



# Chemical reactor models of optimal digestion efficiency with constant foraging costs

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## Abstract

We develop quantitative optimization criteria for transient digestion processes in simple animal tracts that can be modeled by a semi-batch reactor or plug flow reactor. Specifically, we determine the residence time that optimizes the average net energy intake over the total residence time. The net energy is measured by the total energy intake, less the cost of foraging and digestion. Precise values for optimal residence times are presented for different chemical kinetics of substrate breakdown and of absorption. Both first-order kinetics and Michaelis–Menten kinetics are examined and compared, and it is determined how these residence times vary with foraging costs.

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## 1. Introduction

Understanding nutrient acquisition and digestion in individuals form important components in an overall program of ecological modeling. Nutrient acquisition by animals can be roughly categorized into four serial steps (Woods and Kingsolver, 1999): consumption, digestion into small units, absorption, and use of newly acquired nutrients for general metabolism (e.g. tissue construction). The digestive process integrates chemical processing, transport and compartmentalization of digesta in the gut, and ultimately absorption such that large molecules (carbohydrate, proteins, fats) are cleaved into smaller units that can be trans-

ported across the gut boundary (absorption) to then be distributed within an individual for use in general metabolism. The digestive process can be quite complex. Large numbers of enzymes and buffering systems (Dahlquist, 1968; Applebaum, 1985; Christopher and Mathavan, 1985; Terra et al., 1994; Marana et al., 1995) coupled to specialized organ-level responses (Chapman, 1985a,b; Terra, 1990; Perrin, 1992; Yang and Joern, 1994c) and organism-level regulation of movement of substrate and products through the gut (Terra, 1990; Yang and Joern, 1994a) are all required. Appropriate regulation of the digestive process (Chapman, 1985b), longitudinal and countercurrent movements of digesta through the gut (Terra, 1990) and of products of digestion to sites of absorption (Turunen, 1985; Wright et al., 1994) are the primary processes. Additional regulation and feedbacks at the whole organism level comprise the rest of the picture.

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These include dietary influences of redox and pH regulation and absorption (Harrison and Kennedy, 1994; Frasier et al., 2000), or feeding activity regulated by nutrient titers in body tissue (e.g. in the hemolymph in insects; Bernays, 1985; Simpson and Raubenheimer, 1993) that contribute to a consumer's success in obtaining sufficient nutrition.

Food varies greatly in both availability and nutritional quality, especially to herbivores, and organismal needs change depending on physiological and biochemical requirements. Moreover, organisms often actively control the movement of digesta in the gut depending on the amount and quality of available food and the current physiological state of the individual (Yang and Joern, 1994a). At issue is the degree to which individuals optimize digestion rate in such a dynamic environment, and which points in the series of digestive events limit or regulate digestion to effect this goal, if indeed consumers optimize digestion (Sibly, 1981; Cochran, 1987). We develop a mathematical model of digestion using chemical reactor theory (Penry and Jumars, 1986, 1987; Dade et al., 1990; Karasov and Hume, 1997; Woods and Kingsolver, 1999; Jumars, 2000a,b) to provide a conceptual framework to study possible optimal digestion strategies in a mechanistic framework. This chemical reactor model is evaluated in the context of how individuals best meet nutritional needs in an optimizing framework (Sibly, 1981; Cochran, 1987). Chemical reactor theory is now used regularly to analyze relationships among diet composition, food processing, and gut morphology, yielding diverse conclusions regarding how digestion interrelates with foraging for a variety of taxa (Penry and Jumars, 1986, 1987; Martínez del Río and Karasov, 1990; Karasov and Cork, 1994; Karasov and Hume, 1997; Woods and Kingsolver, 1999; Whelan and Schmidt, 2003).

