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Chapter 5

Digestion Theory Applied to Deposit Feeding

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Introduction

As many of the contributions to this volume show, consideration of deposit feeding leads quickly to questions of digestion. There are spectacular variations in feeding rate both among species (Cammen, 1980) and within individuals (Taghon and Jumars, 1984), respectively demanding digestive diversity and flexibility. Intuitively, it seems likely that organisms eating sand and mud might more often be limited by processing ability and food quality – i.e., by the rate at which digestive products can be formed – than by acquisition rate. When one looks for theoretical guidance to design measurements and experiments regarding this interspecific diversity and intraspecific flexibility, comparatively little is available (Milton, 1981; Sibly, 1981; Taghon, 1981; Troyer, 1984). Theories of how an organism should forage and what it should ingest are abundant, but comparably general optimization approaches to predict how it ought to digest what it captures are not. The need is clear for animals in general and for deposit feeders in particular: Variations in fitness can result from variations in digestion just as readily as they can from differences in acquisition.

While browsing in a bookstore, one of us stumbled across remarkable par-

allels between chemical reactor design approaches for maximizing production rate (or efficiency) of a given chemical product (Froment and Bischoff, 1979) and the problem of maximizing rate (or efficiency) of digestive product formation. We pursued this analogy far enough to find that digestion in guts is homologous with conversion in chemical reactors (Penry and Jumars, 1986, 1987). Just as with early applications of foraging theory, however, the costs of digestion and subsequent utilization appear difficult to parameterize and difficult to measure – certainly more so than the costs of building, maintaining, and operating commercial chemical reactors. Net profit in fitness terms of incorporation into somatic growth or reproductive output depends on digestion, on absorption, and on synthesis of new tissues (Kjørboe et al., 1985), including both gross costs and gross gains. To maximize fitness, both foraging and digestion must be optimized, and theory clearly is not yet well enough developed to couple all costs and benefits in a realistic way.

These latter sentences are intended to give an impression of the level of development of this theoretical approach. It is too soon to make apologies, however, because no data can yet be found to contradict the theory's predictions. More to the point, the theory both identifies important digestive variables and links them together in a functional, mechanistic way that allows prediction. It is unfair to use old data to "test" these predictions because the theory is moderately complex; past data can be fitted to predictions simply by allowing those model variables not simultaneously measured to vary. We consequently will not rummage through the deposit-feeding literature for hollow demonstrations of adequate fits.

A major benefit of an explicit digestive theory is the specification of what needs to be measured, how well, and in what time sequence to provide a strong test. At the present level of development it seems most appropriate to make such predictions for gross gains in digestive product formation rate under mild constraints of volume and time. Until they are better parameterized and measured, we will implicitly assume that fixed, unavoidable digestive costs (present even with an empty gut) scale roughly linearly with gut volume and time and that the other costs of digestion (accounting for "specific dynamic action" sensu Kjørboe et al., 1985) scale with processing rate (vol time^{-1}) to some small exponent (greater than or equal to 1). If these assumptions are roughly correct, then gross rate of gain from digestion can give substantial insight into net gain.

Because it permits explicit solution without formulation of any cost functions, the most convenient premise against which to compare alternatives is that of digestive homeostasis. By analogy with the among-species, among-

environment trends he observed, Cammen (1980) suggested that individual deposit feeders would maintain constant rates of organic matter intake. We translate Cammen's original idea of foraging homeostasis or constant rate of intake into digestive homeostasis or constant rate of digestive product formation ($\text{mol s}^{-1}\text{cm}^{-3}$ of gut). We thus do not suggest that the homeostasis premise we examine is identical to that proposed by Cammen. We pose two alternatives, those of rate ($\text{mol s}^{-1}\text{cm}^{-3}$ of gut) and conversion efficiency ($\text{mol product mol}^{-1}$ of reactant) maximization. The former is the digestive analog of energy optimization in optimal foraging, while the latter is an alternative approach used in chemical engineering when reactants are expensive or difficult to obtain. By analogy, the latter might apply where food abundance (not quality) has been severely limiting over the evolutionary history of the organism.

