M., Fuhrman, J. A. 1984. Diel changes in bacterial biomass and growth rates in coastal environments, determined by means of thymidine incorporation into DNA, frequency of dividing cells (FDC), and microautoradiography. *Mar. Ecol. Prog. Ser.* 17:227-35
108. Roberts, F. S. 1976. *Discrete Mathematical Models*. Englewood Cliffs, NJ: Prentice-Hall 559 pp.
109. Sanders, G. W. 1976. See Ref. 7, pp. 341-73
110. Seiderer, L. J., Newell, R. C., Schultes, K., Robb, F. T., Turley, C. M. 1987. Novel bacteriolytic activity associated with the style microflora of the mussel *Mytilus edulis* (L.). *J. Exp. Mar. Biol. Ecol.* 110:213-24
111. Self, R. F. L., Jumars, P. A. 1988. Cross-phyletic patterns of particle selection by deposit feeders. *J. Mar. Res.* 46:119-43
112. Sibly, R. M. 1981. Strategies of digestion and defecation. In *Physiological Ecology: an Evolutionary Approach to Resource Use*, ed. C. R. Townsend, P. Calow, pp. 109-39. Sunderland, Mass: Sinauer
113. Sibuet, M., Khrpounoff, A., Deming, J., Colwell, R., Dinet, A. 1982. Modification of the gut contents in the digestive tract of abyssal holothurians. In *Int. Echinoderms Conf.*, Tampa Bay, ed. J. M. Lawrence. Rotterdam: A. A. Balkema
114. Sinsabaugh, R. L., Linkins, A. E., Benfield, E. F. 1985. Cellulose digestion and assimilation by three leaf-shredding aquatic insects. *Ecology* 66:1464-71
115. Smith, C. R., Jumars, P. A., Demaster, D. J. 1986. In situ studies of megafaunal mounds indicate rapid sediment turnover and community response at the deep-sea floor. *Nature* 323:251-53
116. Stauffer, D. 1985. *Introduction to Percolation Theory*. London: Taylor & Francis, 124 pp.
117. Szabo, I., Marton, M., Buti, I. 1969. Intestinal microflora of the larvae of St. Mark's fly. IV. Studies of the intestinal bacterial flora of a larva-population. *Acta Microbiol. Acad. Sci. Hung.* 16:381-97
118. Taghon, G. L. 1988. The benefits and costs of deposit feeding in the polychaete *Abarenicola pacifica*. *Limnol. Oceanogr.* 33:1166-75
119. Taylor, E. C. 1982. Role of aerobic microbial populations in cellulose digestion by desert millipedes. *Appl. Environ. Microbiol.* 44:281-91
120. Tenore K. R., Cammen, L., Findlay, S. E. G., Phillips, N. 1982. Perspectives of research on detritus: do factors controlling the availability of detritus to macroconsumers depend on its source? *J. Mar. Res.* 40:473-90
121. Terra, W. R., Ferriera, C., de Bianchi, A. G. 1979. Distribution of digestive enzymes among the endo- and ectoperitrophic spaces and midgut cells of *Rhynchosciara* and its physiological significance. *J. Insect Physiol.* 25:487-94
122. Ulitzur, S. 1974. *Vibrio parahaemolyticus* and *Vibrio alginolyticus*: Short generation-time marine bacteria. *Microb. Ecol.* 1:127-35
123. Wainwright, P. F., Mann, K. H. 1982. Effect of antimicrobial substances on the ability of the mysid shrimp *Mysis stenolepis* to digest cellulose. *Mar. Ecol. Prog. Ser.* 7:309-13
124. Wavre, M., Brinkhurst, R. O. 1971. Interactions between some tubificid oligochaetes and bacteria found in the sediments of Toronto Harbour, Ontario. *J. Fish. Res. Bd. Can.* 28:335-41
125. Webster, J. R., Benfield, E. F. 1986. Vascular plant breakdown in freshwater ecosystems. *Annu. Rev. Ecol. Syst.* 17: 567-94
126. Westrich, J. T., Berner, R. A. 1984. The role of sedimentary organic matter in bacterial sulfate reduction: the G model tested. *Limnol. Oceanogr.* 29:236-49
127. Wheatcroft, R. A., Jumars, P. A., Smith, C. R., Nowell, A. R. M. 1990. A mechanistic view of the particulate biodiffusion coefficient: step lengths, rest periods and transport directions. *J. Mar. Res.* 48:177-207
128. Wimpenny, J. W. T. 1981. Spatial order in microbial ecosystems. *Biol. Rev.* 56:295-342
129. Yokoe, Y., Yasumasu, I. 1964. The distribution of cellulase in invertebrates. *Comp. Biochem. Physiol.* 13:323-38
130. Yonge, C. M. 1928. Feeding mechanisms in invertebrates. *Biol. Rev.* 3:21-76
131. Zhukova, A. I. 1963. On the quantitative significance of micro-organisms in nutrition of aquatic invertebrates. In *Symposium on Marine Microbiology*, ed. C. H. Oppenheimer, pp. 699-710. Springfield, Ill: Thomas
132. Hume, I. D., Warner, A. C. I. 1980. Evolution of microbial digestion in mammals. In *Digestive Physiology and Metabolism in Ruminants*, ed. Y. Ruckebusch and X. Thivend, pp. 665-84. Lancaster: MTP Press