

## MODELING ANIMAL GUTS AS CHEMICAL REACTORS

DEBORAH L. PENRY AND PETER A. JUMARS

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

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The digestive tactics open to an animal constrain its foraging. If an animal "operates" to maximize its net rate of gain of energy or nutrients, the optimality of "operating policies" must be defined with respect to both foraging and digestion. Optimality models have generally neglected digestion, although the need to identify digestion parameters has become increasingly apparent (Milton 1981; Sibly 1981; Taghon 1981; Troyer 1984). We (Penry and Jumars 1986) suggested that principles of chemical-reactor theory (from which the idea of operating policies comes) can be used to formulate optimization constraints in a general theory of digestion. In this paper we follow those principles to develop explicit models of digestion.

To design a process of chemical conversion, whether it be industrial ammonia synthesis or digestion of food materials by an animal, is to ask what type and size of reactor and what operating conditions are required to achieve a given extent of a desired reaction. The answer, the process design of a reactor, is obtained as follows.

1. Reactions of interest are identified, and models of reaction kinetics are developed from which rate equations for the reaction are derived.
2. With reaction kinetics specified, the ideal reactor configuration for accomplishing the given reaction is determined.
3. Operations of real reactors are compared with operations of corresponding ideal models, and deviations of real reactor performance from the ideal are analyzed.
4. There are then two options: modify the real reactor to better approximate the ideal model; or modify the model to account for deviations from ideal operations and use the modified model to achieve improved predictions of real reactor performance.

This design sequence serves as the general outline for our development. We first derive forms for digestive-reaction-rate equations and model guts as ideal reactors. We then compare marine deposit feeders (e.g., polychaete annelids) and mammalian foregut fermenters (e.g., kangaroos, cows, sheep) and hindgut fermenters (e.g., horses, rabbits) with the ideal models. Deposit feeders promise to

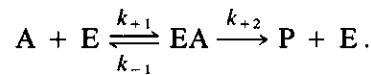
be amenable to simple modeling (Jumars and Penry, in press), and mammalian fermenters have the richest literature for comparison with reactor theory. Finally, since building the ideal worm or cow is not yet a viable option, we suggest generic modifications of ideal gut-reactor models to achieve improved predictions of real reactor performance.

#### MODEL DERIVATION

##### *Digestive Reaction Kinetics and Rate Equations*

Analysis of any chemical process begins with a theoretically or empirically derived kinetic model to provide a form for the reaction-rate equation. Reactions are described as either homogeneous or heterogeneous with respect to phases (gaseous, liquid, solid): homogeneous reactions occur in only one phase, but heterogeneous reactions involve more. General rate equations for the latter include, in addition to reaction kinetics, terms that describe mass transfer between phases.

Digestion, the process that transforms ingested food materials into assimilable components, proceeds through various reactions catalyzed by enzymes and mediated by microbes. These reactions, involving proteins of high molecular weight and other macromolecules, are intermediate between homogeneous and heterogeneous reactions, and the description chosen is the one most useful in a given situation (Levenspiel 1972). We begin by assuming that digestive reactions are homogeneous with rates limited only by chemical kinetics. The basic form proposed for reactions catalyzed by enzymes is



Food component A and enzyme E combine reversibly to form complex EA, which then dissociates irreversibly into product(s) P and free enzyme E. The rate equation (after Briggs and Haldane 1925) is of the form

$$-r_A = \frac{k_{+2} C_E C_A}{[(k_{-1} + k_{+2})/k_{+1}] + C_A}, \quad (1)$$

where  $C_E$  and  $C_A$  are, respectively, concentrations of enzyme and of food component A, and  $k_{-1}$ ,  $k_{+1}$ , and  $k_{+2}$  are the rate constants. This equation simplifies to the more familiar Michaelis-Menten form when  $C_E$  is constant:

$$-r_A = v_{\max} C_A / (K_m + C_A), \quad (2)$$

where  $v_{\max} = (k_{+2} C_E)$  and  $K_m = (k_{-1} + k_{+2})/k_{+1}$ . Digestive reactions catalyzed by an animal's own enzymes are described with this rate equation.

Digestive reactions involving microbial fermentation are autocatalytic: a reaction product (microbes) acts as a catalyst, and the reaction rate is a function of the concentrations both of microbes and of food materials. The modified Michaelis-Menten rate equation often used to describe such autocatalytic biological reac-

tions (Bischoff 1966) is of the form

$$-r_A = v_{\max} C_A C_M / (K_m + C_A), \quad (3)$$

where  $C_M$  is the concentration of microbes.

The basic Michaelis-Menten equation (hereafter termed the catalytic equation) and the modified form for autocatalytic, fermentation reactions (hereafter, the fermentation equation) relate digestive reaction rates to concentrations (of food substrates, enzymes, and microbes). Rates of digestive reactions may also be affected, however, by changes in temperature, pH, and the composition of the microbial community in the gut. We avoid these complications by formulating reactor models for animal guts operating at steady state. In a steady-state model, temperature, pH, and the composition of the microbial community are assumed constant over time at any given point within the gut. The need to ensure that these steady-state assumptions are met then becomes an important consideration when designing experimental tests of model predictions.

#### *Mass Balance*

Having chosen kinetic models, the next step is to identify the ideal method for processing reactants. Our objective in this exercise in reactor design is to identify the gut (reactor) configuration and digestive (operating) strategy that maximize an animal's net rate of production of energy and nutrients from food.

We use conservation principles to predict reactor performance. Phenomena occurring in chemical reactors are reactions and transfers of mass, energy, and momentum. In contrast to many industrial situations, both temperature and pressure variations within an animal's gut are generally negligible relative to compositional changes. Reaction and mass transfer are the dominant processes, and reactor-specific equations for conservation of mass suffice. Formulation of reactor-specific equations begins with a general mass-balance expression written for any component, reactant, or product, over an arbitrary element of reactor volume:

$$I = E + R + W, \quad (4)$$

where  $I$  is input of component in moles per unit of time;  $E$ , output in moles per unit of time;  $R$ , disappearance in moles per unit of time; and  $W$ , accumulation in moles per unit of time. Simplification of this general equation for a given reactor type yields the mass-balance equation describing that reactor's performance. There are three ideal reactors, which differ primarily in the way reactants are processed. Although mass-balance equations for each can be obtained from any chemical-engineering text (e.g., Levenspiel 1972; Froment and Bischoff 1979; J. Smith 1981), we include derivations to provide the foundation for understanding gut-reactor models as well as to allow specific modifications for digestive processes. Our notation follows that of Levenspiel (1972).

#### *The Batch-Reactor Performance Equation*

The batch reactor (fig. 1), as its name implies, processes reactants in discrete batches. Production periods are separated by idle periods, during which the

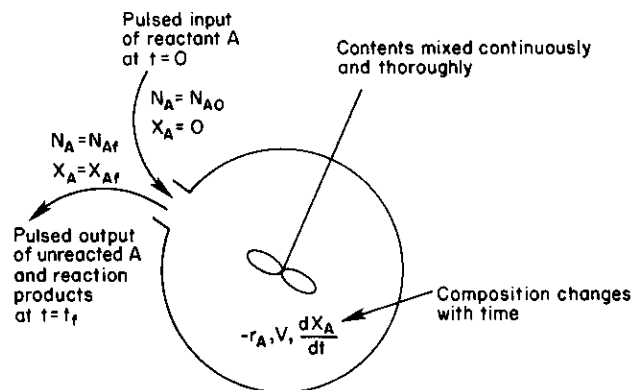


FIG. 1.—The ideal batch reactor operates intermittently. Reactants are loaded at time  $t = 0$ . After the reaction occurs, the resulting reactant-product mixture is unloaded at  $t = t_f$ . At  $t = 0$ , the amount of reactant A added to the reactor is  $N_{A0}$ ; the proportion of reactant A converted to products,  $X_A$ , is initially zero. At  $t = t_f$ , the amount of A that has not reacted is removed from the reactor ( $N_{Af}$ ); the final conversion of A to products is  $X_{Af}$ .  $V$  is reactor volume;  $-r_A$  represents an equation for reaction rate.