Our intent in this paper is to provide explicit parameterizations, based on reactor theory, of measurable features of digestion in deposit feeders and then to make predictions under each of the three alternative premises of production-rate maximization, homeostasis, and efficiency maximization. In other words, our goal is to take our previously developed theory (Penry and Jumars 1986, 1987) and put it in the form that we believe will be the most useful in designing and interpreting experiments. We hope that others will join us in testing both the parameterizations and the predictions.

As a byproduct, the reactor-theory approach provides a useful mechanism for systematizing both the formation of (digestive) functional groups and the study of microbial (digestive) symbioses of deposit feeders. The bewildering diversity of deposit feeders appears to fall into three distinct classes of reactor types and along one axis of mean particle residence time in the gut. As chauvinists of the study of deposit feeding, we point out that deposit feeders turn out to be fortunate choices for application of reactor theory to digestion: The governing equations can be simplified substantially by assuming that digesta volume does not change significantly during digestion. If structural and kinematic similarity with chemical reactors is found to reflect functional similarity, then seemingly esoteric reactor theory has immediate applications beyond feeding ecology. It should be useful in choosing species and generalizing results for evaluation of geochemical transformations occurring in animal guts. In an applied context it could provide an objective way to choose model systems for examining dietary pathways of pollutants.

A Classification of Chemical Reactors

Chemical reactors are classified on the bases both of time variation of reactant input (continuous or discontinuous) or throughput and of the pattern or method in which reactants are brought together (with or without mixing) (e.g., Levenspiel, 1972). In terms of time variation there are batch, continuous-flow, and semi-batch reactors. In a batch reactor, all reactants are added instantaneously, the reaction is allowed to proceed for a set period, and then products and unreacted material are all removed. The empty batch reactor then can remain idle for a period or be refilled. In continuous flow, reactants are continuously introduced and products, removed. Anything in between is referred to as semi-batch.

One kind of batch reactor and two kinds of continuous-flow reactors are recognized as ideal (in the sense of being described accurately by simple equations) on the basis of patterns of reactant mixing. In ideal batch reactors, contents are instantaneously and continuously mixed, so that concentrations are spatially uniform and vary only in time.

In continuous, plug-flow reactors (hereafter PFRs), material does not mix along the flow axis, so that at steady state (no variation at any point in the reactor over time) concentrations vary in a continuous gradient from inlet to outlet of the reactor. In continuous-flow, stirred-tank reactors (hereafter CSTRs), material is continuously and completely mixed, such that concentrations vary neither in space nor in time and are the same at the inlet as at the outlet. Reactions go on, of course, but products are mixed instantaneously with newly introduced reactants, while the volume of newly introduced material displaces an equivalent volume of material from the outlet. A familiar oceanographic application of the CSTR is the chemostat, the theory of which comes directly from the literature of reactor analysis and design.

In the ideal batch reactor reactant concentration is constant in space and varies in time, in the ideal PFR concentration varies in space and is constant (at any point along the flow path) in time, and in the ideal CSTR concentration is constant in both space and time. In the gut of the real deposit feeder, however, food reactant concentration most likely varies in both space and time as digestive enzymes and products diffuse into and out of sediments passing through the gut. In short, the situation may well not be ideal in the sense of producing simple, general equations. Some insight into non-ideal and unsteady behavior can be gained nonetheless by using ideal batch- and continuous-processing models to define end members. Further, to

$$\begin{array}{cc} \text{Batch Reactor and PFR} & \text{CSTR} \\ t = \tau = C_{AO} \int_0^{X_{Af}} \frac{dX_A}{-r_A} & \tau = \frac{C_{AO} X_{Af}}{-r_A} \end{array}$$

t	=	holding time (batch reactor) (time)
τ	=	throughput time (PFR and CSTR) (time)
C_{AO}	=	initial concentration of reactant A in ingested food (mol volume ⁻¹)
X_A	=	conversion of reactant A into products (dimensionless fraction)
X_{Af}	=	final conversion of reactant A after holding or throughput time
$-r_A$	=	reaction rate, given as the disappearance rate of reactant A (mol volume ⁻¹ time ⁻¹)