Chemical reactor models of digestion include standard models of chemical engineering (Nauman, 1987): batch reactors (BRs), continuously stirred tank reactors (CSTRs), plug flow reactors (PFRs), and various serial combinations of these. Authors use mass balance laws and simple chemical kinetics to obtain relations involving throughput rate, volume and rate constants for reactors operating at steady state. Jumars (2000a) determined the optimal throughput time for such reactors and introduced axial variation in a tubular gut by modeling it as a sequence of discrete CSTRs con-

nected in series (Jumars, 2000b). With chewing insect herbivores in mind, Logan et al. (2002) developed a time-dependent model for a tubular gut that has variable cross-sectional area, spatial variation in its absorptive abilities, and temperature-dependent reaction rates. For insects, this model has been extended to couple a crop-like structure (CSTR) connected in series to a tubular gut (PFR) (Wolesensky et al., 2003); nutrients are absorbed into the hemolymph (CSTR) and concentration thresholds feedback to initiate feeding. In this paper we use chemical reactor models to examine an optimal, transient digestion process in a simple organism whose gut structure is either sacular (BR) or tubular (PFR). We focus on analyzing the strategy of maximizing digestibility (fraction of nutrient absorbed), less the foraging and digestion costs, as a function of the total residence time of the digesta in the gut. Residence time is inversely proportional to the throughput speed.

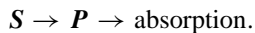
Other digestion strategies have also been proposed. Jumars (2000a) maximizes the absorption rate as a function of the flow-through rate under steady-state conditions. Other work with batch reactor models generally assume steady-state operating conditions with constant inflow and outflow and no volume change, or that the contents undergo reaction before emptying (simple batch reactor). Under the more likely transient conditions, however, the absorption rate is time dependent and no simple optimization criterion for absorption rate exists based on a single flow through speed; this is one topic we develop in this paper. An optimization strategy for transient digestion processes based on a performance criteria of maximizing the net average energy intake over the residence time of the digesta in the reactor is examined for digestion of sugars in nectar-eating birds (Martínez del Río and Karasov, 1990) and more generally by Raubenheimer and Simpson (1996). In this paper we give simple algebraic formulas to calculate the optimal strategy for a transient model and compare the results with expectations from steady-state models of Jumars (2000a). Another possible consumer strategy, especially for certain insects, is to reach a nutritional goal, rather than a rate of nutrient gain (Simpson and Raubenheimer, 1993). That is, concentrations of nutrients in the hemolymph may regulate nutrient intake, resulting in an absorption rate that meets targeted nutrient concentrations or ratios of nutrient concentrations. Moreover,

some experiments challenge predictions of previous chemical reactor models (Karasov and Cork, 1994; Karasov and Hume, 1997). New time-dependent chemical reactor models included herein may provide new insights into the process.

The digestion systems analyzed in this paper represent extremes, although specific animal taxa exhibit unique features depending on diet and environmental constraints. For the case of the sacular gut structure, we assume that it is initially loaded with a volume  $V_0$  of a substrate  $S$  with molar concentration  $s_0$ . The contents are removed at a constant volumetric flow rate (digestion speed) until the gut is emptied. The chemical dynamics include substrate breakdown into a nutrient product that is then absorbed across the boundary of the gut. This process models animals that eat discrete meals by filling the gut quickly, and then digesting the contents as it flows from the gut. It can also model a single gut structure, like the crop in some terrestrial arthropods, that empties into another gut structure, like the midgut. The latter is illustrated by a grasshopper whose crop fills in minutes, but the emptying process of the entire crop and midgut system may be on the order of hours (Yang and Joern, 1994b). For the tubular gut, we load an initial segment of the gut with substrate and permit the digesta to flow through the gut at a constant speed until the gut empties. In both gut structures our goal is to find the throughput rate that optimizes the average, net intake and develop specific formulas that express this digestion strategy.