reactor is emptied of products from the preceding reaction cycle, reloaded with reactants, and prepared for the next cycle. The ideal batch reactor is spatially homogeneous at any one time: its contents are perfectly mixed, and changes in composition occur only with respect to time. Thus, the mass balance of any key component, here designated reactant A, can be written over the entire reactor volume. Since material neither enters nor leaves the batch reactor during reaction ( $I = E = 0$ ), the general mass balance (eq. 4) simplifies to two terms:

$$R = -W, \quad (5)$$

where  $R$  is the disappearance of A by reaction (moles·time<sup>-1</sup>) and  $W$  is the accumulation of A in the reactor. The amount of reactant A consumed by reaction per unit of time is a function of reaction rate,  $-r_A$ . When  $-r_A$  is expressed per unit of volume,

$$R = -r_A V, \quad (6)$$

where  $R$  is the amount of A reacted (moles·time<sup>-1</sup>);  $-r_A$ , the reaction rate (moles·volume<sup>-1</sup>·time<sup>-1</sup>); and  $V$ , the reacting volume. The amount of reactant A accumulated (i.e., unreacted) per unit of time is

$$W = -N_{A0} dX_A/dt, \quad (7)$$

where  $W$  is the amount of A accumulated (moles·time<sup>-1</sup>);  $N_{A0}$ , the initial amount of A introduced (moles); and  $dX_A/dt$ , the time rate of change ( $d/dt$ ) of the fraction of A converted to products ( $X_A$ ) (time<sup>-1</sup>). Substituting equations (6) and (7) into equation (5), rearranging terms, and integrating the entire expression yields the performance equation (eq. 8) for an ideal batch reactor. The holding or reaction

time ( $t$ ) required to achieve a given conversion ( $X_{Af}$ ) of reactant A to products in a batch reactor is

$$t = N_{A0} \int_0^{X_{Af}} \frac{dX_A}{-r_A V}. \quad (8)$$

If we assume that an animal ingests enough food to fill its gut, the volume of reacting food material equals gut volume, and  $V$  is the total gut volume. As digestion proceeds, however, the volume of food material decreases relative to gut volume as digestive products are absorbed. Such deviations from ideal batch-reactor operations can be incorporated into modified batch-reactor models, but it is reasonable to begin with a consideration of the least-complex case and initially neglect deviations from the ideal. If we assume that volume variations resulting from absorption are negligible, a justifiable assumption for some animals we discuss (e.g., deposit feeders), we can further simplify the batch-reactor performance equation. After removing the reactor volume  $V$  from under the integral,

$$t = C_{A0} \int_0^{X_{Af}} \frac{dX_A}{-r_A}, \quad (9)$$

where  $C_{A0} = N_{A0}/V$ , the initial concentration of reactant A. For an animal with a batch-reactor gut, equation (9) can be solved for the gut holding time ( $t$ ) necessary to achieve a specified conversion ( $X_{Af}$ ), or it can be solved for the conversion that can be achieved in a given holding time ( $-r_A$ ,  $C_{A0}$  given in each case). Solutions to equation (9) (i.e., solution for  $t$  given  $-r_A$ ,  $C_{A0}$ ,  $X_{Af}$ , or solution for  $X_{Af}$  given  $-r_A$ ,  $C_{A0}$ ,  $t$ ) can then be used to determine the gut volume required to achieve a specified rate of production of digestive products.

#### *The Plug-Flow-Reactor Performance Equation*

The plug-flow reactor (PFR; fig. 2) is characterized by a continuous, orderly flow of material through the (usually tubular) reaction vessel. Since perfect radial mixing is assumed, reactants are uniform in any cross section. Axial mixing and axial diffusion rates are, by definition, negligible in comparison with axial flow rate, and material composition varies only along the flow path. The mass balance for a key component, reactant A, in a PFR operating at steady state must, therefore, be made over a differential volume element. Since material flows continuously through the reactor, there can be no accumulation of A within the reaction vessel ( $W = 0$ ), and the general mass balance (eq. 4) becomes

$$I = E + R. \quad (10)$$

The input of A into volume element,  $dV$ , (fig. 2) is

$$I = F_A, \quad (11)$$

where  $F_A$  is the input rate of A in moles·time<sup>-1</sup>; and the output of A from  $dV$  is

$$E = F_A + dF_A. \quad (12)$$

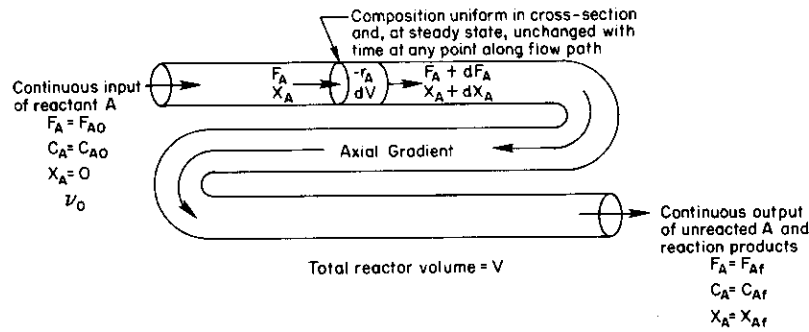


FIG. 2.—The ideal plug-flow reactor operates continuously. The volume of material flowing through the reactor per unit of time is the throughput rate,  $v_0$ . The input rate of reactant A is  $F_{A0}$ ; the initial concentration of A is  $C_{A0}$ ; and the proportion of A converted to products,  $X_A$ , is initially zero. The output rate of A is  $F_{Af}$ ; the final concentration of A is  $C_{Af}$ ; the final conversion of A to products is  $X_{Af}$ . The characteristics of the ideal PFR require that a mass balance be written over a differential volume element,  $dV$ , and then integrated over the entire reactor volume,  $V$ .  $-r_A$  represents an equation for reaction rate.

The amount of A consumed is a function of reaction rate,  $-r_A$  (moles·volume<sup>-1</sup>·time<sup>-1</sup>):

$$R = -r_A dV. \quad (13)$$

Substituting equations (11)–(13) into equation (10),  $F_A = (F_A + dF_A) + (-r_A)dV$ ; and rearranging,

$$0 = dF_A + (-r_A)dV. \quad (14)$$

The incremental change in the amount of A,  $dF_A$ , can be expressed in terms of  $F_{A0}$ , the input rate of A, and  $dX_A$ , the incremental change in the fraction of A converted to products:

$$dF_A = d[F_{A0}(1 - X_A)] = (-F_{A0})dX_A. \quad (15)$$

Substituting equation (15) into equation (14), rearranging terms, and integrating the entire expression yields the ideal PFR performance equation:

$$\frac{V}{F_{A0}} = \int_0^{X_{Af}} \frac{dX_A}{-r_A}$$

or

$$\tau = \frac{V}{v_0} = C_{A0} \int_0^{X_{Af}} \frac{dX_A}{-r_A}, \quad (16)$$

where  $F_{A0}$  is replaced by  $C_{A0}$  times  $v_0$ , the initial concentration of A (moles·volume<sup>-1</sup>) times the volumetric flow rate (volume·time<sup>-1</sup>).

Space-time ( $\tau$ , in units of time), the ratio of reactor volume ( $V$ ) to volumetric

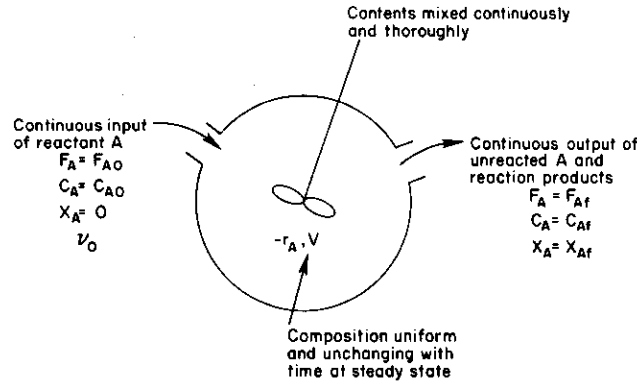


FIG. 3.—The continuous-flow, stirred-tank reactor operates continuously. Variables are the same as for figure 2.

flow rate ( $v_0$ ), is the time required to process one reactor volume of material input. In reactor models for animal guts,  $\tau$  is throughput time, the time for one gut volume of food to be processed. Throughput time is the ratio of gut volume ( $V$ ) to throughput rate ( $v_0$ ).

*The Performance Equation for a Continuous-Flow, Stirred-Tank Reactor*

The continuous-flow, stirred-tank reactor (CSTR; fig. 3) is characterized by a continuous flow of material through, and perfect mixing of material within, the reaction vessel. Since the composition of material within a CSTR operating at steady state is spatially homogeneous and constant with time, the mass balance for reactant A is written over the entire reactor volume,  $V$ . With continuous flow and perfect mixing, A does not accumulate in an ideal CSTR ( $W = 0$ ), and the general mass balance (eq. 4) is

$$I = E + R. \tag{17}$$

The input of A is

$$I = F_{A0}, \tag{18}$$

and the output of A is

$$E = F_{A0}(1 - X_A). \tag{19}$$

The amount of A that disappears by reaction is

$$R = -r_A V. \tag{20}$$

Substituting equations (18)–(20) into equation (17),  $F_{A0} = F_{A0}(1 - X_A) + (-r_A)V$ ; then, rearranging terms yields the performance equation for an ideal CSTR:

$$V/F_{A0} = X_A/(-r_A). \tag{21}$$

The input rate of A,  $F_{A0}$ , is  $C_{A0}v_0$ , the initial concentration of A times volumetric

flow rate. The ideal CSTR performance equation (21) can therefore be expressed in terms of  $C_{A0}$  and  $v_0$ :

$$\tau = V/v_0 = C_{A0}X_A/(-r_A). \quad (22)$$

As defined earlier,  $\tau$  is throughput time in our gut-reactor models. Throughput time for a CSTR gut, as for a PFR gut, is the ratio of gut volume ( $V$ ) to volumetric throughput rate ( $v_0$ ).