Table 5.1: Reactor-theory solutions for digestive equations in batch reactors, plug-flow reactors (PFRs), and continuous-flow stirred-tank reactors (CSTRs), assuming insignificant change in volume of gut contents during digestion.

make testing of predictions as easy as possible, we give the simplest models that cannot yet be refuted by observations.

We give the most compact and general (assuming no volume reduction during digestion) forms of the reactor equations for the three ideal reactor types in Table 1. We will not give derivations here, for they are available elsewhere (Levenspiel, 1972; Penry and Jumars, 1987). We note that the solution for batch-reactor holding time when there are no idle periods between batches is identical to the solution for the throughput in a PFR of equivalent volume. For the remainder of this chapter, we will describe these two reactors with the same equation, implying that the batch reactor is instantaneously emptied and refilled. Graphical solutions for batch reactors with varying idle periods (search times between meals) are given by Penry and Jumars (1986).

We also will not give the more general formulations in which volume can change during digestion. Tests of predictions resulting from the formulations given here should thus focus on animals that do not digest an appreciable proportion of the volume they ingest; i.e., they should avoid the smaller species or life stages that may verge on macrophagy and avoid any species that succeed in being so selective that they ingest primarily digestible material. Such species fall outside our intentionally narrow definition of deposit feeding.

There are some other inherent assumptions, however, that bear close scrutiny, specifically, the mixing patterns of digesta during throughput. If predictions are not met, it is worth knowing whether the approach as a whole lacks merit, or whether the assumptions need modification. We thus will try to point out sensitive assumptions as they are made.

A Gut Reactor Classification of Deposit Feeders

Where (if anywhere) among deposit feeders are guts that may operate as these varieties of ideal chemical reactors seen? We often have to rely on morphology because patterns of digesta throughput have been so little studied. Guts with one opening are suggestive of batch processing, though the converse need not be true. Among the Ophiuroidea and Asteroidea, members have been classed as deposit feeders (e.g., Shick et al., 1981), although we do not know the extent to which volume reduction due to selective ingestion of digestible material (e.g., Scheibling, 1981) occurs. If the gut is filled in one event (rather than as a series of smaller meals), if the contents are mixed upon filling and continually thereafter, and if, after some period of digestion, the gut is completely emptied, ophiuroid and asteroid guts can be modeled as batch reactors. It is obvious, in this case, that the patterns of gut filling, mixing and emptying need to be described. The literature is virtually silent on this issue because the need for such information was not apparent prior to digestive modeling. The most common kind of deposit-feeder gut is a straight tube in which little axial mixing occurs. Evidence of good fit to plug flow is given by Cammen (1980) for *Nereis succinea*, by Miller (1984) for *Corophium* spp. and by Jumars and Self (1986) for *Pseudopolydora kempji japonica*. Our unpublished tracer experiments add *Abarenicola pacifica*, *Parastichopus californicus*, and *Pygospio elegans* to the list. We expect this pattern to be found frequently because, under most conditions, plug flow provides the greatest rate of digestive product formation in minima of time and volume (Penry and Jumars, 1987). Peristalsis, so long as it produces mixing cells of small axial extent, does not substantially affect the predictions from pure plug flow (Penry and Jumars, 1987).