## 2. Sacular gut structure

In both types of gut structures (sacular and tubular), the complex chemical kinetics of digestion is modeled by a simple two-step reaction



That is, a substrate  $S$  containing a nutrient breaks down (say, by hydrolysis) into the nutrient product  $P$ , which is then absorbed across the gut epithelium into the organism's circulatory system. For example, in hornworms, protein substrate is broken down by proteolytic enzymes into small and medium-sized peptides, followed by a breakdown into free amino acids and smaller units by membrane-bound hydrolytic enzymes. These products are then absorbed into the ep-

ithelium by diffusion or by amino acid symporters in the membrane; from there amino acids are distributed in the hemolymph (Santos et al., 1983). In the first case, we model the substrate breakdown by a linear (first-order) reaction rate ( $\text{mol cm}^{-3} \text{min}^{-1}$ ) of the form

$$R_{S \rightarrow P} = kS, \quad (1)$$

where  $k$  is the rate constant ( $\text{min}^{-1}$ ) and  $S$  is the substrate concentration ( $\text{mol cm}^{-3}$ ). We are initially choosing a linear rate for mathematical simplicity; it may be more appropriate in some circumstances to model the enzyme action by Michaelis–Menten kinetics (Section 3). For the absorption process across the gut wall we model the kinetics by either first-order kinetics (this section) or Michaelis–Menten kinetics (Section 3). Therefore, in the first instance

$$R_{P \rightarrow \text{absorp}} = aP, \quad (2)$$

where  $P$  is the nutrient product concentration and  $a$  ( $\text{min}^{-1}$ ) is the absorption rate constant. The analysis can be carried out in terms of a single dimensionless ratio of the rate constants

$$r = \frac{a}{k}. \quad (3)$$

In the case  $r \ll 1$  the process is *absorption limited*. That is, absorption is slower than substrate breakdown; for example, the number of active sites on the epithelium may be limited. When  $1 \ll r$  the process is *digestion limited*. For example, it may be difficult to extract nutrients from the substrate. When  $r \approx 1$  digestion and absorption are balanced. There are other possible limitations that we do not consider in our analysis, for example, post-absorption limitations (the absorbed nutrients are supplied faster than the organism's energy budget demands) and pre-digestion limitations (consumption rate, foraging success, and so on).

We now consider the case of a sacular gut (Fig. 1), which we model as a BR. This type of gut structure is characteristic of some invertebrates, including hydra and coelenterates. We assume it is loaded at time  $t = 0$  with a substrate  $S$  of molar concentration  $s_0$  ( $\text{mol cm}^{-3}$ ) and volume  $V_0$  ( $\text{cm}^3$ ). For  $t > 0$  the contents of the gut are assumed to be perfectly mixed and the reactor empties at constant ejection rate  $q$  ( $\text{cm}^3 \text{min}^{-1}$ ); there is no inflow (ingestion) during the emptying stage. The volume of the contents is therefore  $V(t) = V_0 - qt$ ,  $0 < t < V_0/q$ . Letting  $S = S(t)$

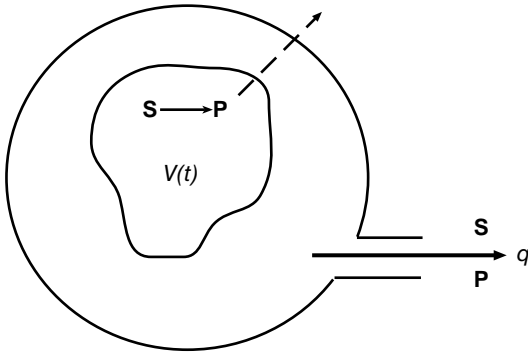


Fig. 1. A digestive structure modeled by a semi-batch reactor. The reactants  $S$  are loaded at time zero and reaction and absorption of the products  $P$  occur as digesta in the gut is ejected at a constant flow rate  $q$ . At all times the mixture, which has volume  $V(t) = V_0 - qt$ , is perfectly stirred.

and  $P = P(t)$  denote the molar concentrations of  $S$  and  $P$ , respectively, as functions of time, we can balance the number of moles of  $S$  and  $P$  in the reactor at time  $t$ . In the usual manner (Nauman, 1987; Edelstein-Keshet, 1988), we obtain the dynamical equations for the concentrations with the given initial conditions:

$$\begin{aligned} (V(t)S)' &= -qS - kV(t)S, \\ (V(t)P)' &= -qP + kV(t)S - aV(t)P, \\ S(0) &= s_0, \quad P(0) = 0. \end{aligned}$$