#### *Throughput Time and Conversion*

“Gut-clearance time” is not a synonym for space-time or throughput time. It refers specifically to the time required for an animal entering starvation to evacuate its gut completely. Gut-clearance time is thus throughput time measured under unsteady conditions that are both unnatural and difficult to model, especially for animals ordinarily feeding in a more or less continuous manner. Note also that neither “gut-residence time” nor “gut-passage time” is equivalent to throughput time or batch-reactor holding time. Residence time ( $\theta$ ) is the time an individual material element spends in a reactor or a gut. Gut-passage time—also erroneously called “gut-passage rate” even when measured as time<sup>+1</sup>—is actually mean gut-residence time ( $\bar{\theta}$ ). Since mean residence time can be precisely and unambiguously defined (e.g., J. Smith 1981), its use is preferable.

For a PFR gut in which throughput rate is constant, throughput time, residence time, and mean residence time are all equal. In fact, the equation  $\theta = \bar{\theta}$  is a necessary condition for plug flow (Levenspiel 1972). In contrast, residence times of individual material elements in a CSTR may differ, and effective description requires a residence-time distribution. Mean residence time and throughput time are equal in an ideal CSTR. Since batch-reactor operation does not involve the flow of material into or out of the reactor, we use holding time rather than throughput time. The characteristics of ideal batch-reactor operation require that holding time, residence time, and mean residence time all be equal for any given batch.

We express performance equations for all three ideal reactors (eqs. 9, 16, and 22) in terms of conversion ( $X_A$ ), the fraction of reactant A that reacts to form products. It is important to future tests of gut-reactor models that we define conversion in terms of experimentally measurable quantities. If we assume that digestion is a constant-density (mass·volume<sup>-1</sup>) system, conversion can be defined as

$$X_A = 1 - C_A/C_{A0}. \quad (23)$$

The boundary conditions we use are (1) initial conversion of food material,  $X_{A0} = 0$ , and (2) final conversion,  $X_{Af} = 1 - C_{Af}/C_{A0}$ , where  $C_{Af}$  is the concentration of A in egested material, and  $C_{A0}$  is the concentration of A in ingested material. These boundary conditions are arbitrary and may be changed as appropriate. For example, ( $X_{A0} = 0$ ) may not hold when, as in some spiders, breakdown of food materials begins before food is ingested. Equation (23) can also be used to convert reaction-rate equations (eqs. 2 and 3) from the functions of concentration ( $C_A$ ) initially derived to known functions of conversion ( $X_A$ ).

*Ideal Reactor Designs with Respect to Digestion*

As previously stated, our design objective for digestive reactions is to identify gut (reactor) configurations and digestive (operating) strategies that maximize the production rate of energy and nutrients from food. In terms of design variables we have defined, our objective is to identify the gut-reactor configuration in which the maximum conversion ( $X_{Af}$ ) of ingested food to assimilable products is achieved in minima of time ( $t$  or  $\tau$ ) and gut-reactor volume ( $V$ ). Note that reaction rates,  $-r_A$ , are expressed as functions of conversions,  $X_A$ .

Holding time in a batch reactor and throughput time in a PFR are compared as areas under the curve of the reciprocal of reaction rate versus conversion (where  $C_{A0}$  is constant). Since we have assumed that the volume of reacting food material equals gut volume and does not change significantly during the course of reaction, the performance equations for ideal batch and plug-flow reactors are interchangeable:  $t = \tau_{PFR}$ , where  $C_{A0}$  is constant. For any given reaction, the time ( $t$ ,  $\tau_{PFR}$ ) and the reactor volume required to achieve a specified final conversion are identical for the two ideal reactors (fig. 4).

The contrast between batch and plug-flow reactors becomes one of discontinuous versus continuous operation. In the batch reactor, production (reaction) periods are interrupted by discharge and idle periods, whereas the PFR is continuously productive. To compensate for intermittent operation, a larger volume is required for the batch reactor to match the production-rate capabilities of the PFR. Our design objective is, therefore, better satisfied by a gut-reactor configuration that allows continuous processing of food.

The ratio of throughput time in a PFR,  $\tau_{PFR}$ , to throughput time in a CSTR,  $\tau_{CSTR}$ , is shown graphically by the ratio of the areas designated in figure 5. For reactions with rates that fall monotonically as reactant concentration decreases, a greater throughput time (or if throughput rate is constant, a greater reactor volume) is always required to achieve a given conversion with stirred flow than with plug flow. Since catalytic digestive reactions (eq. 1) belong to this category, our design objective for them is best satisfied by a gut that functions as an ideal PFR.

Development of the PFR model for animal guts, however, does more than confirm the obvious. It provides concrete physical and chemical reasons why animal guts should operate as PFR's. The PFR design represents the better method of accomplishing catalytic digestion because it maintains a gradient in reactant concentration, and therefore in reaction rate, from higher values near the reactor entrance to lower values near the exit. In contrast, the high reactant concentration entering a CSTR is diluted immediately to some lower, constant level by material recirculating in the reactor.

Determination of the ideal gut-reactor configuration for autocatalytic reactions is easily solved with graphical representations of the ideal reactor performance equations. When digestion involves microbial fermentation, these reactions are only one component of the process, but we first consider the simpler case in which autocatalytic reactions comprise the entire process. For autocatalysis, the curve of reciprocal reaction rate versus conversion has a characteristic minimum (fig.

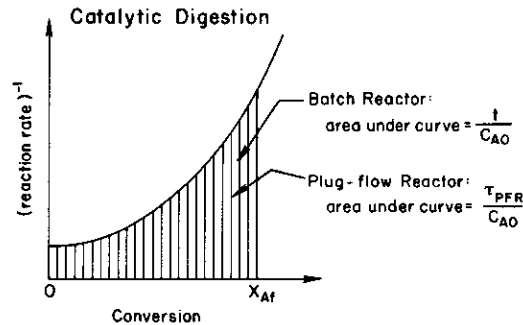


FIG. 4.—A comparison of ideal batch-reactor and plug-flow-reactor performances with respect to catalytic digestive reactions, where reaction kinetics are given by the Michaelis-Menten enzyme model. If  $C_{A0}$ , initial concentration of reactant A, is constant, batch-reactor holding time ( $t$ ) and plug-flow-reactor throughput time ( $\tau_{PFR}$ ) are identical.

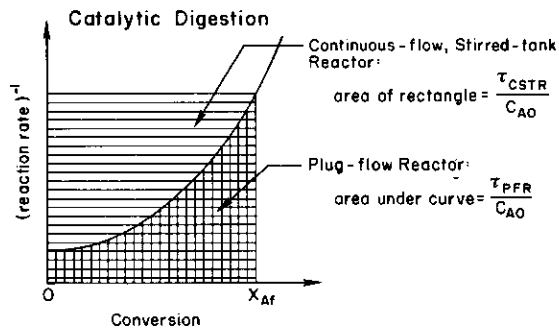


FIG. 5.—A comparison of the performances of an ideal plug-flow reactor and a continuous-flow, stirred-tank reactor with respect to catalytic digestive reactions, where reaction kinetics are given by the Michaelis-Menten enzyme model. If  $C_{A0}$ , the initial concentration of reactant A, is constant, the plug-flow-reactor throughput time ( $\tau_{PFR}$ ) required to achieve any final conversion ( $X_{Af}$ ) is always less than the throughput time of a continuous-flow, stirred-tank reactor ( $\tau_{CSTR}$ ) required to achieve the same conversion.

6a), the point of maximal reaction rate. As before, comparison of the ratio of throughput time in a PFR to throughput time in a CSTR is used to identify the reactor configuration that best satisfies our design objective. At low conversions of reactants to products, the CSTR requires the smaller throughput time or, if throughput rate is constant, the smaller reactor volume (fig. 6a). As conversion increases, PFR performance equals, and then surpasses, the CSTR (fig. 6b). To maximize conversion and minimize total throughput time or reactor volume ( $v_0$  constant), the ideal design for a single autocatalytic reaction is to use the two reactors in series: a CSTR followed by a PFR (fig. 6c).