We have found via tracer experiments, however, that mixing is much more substantial in some deposit feeders. In *Amphicteis scaphobranchiata* (Penry, in prep.) and *Hobsonia florida* (Jumars and Self, 1986) substantial mixing goes on in an expanded anterior portion of the gut. We assume that similar mixing goes on in the expanded anterior chambers of other tere-

bellimorph polychaetes (e.g.: Dales, 1955; Dales and Pell, 1970). We have suggested (Penry and Jumars, 1987) that these animals' guts can be modeled as CSTR-PFR series, as is clearly the case with ruminants (Penry and Jumars, 1986). We have suggested that the mixing chamber serves to overcome problems of diffusing enzymes into food when food is of low porosity or gut diameter is large (Penry and Jumars, 1987). If microbial fermentation does prove to be important in digestion, then these mixing chambers would be more likely places to look for unattached symbiotic microbes than would tubular PFR segments of guts. Degree of mixing in both batch reactor and CSTR-PFR guts must be quantified. If it is incomplete as it is in some commercial reactors, the actual degree of mixing can be quite easily incorporated into models (e.g.: Bailey and Ollis, 1977; Smith, 1981) when making predictions. At this point, we assume that mixing is complete in batch reactor guts and the CSTR portions of CSTR-PFR guts and use the unmodified, ideal reactor equations. Similarly, we do not deal here with complications such as digestive caeca. Again, the models can be easily modified (Penry and Jumars, 1987), should early results indicate that it is necessary.

Predictions

To make predictions explicit, one must stipulate reaction kinetics. In the continuing spirit of choosing the simplest model that cannot be discredited with existing data, we use the Michaelis-Menten model for digestive-enzyme reaction kinetics:

$$-r_A = \frac{V_{max}C_A}{K_m + C_A}, \text{ where}$$

V_{max} is the maximal rate of reaction, C_A is the concentration of substrate, and K_m is the concentration when the rate of reaction is one half its maximal value. Enzyme concentration is assumed constant, and reaction rate reaches V_{max} when all available enzyme is saturated with substrate. Substituting this expression for $-r_A$ in the equations of Table 1, the ideal reactor performance equations can be solved for throughput time in terms of the Michaelis-Menten parameters and the extent of conversion (X_A) of reactant into product (Table 2A).

In designing experiments to test the predictions derived from the three premises, homeostasis, energy maximization, and efficiency maximization, the most straightforward approach we have envisioned proceeds as follows: First, an animal ingests a food substance with a well defined initial concentration (C_{A0}) of some component. To avoid semantic difficulties later, we

call this food concentration the "conditioning" concentration. The extent of conversion is measured as the concentration of food remaining ($[1 - X_A]C_{A0}$) in the fecal material and, perhaps, at various points along the gut. Measurements are carried out until it is established that feeding rate and conversion no longer change with time (constant V_{max} and K_m). Concentration of the food component is then altered from the conditioning concentration to a new level (C'_{A0}), and measurements are made again.

There is one unique solution for digestive homeostasis (Table 2B), both in terms of the expected conversion and of throughput time under the new food condition (C'_{A0}), assuming that enzyme kinetics (i.e., V_{max} and K_m) remain constant over the short-term course of the perturbation experiment. For the CSTR neither V_{max} nor K_m is required to specify the predicted extent of conversion (X'_{Af}) or the relative throughput time (τ'/τ). For the PFR and batch reactor, the same is true of conversion, but the value of K_m is required to solve for relative holding (t'/t) or throughput (τ'/τ) time (see Table 2B). The solution for a batch reactor that is not immediately refilled upon emptying is obtained by adding the amount of time the gut remains idle to the holding time that appears in the denominator for the instantaneously refilled batch-reactor equation (equivalent to the PFR equation) of Table 2B.

To better illustrate the behaviors of both PFRs and CSTRs and to allow comparison between them, we present (Fig. 1) graphs of absolute conversion and of relative throughput time, both plotted against relative concentration of substrate in the ingested food (C'_{A0}/C_{A0}). Only the relative throughput-time curve for the PFR (= the holding-time curve for a batch reactor with no idle periods) requires stipulation of absolute conditioning and new substrate concentrations (rather than simply their ratios). Since we must stipulate these absolute concentrations, we express them in the way that is least restrictive, as concentrations relative to (i.e., divided by) K_m . For purposes of illustration, we take the conditioning concentration of substrate (C_{A0}) as equal to K_m . Again, this restriction is necessary only for the throughput curves for PFRs (and holding times for batch reactors). The curves drawn in Fig. 1 are explicitly for the premise of digestive homeostasis, and describe how conversion and relative throughput time should change in response to the conditioning concentration if an animal is to maintain a constant rate of digestive product formation ($\text{mol s}^{-1} \text{cm}^{-3}$). Departures that fall below the curves (assuming unchanged enzyme kinetics) suggest that the animal is achieving a greater rate of digestive product formation on the new food concentration (C'_{A0}) than it was on the conditioning concentration, and de-