Expanding the derivatives on the left sides and simplifying gives

$$\begin{aligned} S' &= -kS, \quad P' = kS - aP, \\ S(0) &= s_0, \quad P(0) = 0. \end{aligned} \quad (4)$$

We observe that the volume drops out when it is a linear function of time (for nonlinear functions of time this cancellation does not occur and the problem is more complicated). We now nondimensionalize the problem by introducing scaled, dimensionless variables. In many prior works on digestion modeling this step is not performed and authors retain the physical, dimensioned quantities. However, scaling can greatly simplify a problem by reducing the number of independent constants (Gurney and Nisbet, 1998; Logan, 1997). We introduce new, dimensionless, variables via

$$\tau = kt, \quad s = \frac{S}{s_0}, \quad p = \frac{P}{s_0}. \quad (5)$$

So, the concentrations are measured relative to the initial substrate concentration, and time is measured relative to time of substrate breakdown. In terms of these scaled variables, the dimensioned problem (4) can be written in dimensionless form as

$$\frac{ds}{d\tau} = -s, \quad \frac{dp}{d\tau} = s - rp, \quad s(0) = 1, \quad p(0) = 0, \quad (6)$$

where  $0 < \tau < T$ , and

$$r = \frac{a}{k}, \quad T = \frac{kV_0}{q} \quad (7)$$

are dimensionless parameters;  $r$  is the ratio of the absorption rate to the reaction rate, and  $T$  is the scaled time to empty the gut (the scaled residence time). Thus, nondimensionalizing reduces the number of parameters from three to two.

The solution of this linear system can be found by straightforward methods (Boyce and DiPrima, 2001). We obtain

$$s = e^{-\tau}, \quad p = \frac{1}{r-1}(e^{-\tau} - e^{-r\tau}), \quad \text{if } r \neq 1, \quad (8)$$

$$s = e^{-\tau}, \quad p = \tau e^{-\tau}, \quad \text{if } r = 1. \quad (9)$$

Upon setting  $p' = 0$  and solving for  $\tau$  shows that the product concentration  $p$  is maximized at the scaled time

$$\tau_{\max} = \begin{cases} \frac{\ln r}{r-1}, & \text{if } r \neq 1, \\ 1, & \text{if } r = 1. \end{cases} \quad (10)$$

The maximum product concentrations are

$$p_{\max} = \begin{cases} r^{r/(1-r)}, & \text{if } r \neq 1, \\ e^{-1}, & \text{if } r = 1. \end{cases}$$

Fig. 2 shows the scaled product concentrations (8) for various values of  $r$ . We observe that as  $r$  increases (digestion limited) the maximum product concentration occurs at an earlier time; as  $r$  decreases (absorption limited), the maximum occurs at later times. These conclusions correspond to the results of Woods and Kingsolver (1999) for a PFR operating at steady state; in the digestion limited case the maximum nutrient concentration occurs earlier in the tubular gut and in