We have proposed that the ruminant gut be modeled as a CSTR-PFR reactor series because observed tracer residence-time distributions are exactly explained by this model (Penry and Jumars 1986). We now provide additional physical and

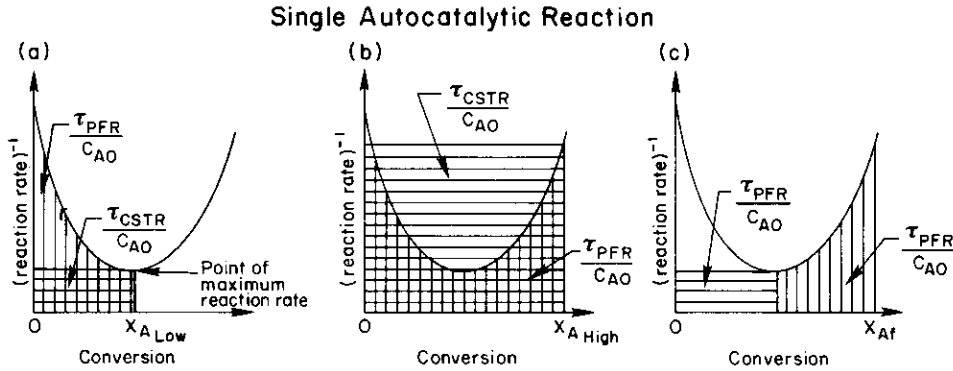


Fig. 6.—A comparison of the performances of an ideal plug-flow reactor and a continuous-flow, stirred-tank reactor with respect to any autocatalytic reaction.  $C_{A0}$ , initial concentration of reactant A, is constant among all comparisons. *a*, At low conversions, the CSTR throughput time,  $\tau_{CSTR}$ , is less than the PFR throughput time,  $\tau_{PFR}$ . *b*, At high conversions, however, CSTR throughput time exceeds PFR throughput time. *c*, High conversions of reactants to products via an autocatalytic reaction can be achieved in minima of total throughput time or total reactor volume if a CSTR-PFR series is used.

chemical justifications. The primary fermentation site in ruminants (e.g., cows, sheep, goats, deer) is the foregut. Our discussion generalizes to other foregut fermenters as well (e.g., hippos, kangaroos, monkeys of the subfamily Colobinae).

As we have shown, fermentation rate is maximized in minimal throughput time or gut-reactor volume ( $v_0$  constant) if the foregut (rumen or stomach) functions as a CSTR (fig. 6*a*). However, in contrast to the simple case of a single, autocatalytic reaction just analyzed, acid treatment in foregut fermenters stops fermentation as material leaves the CSTR chamber. Digestion then proceeds primarily through catalysis, better accomplished in a PFR (fig. 5). Thus, digestion in foregut fermenters involves two consecutive reaction types, microbial fermentation and enzymatic catalysis, in a CSTR-PFR series (fig. 7*a*).

Suppose catalytic digestive reactions precede fermentation. In this case the entire digestive process is best accomplished in a PFR-CSTR series (fig. 7*b*), and we have designed a hindgut fermenter (e.g., elephants, rhinos, horses, koalas, rabbits, gallinaceous birds, monkeys of the family Indriidae, some aquatic, leaf-shredding insects, wood-boring bivalves of the subfamily Xylophaginae). Differences between the two digestive strategies are direct consequences of the order in which the reactions occur. Since the exact curves of reciprocal reaction rate versus conversion are unknown, we cannot further compare foregut and hindgut fermentation strategies using the graphical approach.

Two very general predictions thus result from our simple application of chemical-reactor analysis to the study of digestion. Under the assumptions given, an animal's net rate of production of energy and nutrients from food via catalytic digestive reactions (eq. 2) is maximized when its gut is an ideal PFR. If, in addition to catalytic digestive reactions, fermentation reactions (eq. 3) are important diges-

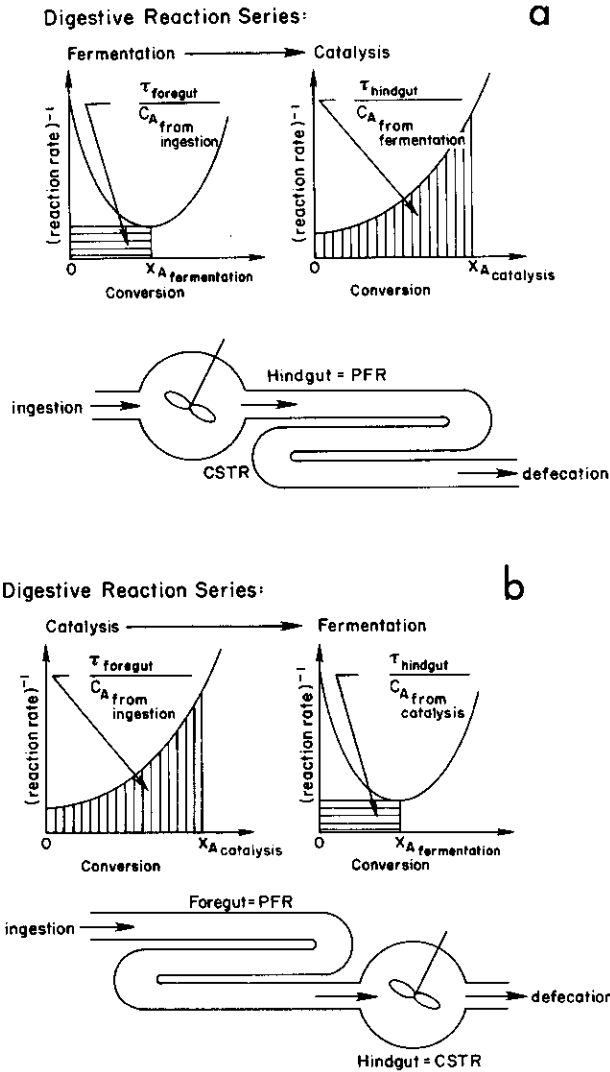


FIG. 7.—A determination of gut-reactor configurations when digestion involves both auto-catalytic fermentation reactions and catalytic enzyme reactions. *a*, When fermentation precedes catalytic digestion, high conversions of food to assimilable components can be achieved in minima of throughput time and gut volume if the gut operates as a CSTR-PFR series. This gut-reactor configuration is the basic representation for any foregut fermenter. *b*, When catalytic digestion precedes fermentation, the gut should operate as a PFR-CSTR series. This gut-reactor configuration is the basic representation for any hindgut fermenter.

tive components, fermentative production rate is maximized when a portion of the gut is a CSTR.

#### COMPARISON WITH REAL REACTORS

It takes only a brief, qualitative review to substantiate both the above predictions. Tubular guts predominate among more complex, multicellular animals, and the flow of digesta through tubular guts can be described quite reasonably by the plug-flow model. Large chambers are important features of animal guts using fermentation. The flow of digesta through these chambers—for example, through the rumen of cows (Balch 1950; Van Soest 1982; Demment and Van Soest 1985) or the caecum of rabbits (Pickard and Stevens 1972; Stevens et al. 1980)—can be approximated by flow through a CSTR. Additional value of the formal use of reactor theory lies in our ability to deal with more-specific cases (e.g., more narrowly defined feeding or digestive guilds or more-quantitative prediction) and with exceptions to our two general predictions.

#### *Deposit Feeding*

Using chemical-reactor analysis to study deposit-feeder digestion illustrates the effectiveness of reactor models in generating specific predictions for future experimentation and measurement. Of all animals, deposit feeders are most likely to conform to the assumption that volume changes are negligible during digestion; the volumetric bulk of food ingested is in mineral grains. We postulate initially that deposit-feeder digestion involves only catalytic digestive reactions and consequently predict that deposit-feeder guts should operate as ideal PFR's. Qualitative observations of tracer movements through guts of representatives of three deposit-feeding taxa have shown approximation to plug flow: *Nereis succinea* (a polychaete; Cammen 1980), *Corophium* spp. (amphipods; Miller 1984), and *Pseudopolydora kempj japonica* (a polychaete; Jumars and Self 1986). Our unpublished tracer observations add two more polychaetes, *Abarenicola pacifica* and *Pygospio elegans*, and one holothuroid, *Parastichopus californicus*, to this list. Axial mixing was observed to be negligible in all these species, thus fulfilling the most important assumption of the ideal plug-flow model and confirming the results of our theoretical analysis.