A. Solutions for holding time (batch reactor) or throughput time in terms of X_{Af} and C_{AO} .

Batch reactor and PFR:

$$t = \tau = \frac{k_m}{V_{\max}} \left[-\ln(1 - X_{Af}) + \frac{C_{AO} X_{Af}}{K_m} \right]$$

CSTR:

$$\tau = \frac{K_m}{V_{\max}} \left(\frac{X_{Af}}{1 - X_{Af}} + \frac{C_{AO} X_{Af}}{K_m} \right)$$

B. Solutions for homeostasis (mol product produced time⁻¹ = constant) with varying C'_{AO} , where V = volume of gut contents = constant.

$$\frac{X_{Af} C_{AO} V}{t \text{ or } \tau} = \text{constant} = \frac{(\text{dimensionless fraction})(\text{mol volume}^{-1})(\text{volume})}{\text{time}}$$

$$\text{Therefore } \frac{X'_{Af} C'_{AO} V}{t' \text{ or } \tau'} = \frac{X_{Af} C_{AO} V}{t \text{ or } \tau}, \text{ and}$$

1. X'_{Af} in terms of C_{AO} , C'_{AO} and X_{Af} :

$$\text{Batch reactor and PFR (solved iteratively): } (1 - X'_{Af})^{X_{Af}} = (1 - X_{Af}) \frac{C'_{AO} X'_{Af}}{C_{AO}}$$

$$\text{CSTR: } X'_{Af} = \left[\frac{C_{AO}}{C'_{AO}} (X_{Af} - 1) \right] + 1$$

2. t'/t or τ'/τ in terms of C_{AO} , X_{Af} , C'_{AO} , X'_{Af} , and K_m :

$$\text{Batch reactor and PFR: } t'/t = \tau'/\tau = \frac{-\ln(1 - X'_{Af}) + \frac{C'_{AO} X'_{Af}}{K_m}}{-\ln(1 - X_{Af}) + \frac{C_{AO} X_{Af}}{K_m}}$$

$$\text{CSTR: } \tau'/\tau = \frac{C'_{AO} C'_{Af}}{C_{AO} X_{Af}}$$

Table 5.2: Experimentally useful solutions of the digestive equations, assuming that Michaelis-Menton kinetics limit the rate of digestion. Unprimed variables refer to the conditioning period, while primed (t) variables refer to expectations under the new initial food concentration (C'_{AO}). See Table 1 and text for explanation of other symbols.