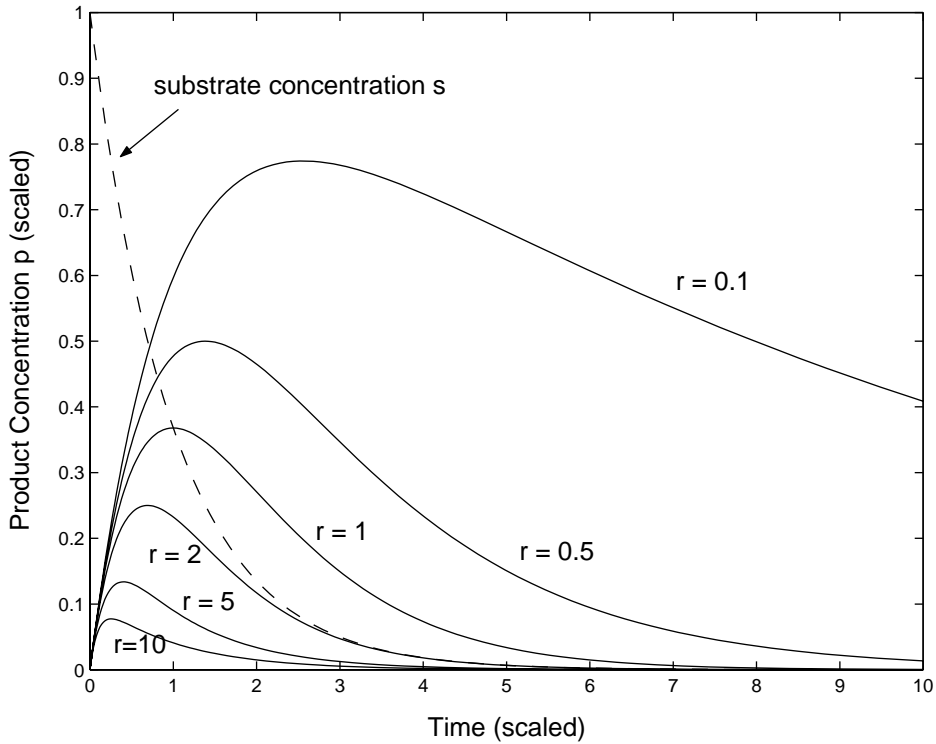


Fig. 2. Scaled  $p(\tau)$  concentration–time curves for different values of the ratio  $r$ , and the scaled substrate concentration  $s(\tau)$ .

the absorption limited case the maximum occurs farther down in the gut.

To examine the optimization problem, we compute the fraction of the initial substrate that is absorbed, i.e. the *digestibility*. The rate of absorption is given by  $aP(t)V(t)$ , so the total amount absorbed (mol) is given by

$$A = \int_0^{V_0/q} aP(t)V(t) dt.$$

This can be written (first, for the case  $r \neq 1$ ) using dimensionless quantities as

$$\begin{aligned} A &= \frac{aqs_0}{k^2(r-1)} \int_0^T (e^{-\tau} - e^{-r\tau})(T-\tau) d\tau \\ &= \frac{aqs_0}{k^2(r-1)} \left( \frac{-1}{r^2} e^{-rT} - \frac{T}{r} + \frac{1}{r^2} + e^{-T} + T - 1 \right). \end{aligned}$$

Therefore, the digestibility  $D(T) = A/s_0V_0$  (amount absorbed per unit mole of initial reactant) is, in terms

of the residence time  $T$ ,

$$\begin{aligned} D(T) &= \frac{1}{r(r-1)T} \\ &\quad \times (r^2 e^{-T} - e^{-rT} - rT + 1 + r^2 T - r^2), \\ &\quad r \neq 1. \end{aligned} \quad (11)$$

We observe that

$$D(T) \rightarrow 1, \quad \text{as } T \rightarrow \infty,$$

which states that total conversion occurs as the residence time gets large. The right side of (11) is undefined at  $T = 0$ . To find the behavior for short digestion times, we expand the right side of (11) in a Taylor series about  $T = 0$ :

$$D(T) = \frac{r}{6} T^2 + O(T^3), \quad \text{as } T \rightarrow 0.$$

Thus, for small residence times, the graph of the digestibility  $D(T)$  is nearly parabolic; the accumulated absorption is small at early times. Fig. 3 shows the digestibility as a function of time for various values of