Deviations from plug flow have been observed, however, in guts of the ampharetid polychaetes *Amphicteis scaphobranchiata* and *Hobsonia florida*. Qualitative tracer observations in conjunction with gut dissections (Jumars and Self 1986; Penry, pers. obs.) indicate that anterior mixing occurs in these ampharetid guts and presumably in those of anatomically similar terebellimorphs (e.g., Dales 1955; Dales and Pell 1970). Tracer results and gut morphology are consistent with a CSTR-PFR series. In addition to the already discussed disadvantages of a CSTR compared to a PFR in catalytic digestion, a CSTR incurs the energetic costs of mechanical mixing.

Under what environmental conditions is a CSTR-PFR gut necessary or advantageous for survival? Deposit feeders having guts with mixing chambers tend to be large or to ingest fine sediments of low permeability (Jumars, pers. obs.). The

rates at which digestive enzymes diffuse to food particles may limit reaction rates in the absence of mixing. Under these conditions, the advantages of a gut with a mixing chamber may outweigh the twin disadvantages of a greater energy requirement for mixing and a reduction in effective reactant concentration through dilution with previously ingested and partially digested material. A less likely alternative, mentioned because of its relevance to ruminants and mammalian caecal fermenters, is that mixing is the byproduct of a gut sorting mechanism that selectively retains some particles for further digestion. Sorting within the gut has been seen in *Hobsonia florida* (Self and Jumars 1978). We cannot discount the possibility that fermentation occurs in the CSTR, but, at the shorter throughput times observed, its nutritional importance is probably negligible (Taghon and Jumars 1984).

The hypothesis that the diffusion of digestive enzymes constrains deposit-feeder digestion suggests specific couplings of body size with foraging and digestive strategies. Relatively large deposit feeders with mixing guts may ingest and process sediments of relatively low permeability. Deposit feeders with plug-flow guts, however, may be limited to relatively small sizes and gut diameters or to ingesting and processing sediments of relatively higher permeability. Relatively small deposit feeders with plug-flow guts dominate sites of organic enrichment (Pearson and Rosenberg 1978) and the food-poor abyss (Jumars and Gallagher 1982). Food of low permeability—poorly sorted, organic-rich muds in the former case and nearly pure clays (Hessler and Jumars 1974) in the latter—is characteristic of these seemingly disparate environments. The selective abilities of some deposit feeders may ensure the permeability of digesta, and the field distributions of organisms with limited selective abilities may be constrained by sediment permeability.

The relationship between sedimentary parameters and the distribution of *Arenicola marina* (Polychaeta, Arenicolidae) can be reinterpreted in light of this last hypothesis. Longbottom (1970) sampled 10 sites differing in sediment type, sediment organic content, and *Arenicola marina* density. Median grain size and organic content were inversely correlated. Although organic content was highest in the finest sediments, *Arenicola marina* adults were not found below median grain sizes of 80  $\mu\text{m}$ ; only juveniles were. Longbottom suggested that the distributional pattern results from the inability of *Arenicola marina* adults, but not of juveniles, to maintain burrows in fine sediments. We suggest instead that digestive constraints may be responsible.

From its anatomical and functional similarities to *Abarenicola pacifica* (Arenicolidae), a species we have studied, we infer that particle mixing in the *Arenicola marina* gut is insignificant. Although finer sediments are generally higher in organic content than coarser sediments, they are also generally lower in permeability. Because juveniles have small gut diameters, the diffusion of digestive enzymes through sediments probably is not limiting. Juveniles may, however, reach a size at which the diffusion of enzymes into the gut contents (or of digestive products out) becomes limiting, resulting in a net loss of energy or nutrients. Since *Arenicola marina* is a relatively nonselective feeder (Fauchald and Jumars 1979), it similarly may be excluded from areas of poorly sorted sediments irrespective of

median grain size. The data to test these hypotheses do not exist, yet have potentially broad application. Studies of functional morphology and kinematics of deposit feeders' guts with reference to gut-reactor models, feeding strategies, and distributional patterns are needed.

A review of gross gut morphologies of deposit-feeding taxa yields a second apparent exception to the general plug-flow model for deposit feeders. Asteroids and ophiuroids (Echinodermata) include reportedly deposit-feeding representatives, which appear to have batch-reactor guts. The simple, saclike guts have one major opening: material is both ingested and egested through the mouth. Shick et al. (1981) indicated that at least one deposit-feeding asteroid, *Ctenodiscus crispatus* (Gonopectinidae), does operate as a batch reactor (although the egestion behavior observed conceivably could have been a response by *C. crispatus* to the physical disturbance of collection).

Industrial batch reactors are used when their construction and maintenance costs are low or when high conversions are more important than large production rates (i.e., when reactant supply is limiting). Bona fide deposit feeders, however, exploit a very dilute food resource and must, therefore, process large quantities of sediment per unit of time. What characteristics and adaptations may enable these deposit-feeding asteroids to utilize a batch-processing rather than continuous-flow digestive strategy?

In addition to low maintenance requirements (inferred from respiratory requirements), *C. crispatus* has a distensible stomach, which may enable it to process large volumes of sediment (Shick et al. 1981). The Porcellanasteridae, taxonomically related, abyssal, deposit-feeding asteroids, also have large, undivided, sac-like guts that, when filled with sediment, cause their disks to expand greatly (Madsen 1961). Assuming adequate mixing (as the batch-reactor formulation does), the large gut volume and, therefore, the increased amount of sediment processed per batch may result in net production rates comparable to those achieved by a deposit feeder with a smaller, but continuous-flow, gut.

Ophiuroids do not seem to have comparably distensible guts; their disks are generally smaller and more rigid than those of asteroids. They do, however, have adaptations that may minimize their energy requirements. The low metabolic rates of deposit-feeding ophiuroids (Buchanan 1964) indicate that rates at which they need to obtain energy are also low, and their simple, saclike guts are probably energetically inexpensive to maintain. Metabolic rates are especially low with respect to body volume and gut volume, the terms relevant to reactor theory, since much of the body volume is made up of metabolically inactive calcium carbonate. These low energy requirements may make batch processing a viable alternative, but the relatively limited amounts of food-poor material that can be processed per unit of time still cast doubts on the success of a purely deposit-feeding strategy.

It is possible that ophiuroids, although possessing blind guts, are able to ingest and egest material continuously, operating as CSTR's. Ophiuroids' guts may be functionally similar to the guts of scyphozoan medusae; the latter continuously ingest and egest small particles along separate ciliary tracts, but process large particles in batches (Larson 1976). A second possibility is that "deposit-feeding"

ophiuroids are selective, searching for and ingesting food particles of the highest quality available. *Oreaster reticulatus*, an asteroid classified as a deposit feeder, is known to use a selective foraging strategy, concentrating on the food-rich layer at the sediment surface (Scheibling 1981) and perhaps avoiding the need to process large sediment volumes.

"Deposit-feeding" ophiuroids, thus, most probably use a mixture of foraging modes: deposit-feeding, scavenging, and predation. This flexible, opportunistic strategy would enable an ophiuroid to minimize time between meals by deposit feeding to obtain some level of intake while searching for food particles of higher quality. Several deep-sea ophiuroid species are adept at localizing and ingesting carrion (C. Smith 1985), and in the laboratory we have observed active predation by *Ophiura sarsi*, a member of a genus generally considered to consist of deposit feeders and scavengers (Tyler 1980). On intuition, Madsen (1961) similarly has suggested that porcellanasterid asteroids are scavengers and facultative predators as well as deposit feeders. We suspect that animals that prove to be bona fide deposit feeders with small, batch-reactor guts will be highly motile, selecting only the best food patches.

Existing information on foraging and digestion in deposit-feeding asteroids and ophiuroids is limited and often inconclusive. Feeding habits are most often inferred from gut contents or lack thereof, and researchers studying feeding habits of polychaetes point out how misleading gut-contents data can be (Ockelmann and Vahl 1978; Fauchald and Jumars 1979). Direct observations of foraging modes are needed to evaluate our hypotheses. Patterns of movement of material into, within, and out of their guts must be assessed to find out whether they operate more nearly as batch reactors or CSTR's. Determination of conversion and holding time as they relate to food type and concentration are needed to answer questions raised as a result of this very simple reactor analysis.

Although not a focus in this brief analysis, microbially mediated, autocatalytic digestive reactions may also be used by deposit feeders. These digestive reactions could be particularly important in deep-sea environments, where rates of organic input are relatively low and organic material tends to be refractory. It is possible that deep-sea, deposit-feeding bivalves that retain fecal pellets in enlarged hindguts (e.g., *Abra* spp.) and xenophyophores and komokiaceans (Protozoa), which amass fecal pellets (stercomata), are, by fermentation, deriving further nutrition from the organic material remaining in the fecal pellets (Allen and Sanders 1966; Allen 1979; Tendal 1979). Deep-sea, deposit-feeding elapsipod holothuroids (Echinodermata) have large, sediment-filled, hindgut caeca, which similarly may be sites of fermentation.