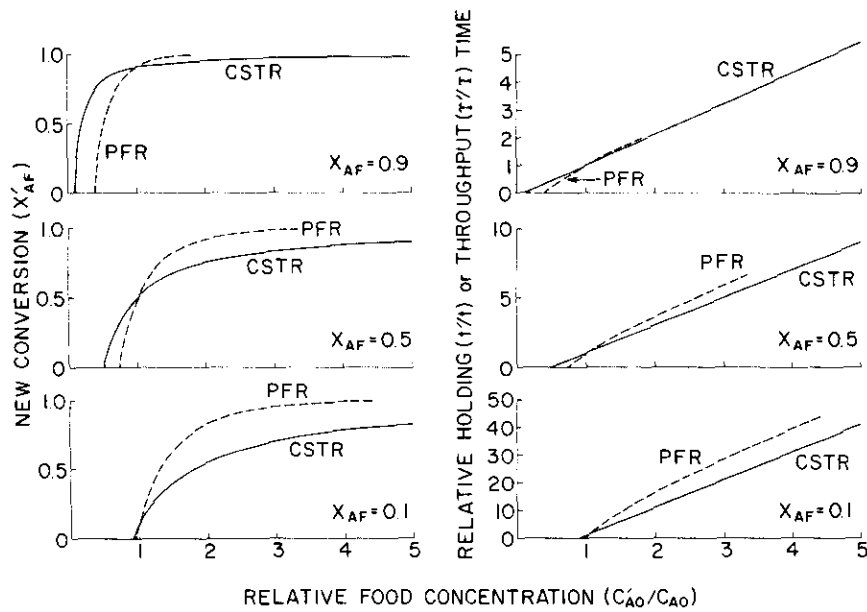


Figure 5.1: Predicted new conversion (X'_{Af}) and relative holding (t'/t) or throughput (τ'/τ) times for digestive homeostasis with three different conditioning conversions (X_{Af}). Predicted new conversions are independent of kinetic parameters of the digestive enzymes; CSTR holding times are as well. Batch reactor relative holding times and PFR relative throughput times, however, depend upon the ratios of both C_{A0} and C'_{A0} to K_m ; for purposes of illustration, the case where $C_{A0} = K_m$ is shown. See text and Tables 1 and 2 for symbols, mathematical solutions and explanations. Dashed lines (PFR and batch reactor) terminate at values of X'_{Af} greater than 0.99 because they appear unrealistic.

partures that fall above suggest the converse. It is extremely important to note that throughput time and conversion can not be varied independently and one is readily calculable from the other if V_{max} and K_m are invariant (Table 2). Thus, when an animal varies its throughput time, it also changes its conversion in a predictable fashion. We give the homeostasis solutions for three specified states characterized by widely different conversion efficiencies ($X_{Af} = 0.9, 0.5, 0.1$) achieved on the conditioning substrate concentration.

There is no explicit solution based only on gross digestive gains for either of the other two premises, since inspection of the equations for Tables 1 and 2 shows that rate maximization should drive throughput times (and conversions) toward zero, while efficiency maximization should push throughput times and conversions very high. Exactly how low or high will be determined by the associated costs, which remain unparameterized. If rate of digestive product formation is an important determinant of net mass or energy gain in a fitness context, however, and if short-term variations of food quality are frequent in the animal's natural environment, one would expect systematic departure downward from the homeostasis curves. If, alternatively, the amount of food (as opposed to the concentration of digestible substrate in it) has frequently been limiting in an organism's evolutionary history, one might expect conversion efficiency to remain high, even at those low food concentrations where both the homeostasis premise and the production-rate maximization premise predict decreased conversion in order to maintain or to increase, respectively, the rate of product formation.

Discussion and Conclusions

An immediate advantage of these very explicit models for digestion is that predictions are made in terms of measurable parameters. The models allow the idea of digestive homeostasis, for example, to be tested through the measurement of both conversion and throughput time. Without this explicit formulation the extent of conversion necessary to maintain digestive homeostasis with increasing food concentration would not be obvious. Likewise, it would not be apparent that increasing throughput times (decreasing feeding rate) with increasing food concentration produce greater rates of digestive conversion ($\text{mol s}^{-1} \text{cm}^{-3}$ of gut), as long as the throughput times increase more slowly than the homeostasis solution curve. More obviously, Michaelis-Menten kinetics assure that unchanging throughput times with increasing food concentration result in increasing rates of digestive conversion.

We have eliminated those segments of the curves that require conversions above 0.99, because they are likely to be unattainable. Should we be wrong, the solutions are easily generated and visualized by extending the present curves. Since we are dealing with organisms of unspecified absolute size, we cannot similarly eliminate segments of the relative throughput time curves for requiring unrealistically fast throughput rates. At some low throughput time, diffusion of digestive products to absorptive surfaces will not have time to occur. Conversion will occur so long as our kinetic reaction description is accurate, but products will go out with the feces. The relevant diffusion times will depend upon absolute gut diameters and the geometries of absorptive sites, so we are unable to specify minimal retention times on the more general (relative retention-time) plots of Fig. 1.