#### *Foregut and Hindgut Fermenters*

When they are primary components of a digestive strategy, fermentation reactions are linked in series with (and may either precede or follow) catalytic digestive reactions. Under the assumptions given, an animal's net production of energy and nutrients from food via this reaction series is maximized in a gut that operates as a series of two reactors, the CSTR and the PFR. The reaction sequence determines the reactor sequence. When fermentation precedes catalytic digestion,

an animal's gut should operate as a CSTR-PFR reactor series; when fermentation succeeds catalytic digestion, an animal's gut should operate as a PFR-CSTR reactor series. These gut-reactor configurations correspond to the digestive processes of foregut fermenters (stomach or rumen as the primary fermentation site) and hindgut fermenters (colon or caecum as the primary fermentation site), respectively.

Gut-reactor models are more successful than previous compartmental models in describing the flow patterns of digesta (Penry and Jumars 1986). In further contrast to compartmental-model parameters of unknown biological significance, gut-reactor operating variables represent biologically important determinants of digestion. Gut architecture, gut capacity, intake level, diet composition, digesta passage rate, and digestion rate are all factors experimentally identified as affecting the digestibility of plant material (Parra 1978); all are represented as operating variables in our gut-reactor models. The extent to which ingested plant material is converted to usable products ( $X_{Af}$ ) is a function of gut-reactor configuration (batch reactor, PFR, CSTR, or some series), gut volume ( $V$ ), throughput rate ( $v_0$ ), initial concentration of some important or limiting component of ingested plant material ( $C_{A0}$ ), throughput time ( $\tau$ ), and digestive reaction rate ( $-r_A$ , catalytic or autocatalytic kinetics). By using reactor theory to analyze digestion we not only have derived the important variables, but also have provided, through the reactor performance equations, biologically meaningful, mathematical descriptions of the necessary relationships among them.

The relationship among digestive conversion, gut volume, and throughput rate, quite apparent in numerous studies of digestion in herbivores and folivores, is now made explicit by the performance equations. Under the assumptions given for digestive reactions, the extent of digestive conversion is completely determined by, and increases with, throughput time. Since throughput time is the ratio of gut volume to volumetric throughput rate, conversion increases as gut volume increases relative to throughput rate, or as throughput rate decreases relative to gut volume. The extent to which fiber (refractory plant material) is digested by herbivores and folivores generally increases with body size (Parra 1978). The gut-reactor performance equations allow us to assert that this pattern exists primarily because gut volume increases relative to throughput rate as body size increases, supporting in part empirical arguments by Demment and Van Soest (1985). Conversely, when gut volume is held constant, as in inter- or intraspecific comparisons of animals of similar body size (e.g., Grovum and Williams 1977), fiber conversion, as predicted, varies inversely with throughput rate.

The relative advantages and disadvantages of foregut versus hindgut fermentation have been much discussed, but a reactor analysis of digestion reveals limitations in these discussions. They have focused on fermentation to the exclusion of catalytic digestion. According to the principles of dynamic programming (Bellman 1957), an entire process is optimal only when each stage functions optimally with respect to the preceding stage. Foregut fermenters ferment ingested materials, and then catalytically digest the fermentation digesta. Thus, in foregut fermenters, fermentation should be optimized with respect to ingested material, and catalytic digestion should be optimized with respect to fermentation products and residue.

In contrast, hindgut fermenters digest ingested material catalytically and then ferment the residue. Understanding the differences between these two digestive strategies requires that the roles of fermentation and catalytic digestion be analyzed in the context of the stage in which they occur.

Within this dynamic-programming framework we can explain, from a reaction-engineering standpoint, observations (summarized in Parra 1978) that throughput rates are smaller in foregut fermenters than in hindgut fermenters of similar size. Until otherwise stated, we assume that digestive-reaction kinetics and diet composition are similar for foregut and hindgut fermenters of similar size. Apparent rates of fermentation are generally slower than apparent rates of catalytic digestion. Thus, optimization of fermentation, the first digestive stage in foregut fermenters, requires relatively long throughput times (larger  $V/v_0$ ), and optimization of catalytic digestion, the first digestive stage in hindgut fermenters, requires shorter throughput times. Foregut fermenters are predicted, and observed, to have larger foregut volumes and smaller throughput rates than those of hindgut fermenters of similar body size.

Throughput rate, determined by optimization of the first digestive stage, must remain constant along a continuous-flow gut, becoming a constraint on the second stage. Given the relatively small throughput rates of foregut fermenters, optimization of the second, catalytic stage requires relatively small hindgut volumes, smaller than the foregut volume required for fermentation. More importantly, if the catalytic kinetics of digestive reactions are similar in foregut and hindgut fermenters, the proportion of total gut volume required by foregut fermenters for catalytic digestion is, as a result of their smaller throughput rates, relatively smaller than the proportion required by hindgut fermenters of similar size. Although the limited data do not show dramatic differences, the proportion of the gut devoted to catalytic digestion is smaller in foregut fermenters than in hindgut fermenters (Parra 1978, table 3).

Over time, foregut fermenters are expected to evolve toward minimizing the proportion of total gut volume required for catalytic digestion in order to maximize the proportion available for fermentation, constrained by throughput rates that are sufficient to meet energy and nutrient requirements. Once the optimal apportionment of total gut volume is achieved, further increases in the extent of fermentative conversion of ingested materials can be achieved only by modifying the fermentative capabilities of the microbial community or by developing mechanisms to increase the mean residence times of selected digesta particles in the fermentation chamber.

Contrary to the arguments of Demment and Van Soest (1985), selective retention mechanisms like those observed in ruminants may not have been prerequisites for the success of larger foregut fermenters. Instead, these mechanisms may have been secondary adaptations to increase the efficiency with which foregut fermenters could exploit diets relatively high in refractory materials. From the above reactor analysis (fig. 6b), we can predict that, at the largest body sizes, longest throughput times, and highest conversion efficiencies, foregut fermentation may be accomplished efficiently in a PFR without an obviously modified fermentation chamber. The conspicuous absence of ruminants from the ranks of

the largest foregut fermenters (Demment and Van Soest 1985, fig. 3) is consistent with this prediction, and the implications for dinosaur herbivory should be noted.

Given that the proportion of total gut volume required by hindgut fermenters for catalytic digestion is larger than that required by similarly sized foregut fermenters and that total gut volume is limited by body size, the proportion available to hindgut fermenters for fermentation is necessarily smaller than that available to foregut fermenters. Since there are no demonstrable differences in the fermentative capabilities of the microbial communities of foregut and hindgut fermenters (Parra 1978), hindgut fermenters should, as a result of their shorter throughput times, exhibit lower conversions of refractory materials than do foregut fermenters of similar size. As predicted, the efficiency of fiber digestion is generally lower in hindgut fermenters, and differences become much less apparent as body size increases (Parra 1978).

In competition with foregut fermenters over evolutionary time, hindgut fermenters appear to have found refuges at either end of the body-size spectrum. With one notable exception, large fermenters are hindgut fermenters. At body sizes larger than 600–1200 kg (Demment and Van Soest 1985), gut volume is sufficiently large, and throughput times thus sufficiently long, for efficient exploitation of diets high in refractory materials, regardless of fermentation strategy. The higher throughput rates of large hindgut fermenters and their corresponding ability to process larger quantities of food per unit of time may have provided a competitive advantage over large foregut fermenters (Janis 1976). Further, our analysis suggests that foregut fermentation is inherently a specialist strategy; whether or not food materials are labile to catalytic digestion, they are first broken down microbially. When food quality is high or variable, hindgut fermenters would appear to have the advantage. Whales, the notable exception in size, are foregut fermenters (Herwig et al. 1984). Too little is known of their food availability, gut kinetics, digestive reactions, and metabolic costs to place them in perspective with terrestrial mammals.

Small fermenters are also hindgut fermenters or, perhaps more accurately, "foregut digesters." Smaller animals, with smaller absolute nutrient and energy requirements, are better able to obtain sufficient quantities of relatively "high-quality" foods (i.e., high in concentrations of enzymatically digestible materials, low in refractory materials requiring fermentation) and minimize their energetic dependence on the fermentation of refractory materials. Because some fermentation products (methane, hydrogen gas, and heat) are not used by the host animal, the fermentation of labile food materials can represent a net loss over catalytic digestion. Since net energy yield is maximized by catalytically digesting foods of relatively high quality, foregut fermentation is disadvantageous at small body sizes (<10 kg) (Parra 1978). For small animals, fermentation may be most important as a source of limiting vitamins and other nutrients (Hörnigke and Björnhag 1980).

To compensate for the reduced throughput times associated with both small size and foregut digestion, small hindgut fermenters have developed tactics to increase effective throughput times and, therefore, the use of fermentation products. Recycling reactants for further reaction, a common tactic in the chemical

industry, exists among animals as coprophagy and caecotrophy. Coprophagy is simply the recycling of digesta by reingesting feces. Caecotrophy, a refinement that increases the overall efficiency of the recycling process, is more complex, involving separation in the gut of more readily fermented materials from less readily fermented materials. The latter bypass the fermentation chamber and are defecated, and only the relatively more valuable components are fermented and then recycled.

In the rabbit, which exhibits caecotrophy (Hörnigke and Björnhag 1980; Pehrson 1983), separation of relatively more-labile components from refractory components occurs before digesta enter the caecum. Refractory components bypass the caecum and are defecated as hard pellets. Labile components are fermented in the caecum, defecated as soft pellets (caecotrophes), recycled for further fermentation in the mucus-wrapped pellet, and digested catalytically. Recycling of energetically and nutritionally valuable components allows small hindgut fermenters to achieve food conversions that would otherwise require larger gut volumes or smaller throughput rates.

Large hindgut fermenters typically do not recycle. How and to what extent are these animals able to use fermentation products? Catalytic digestion of fermentation intermediates and microbes might succeed fermentation as a third stage in digestion, but such mechanisms may not be necessary. Large throughput times may allow fermentation to proceed almost to completion. Large hindgut fermenters, with their low, size-specific metabolic requirements, thus may use easily absorbed fermentation end products like energy-rich, volatile fatty acids (VFA). The recovery of food energy tied up in microbial biomass may not repay its additional costs. Unfortunately, little is known about fermentation in large hindgut fermenters because it has been assumed that the results of studies of foregut fermenters are applicable. Since it is obvious from reactor theory that there may be significant differences, hindgut fermenters deserve special scrutiny.

#### MODIFICATIONS OF IDEAL GUT-REACTOR MODELS

Many foreseeable modifications need not be derived anew, having been encountered in chemical-engineering applications. They involve either reaction modifications (e.g., modified enzyme kinetics, mass-transport limitations, heterogeneous catalysis) or modifications of the assumptions in the ideal models (e.g., variable digesta volume or gut volume, nonideal patterns of digesta mixing and flow).

We began with the simplest known enzyme kinetics, a catalytic Michaelis-Menten model, and the simplest food characterization, the concentration of a single component. Enzyme induction and poisoning, as well as competition for substrates, are likely complications. Mathematically, modified digestive-reaction kinetics (e.g., Lehninger 1970) are readily incorporated in an ideal gut-reactor solution, but semantically, there are problems. By engineering digestive reactions, we highlight these problems, forcing strict definition of loosely defined concepts like food quality.

Quality ultimately reflects a net gain of energy or of some limiting nutrient from

a particular food. It is thus a composite of a number of different factors including concentration of some important or limiting component, susceptibility to degradation by an animal's enzymes or microbes, costs of producing those enzymes or maintaining those microbes, and costs of producing new body tissues from the breakdown products of the particular food. For simplicity we have equated food quality with concentration ( $C_{A0}$ ), but its role in reactor models extends to considerations of enzyme activity and microbial-community activity (both of which can differ with time in the same animal), and to mass-transfer constraints (which can differ among foods of the same chemical composition but in different phases or forms). Food quality thus depends on the enzyme and microbe complements and the nutritional state of the digester as well as on various inherent food properties. Hay is useless to a carnivore. Given the need to characterize digestive reactions accurately, an intuitive sense of what is meant by food quality will no longer suffice; the measurement of its component parameters becomes necessary.

Our initial simplifying assumption that digestive reactions are homogeneous can be relaxed, incorporating modifications that result from considering the transport of (1) enzymes from secretory sites to the bulk fluid; (2) enzymes from the bulk fluid to food particles; (3) enzymes into food-particle pores; (4) products out of food-particle pores; (5) products from particles to the bulk fluid; and (6) products from the bulk fluid to the absorption sites. For example, microbes responsible for cellulose degradation attach to particles of plant material and attack the cell walls, eroding the substratum beneath their attachment points. Microcolonies occupy pits that develop (Costerton et al. 1985, fig. 14). Thus, the overall rate of cellulose degradation may be limited by the rate of microbial attachment or by the rate of diffusion of nutrients into, and metabolites out of, pits containing growing microcolonies. Cellulose degradation and digestive reactions in general, along with most industrial chemical processes, fall into the category of heterogeneous catalysis. Derivations of rate equations for heterogeneous catalysis have been considered in detail (e.g., Carberry 1976; Froment and Bischoff 1979; J. Smith 1981).

Subtidal marine invertebrates and mammals are perhaps uniquely immune to temperature variations resulting from digestive processes or from environmental changes. We thus assumed that reaction and mass transfer are the dominant processes in guts, allowing us to describe performances of gut-reactor models solely by the reactor-specific equations derived from mass-balance considerations. That reptiles use environmental heat in digestion, however, is obvious. If in digestion, as in the chemical industry, adding or removing heat is a major design problem, it can be examined through equations for heat conservation (Levenspiel 1972; Froment and Bischoff 1979; J. Smith 1981).

Another simplifying assumption in our gut-reactor models is that digesta volume is constant and equal to reactor volume. With the exception of deposit feeders, such volume changes are likely to be important in most animals. They may, for example, provide another important difference between foregut and hindgut fermentation of refractory materials. In foregut fermenters, fiber volume is reduced before material undergoes catalytic digestion in the PFR portion of the gut, whereas in hindgut fermenters, fiber occupies space and impedes diffusion in the PFR portion of the gut. Volume changes may be treated as changes in the

density of reacting material or as an additional advective term representing absorption. In either case, the mass-balance approach of reactor design can be used to formulate the solution (e.g., Levenspiel 1972; Hershey 1973). Most commercial reactors have neither secretory nor absorptive walls, but mass-transfer and radial-diffusion constraints (e.g., Aller 1980; J. Smith 1981) can be incorporated in the models based on reactor theory. Similarly, modifying the steady-state assumptions is conceptually easy but mathematically difficult (Levenspiel 1972).

We assumed digesta mixing patterns and flow patterns identical to those of ideal reactor models. If deviations from the ideal occur, gut models based on reactor theory are modified more easily (e.g., Bailey and Ollis 1977; J. Smith 1981) than are less mechanistic, compartmental models. Such modifications may be necessary, for example, to treat size-selective particle retention in the rumen. The basic PFR-CSTR reactor model for hindgut fermenters also is easily modified to incorporate digesta separation and recycling (e.g., Levenspiel 1972; Carberry 1976). Subsequent analyses based on this modified gut-reactor model are sure to include consideration of such chemical-engineering concepts as the "optimal recycle ratio" for small hindgut fermenters (i.e., the ratio of recycled to unrecycled material that results in the greatest net rate of product formation).

The validity of ideal plug flow and the PFR gut model will be questioned by anyone who has observed peristalsis. Cells of longitudinal mixing clearly do result (Macagno and Christensen 1980). A tubular gut with mixing cells might then be modeled as a series of CSTR's. Linking CSTR's in series reduces both the total mixed-flow volume required to achieve a given conversion ( $X_{Af}$ ) and the dilution effect of a single, large CSTR. In fact, as the number of CSTR's in series increases, the behavior of the reactor system rapidly approaches that of plug flow (Levenspiel 1972). Counterintuitively, then, no modification of the ideal PFR model may be required for a tubular gut with mixing cells.

From the PFR model it is immediately apparent that radial elaboration of the mucosal, absorptive surface and lengthening of the gut are not (as claimed in Karasov and Diamond 1985) equivalent tactics. A radial increase in the absorptive surface area increases the uptake of digestive products at any point along the gut. Lengthening the gut increases the surface area but, more importantly, increases the total volume of the gut as well. With all else constant, the resulting increase in throughput time increases the extent to which ingested materials are converted to digestive products. Elaboration of surface area thus affects only the extent of absorption, whereas lengthening the gut affects both the extent of absorption and the extent of reaction.

It is obvious that any number of modifications to the gut-reactor models are possible. Experiments will indicate where necessary modifications lie. Citing Prater's principle of "optimum sloppiness," Carberry (1976) provided some timely advice with respect to the ultimate goals and value of model development. Many processes, industrial or biological, are the interactions of complex arrays of phenomena, often poorly understood. A completely fundamental model may thus be unattainable, but iteration between theory and observation will most efficiently determine acceptable levels of imprecision and inaccuracy.