Since we know of no deposit feeder which operates entirely as a CSTR, the degree to which the CSTR curve is the better (or worse) descriptor of a deposit feeder using a CSTR-PFR series will depend on the relative volume of the CSTR portion of its gut. Note also that the PFR will not receive a concentration of C_{A0} or C'_{A0} , but rather a concentration reduced by both mixing and digestive reaction in the CSTR portion of the gut. The curves might also suggest that CSTRs are the more flexible in situations of rapidly and widely varying food concentration, since the homeostasis solutions do not require as great a range of either conversion or relative throughput time, and since the homeostasis is possible at lower concentrations in CSTRs as compared to PFRs or batch reactors. The reason is simple: Food concentration is reduced immediately to the gut average concentration by mixing. This seeming advantage in a homeostatic sense becomes a disadvantage under the rate-maximization premise, since at the same C'_{A0} and total gut volume a PFR can outproduce a CSTR (Penry and Jumars, 1986).

We again emphasize that the solutions of Fig. 1 are for short-term experiments only. It is very likely, for example, that increasing substrate concentration will induce increased enzyme secretion, increasing V_{max} , and thus changing the homeostasis solution for longer time scales in a manner predictable from the equations of Table 2. Increasing V_{max} with time of exposure to high substrate concentrations (relative to K_m) seems more compatible, however, with the premise of maximizing rate of digestive conversion than with either of the other two premises. Further, such increase is compatible with field data collected to date (Stuart et al., 1985). With two of three species in the laboratory, Taghon and Jumars (1984) found slowing of feeding from initially high rates. Their results would be consistent with induction of enzyme secretion in these two species but not in the third.

An implicit assumption throughout is that the concentration of the limiting nutrient or energy source (or at least of some component well correlated with it) is being measured. For deposit feeders in particular and detritivores in general, either the rate of supply of assimilable nitrogen or the rate of supply of chemical energy can be limiting (Bowen, 1984). If one measures concentrations and conversions of non-limiting food substances in heterogeneous resources when making plots of the sort put forth in Fig. 1, the results may well be uninterpretable. Application of digestion theory emphasizes the need to identify the limiting resource, as pointed out amply in this book.

Lastly, we repeat (Penry and Jumars, 1986, 1987) the caution that digestion is only one phase of the problem of acquiring and utilizing energy and nutrients. Digestion is a phase that can now be attacked with explicit, mechanistic models to determine gross gains, to put useful constraints on the subsequent steps of absorption and assimilation and to balance against costs. There might, for example, be two alternate means of achieving net homeostasis via digestion, one (close to that we have shown in Fig. 1) with comparatively long throughput times balanced against low costs, and one with comparatively shorter throughput times (with higher gross formation rate of product) and consequently higher costs. If digestion is indeed an energetically cheap process (Kjørboe et al., 1985) and if little energy is needed to vary throughput times substantially in deposit feeders (Taghon, this volume), then there is good reason to suspect that of our three premises the idea of conversion-rate maximization is the most likely to be supported by experiment.

Unless an argument firmly grounded in Darwinian selection could be found to contradict it (Calow, 1982) for deposit feeders, we would favor the premise of digestive rate maximization as an *a priori* hypothesis, even if there were strong selective pressure for a constant rate of energy or nutrient supply for growth. If food concentration varies in nature from time to time for any given individual, then a much more reliable way (than digestive homeostasis) of assuring a constant energy or nutrient supply for growth is achievement of conversion in excess of immediate requirements—with absorption and transfer to a storage organ. The storage organ can then supply energy or nutrients at the required rate independent of short-term, external variation. Such arguments, however, can go on *ad nauseam* without any clear scientific benefit. We hope that, rather than fueling continuing debate, our explicit formulation in terms of measurable variables will be used experimentally to extinguish it.

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