We have deliberately focused on the homologies between the analysis of chemical reactors and the analysis of digestion. It is useful to consider how this borrowed modeling tool may need to be modified outside the context of design for commercial reactors. We have touched on some possible changes for treating real animals, but it is worth noting some generic problems for future efforts in tailoring reactor theory for predictions of feeding optimization.

At this point, cost functions remain implicit. In the chemical industry most costs are relatively easy to quantify. Like foraging costs, the parameters that describe digestive costs appear difficult to identify and to measure (Penry and Jumars 1986). Our design objective of maximizing production rate in minima of volume and time implicitly assumes that digestive costs (e.g., energy and nutrients required to maintain digestive tissues and energy to propel digesta) are monotonically increasing functions of reactor volume and time. Based on an analogy with commercial reactor costs, these constraints are reasonable, but digestive costs need to be measured and made explicit. That there may be significant costs associated with maintaining a gut is suggested by the evolutionary reduction or loss of guts by some multicellular animals (e.g., pogonophorans, Southward and Southward 1968, Cavanaugh et al. 1981; and some bivalves, Reid and Bernard 1980). Like gut-maintenance costs, the costs of moving digesta of varying mechanical properties and at varying flow rates are essentially unknown.

On the basis of fitness arguments (Townsend and Hughes 1981) the net rate of the assimilation of energy or limiting nutrients should be maximized, and resources directed primarily into tissues that either enhance individual survival or produce offspring. The relative costs of foraging, digestion, absorption, and production of new tissues will be important in determining an animal's strategy for acquiring energy or material. Absorption and production of new tissues appear, in some cases, to be far more expensive than foraging or digestion (Kiørboe et al. 1985). This cost balance suggests that when food is unlimited and inexpensively obtained, an animal may eat a lot, digest it relatively well, but assimilate products less efficiently. Some terrestrial isopods use such a strategy when food is abundant, but increase assimilation efficiency when food becomes limiting (Hubbell et al. 1965; Wieser 1978).

Our analysis indicates that batch processing is an undesirable digestive strategy and conflicts with the obvious success of animals like ctenophores, jellyfish, hydras, anemones, starfish, brittlestars, some glycerid polychaetes, chaetognaths, and many protozoans that do indeed use such a strategy. What characteristics and adaptations do these animals possess that may enable them to utilize a batch-processing rather than a continuous-flow strategy, or which of our explicit or implicit assumptions are invalid with respect to these animals? Various, though certainly not all, representatives of groups using batch-processing strategies have low metabolic requirements (e.g., Buchanan 1964) and expend relatively little energy in foraging. Many have large bodies (reactors) composed of tissues with little metabolic-support cost (mostly water or calcium carbonate). Anemones, hydras, and those glycerid polychaetes that maintain burrow complexes (Ockelmann and Vahl 1970) are essentially sessile. Batch-processing animals generally

are carnivorous or specialize on labile foods [high  $C_{A0}$ , high  $X_A(t)$ ]. Low energy requirements of sit-and-wait predation (Hughes 1980) and relatively high growth efficiencies (e.g., Ockelmann and Vahl 1970) are probably significant adaptations making batch processing a viable strategy.

Our conclusion that batch processing is an undesirable digestive strategy is partly a consequence of assuming unlimited food supply. The implicit assumption of constant food availability is best met in deposit feeders and large herbivores, animals feeding on food of low quality and consequently high abundance. Continuous-flow guts may be disadvantageous when food supply is low. As throughput rate decreases, for example, the PFR assumption of insignificant axial diffusion breaks down. Predicting aspects of batch-reactor performance when food supply varies is reasonably straightforward (Penry and Jumars 1986), but predicting non-steady-state PFR or CSTR performance is not. We are as yet unable to compare digestive strategies across reactor types under all food-supply conditions. We suspect that batch reactors may be comparatively flexible under varying food supply. If, as evidence indicates (Kiørboe et al. 1985), digestion requires relatively little investment, gut contents digested in batches may be quickly ejected and replaced when better items become available. Continuous-flow guts, especially those with spatially segregated secretory and absorptive sites, have more-complex timing constraints.

We have inferred that animals with one gut opening are likely to be batch processors, although exceptions already are known (Larson 1976). The converse inference should not be drawn: a gut with two openings need not operate as a continuous-flow reactor. Batch processing may thus be much more frequent than our cursory overview suggests. Some carnivores, including some snakes and large cats as well as anemones, slowly digest and efficiently assimilate a single high-quality item. A large item may prevent the mixing assumed in the batch-reactor formulation, but mixing may not be necessary because steep product gradients may form over small spatial distances between a constricting gut wall and the food item. Mathematical models of reactors of varying volume are available (basic treatments in Carberry 1976; Levenspiel 1972) and have been used for processes outside industrial design (B. B. Krieger, pers. comm.).

Batch processing is especially likely in time minimizers constrained to widely separated feeding intervals. The similarity in predictions of optimal foraging behavior for time minimizers and energy maximizers is often noted, but consideration of digestion immediately draws an important distinction (e.g., by using fig. 3*b* of Penry and Jumars 1986). By the end of a foraging period, time minimizers should fill their guts with items that will maximize returns integrated over the entire nonforaging period rather than items with initially rapid but unsustainable returns. Continuously feeding energy maximizers with the flexibility to alter gut throughput times should, in contrast, never reject an item providing a higher-than-average short-term rate of gain.

The engineering approach to process design as applied to feeding emphasizes the interdependence of foraging and digestion. Foraging theory suggests what foods will be available at reasonable energetic expense. Digestion theory, in turn, provides process constraints that must be incorporated into foraging models.

Digestive fermentation, for example, should be included as an initial constraint in optimal foraging models for herbivores. Foraging models for generalist herbivores (e.g., Westoby 1974; Owen-Smith and Novellie 1982) should be adapted for specific consideration of foregut versus hindgut fermenters. Theory that links foraging and digestion must yield a better understanding of energy and nutrient acquisition by animals than can either body of theory alone.

#### SUMMARY

Chemical-reactor theory recognizes three ideal reactor types: batch reactors, which are filled with reactants, continuously stirred during the reaction, and then emptied of products after a given reaction period; plug-flow reactors (PFR's), in which reactants continuously enter and products continuously exit with no mixing along the flow path; and continuous-flow, stirred-tank reactors (CSTR's), in which reactants continuously enter and products continuously leave a stirred vessel. Performance equations for these reactors, together with kinetic models for simple enzymatic catalysis and microbially mediated (autocatalytic) digestive fermentation, reveal necessary functional relationships among initial concentrations of the limiting food component, gut volume, throughput time or gut holding time, and digestive reaction kinetics. We use these models to suggest optimization constraints for digestion, analogous to those of optimal foraging theory.

Two general predictions are possible. To sustain the greatest digestive production rate in minima of throughput time and gut volume, an animal dependent on its own digestive enzymes should function as a PFR. Animals fermenting refractory materials should combine a CSTR and a PFR in series at all but the slowest throughput rates, when a PFR will suffice.

We make specific predictions for deposit feeders because they digest little of the ingested volume, greatly simplifying digestive performance equations and making them ideal subjects for initial tests of our models. The majority conform to the prediction of PFR guts, but some deposit feeders apparently use CSTR-PFR series (terebellimorph polychaetes) and batch processing (asteroids and ophiuroids). We suggest that terebellimorph polychaetes may use the CSTR to overcome digestive-rate constraints imposed by diffusion limitations; asteroids and ophiuroids may use a variety of foraging modes to obtain the highest-quality foods available.

We also apply reactor theory to mammalian fermenters because empirical feeding information is extensive. Specifically, we compare the dynamics of foregut versus hindgut fermentation. Foregut fermenters should optimize fermentation with respect to ingested foods and optimize subsequent catalytic digestion with respect to fermentation products. In contrast, hindgut fermenters should optimize foregut catalytic digestion and then optimize fermentation of the residue. According to the principles of dynamic programming, the first digestive stage in each case sets the pace of digesta throughput: slower in foregut fermenters than in hindgut fermenters of similar size. Hindgut fermentation is seen to be competitive, especially for small animals, when food quality is high or variable or when body size is large and throughput rate set in the foregut is slow enough for hindgut

fermentation to yield high conversion. Coprophagy and caecotrophy, tactics used by small hindgut fermenters to increase throughput time and utilization of fermentation digesta, are easily understood in terms of industrial recycle-reactor equivalents. A great advantage in deriving models of digestion from reactor theory is that many foreseeable modifications (e.g., explicit incorporation of volume changes during digestion or of coprophagy) to ideal models have analogues in diverse industrial reactor configurations already modeled and tested.

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