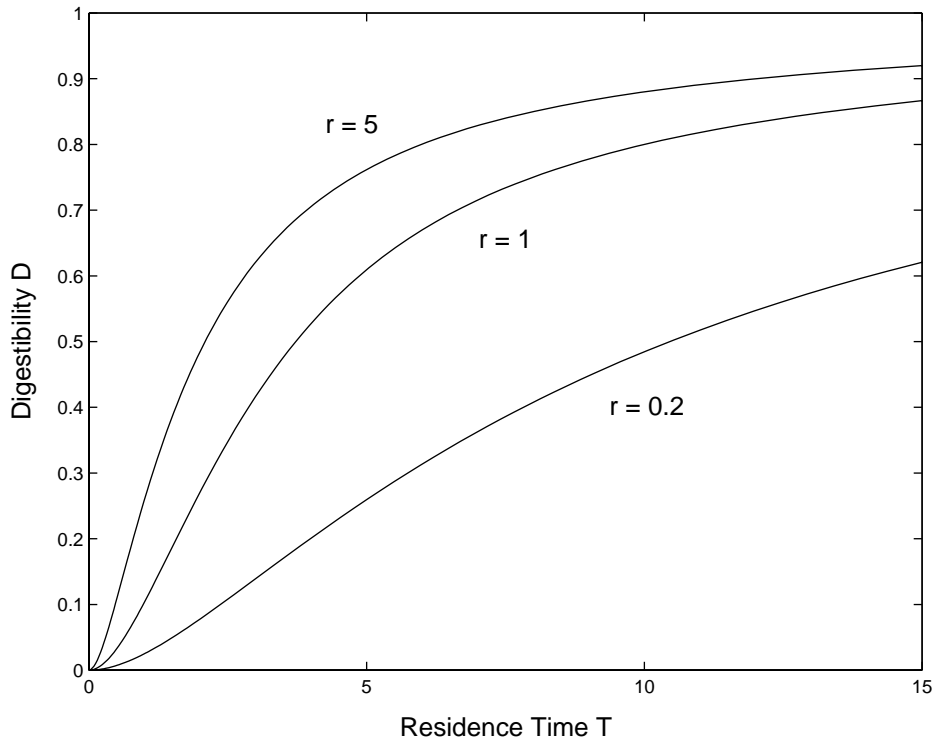


Fig. 3. The digestibility, or fraction of nutrient absorbed vs. time in a sacular structure for various values of  $r$ .

$r$ . Observe that the curves are sigmoid in shape, which confirms the qualitative conclusions made in the literature (Sibly, 1981).

In the special case of  $r = 1$  the digestibility is

$$\begin{aligned} D(T) &= \frac{1}{T} \int_0^T \tau e^{-\tau} (T - \tau) d\tau \\ &= \frac{1}{T} [T - 2 + (T + 2)e^{-T}]. \end{aligned}$$

### 3. Optimal digestion strategy

We now apply optimization methods to determine quantitatively the optimum residence time for the sacular gut model. A similar qualitative analysis is given in different contexts by Sibly (1981), Raubenheimer and Simpson (1996), Martínez del Río and Karasov (1990), but without the accompanying formulas obtained here.

There is an important connection between foraging and digestion (Sibly, 1981; Stephens and Krebs, 1986;

Penry and Jumars, 1986, 1987; Martínez del Río et al., 1994; Karasov and Hume, 1997; Whelan and Schmidt, 2003). When an animal is faced with limited options to select food, through food scarcity or low food quality, there is evidence that it may compensate by altering its digestive tactics to maximize the amount of nutrients it requires to meet its nutritional needs. One strategy is to change its morphology, e.g. the size of the gut; another is to change the flow through speed, or the residence time, of the food that is ingested. Our analysis is focused on the latter. Simply put, there is a cost of avoiding predators, finding, capturing, and handling food (we lump all these interesting components together in a single term, “foraging cost”), and a cost of digesting food; and, a possible strategy is to control the residence time in order to maximize the total intake less the costs of foraging and digestion over the total time it is in the gut. Different strategies have been suggested by others, e.g. that of maximizing the rate of absorption as mentioned earlier (Jumars, 2000a). Another suggested tactic is optimal foraging

theory (Belovsky, 1997) in which relations between allometric quantities, food characteristics, and digestion characteristics (retention time) lead to a constrained optimization problem where time and capacity are limiting quantities. Still other strategies involve regulation of temperature, water, or pH in order to maintain homeostasis. Finally, experiments by Simpson and colleagues indicate that some insects “satisfice”, that is, they digest only to meet certain target concentrations, or ratios of such concentrations (Stephens and Krebs, 1986; Simpson and Raubenheimer, 1993). The quantitative results obtained below can be used in conjunction with experiments to ascertain if a given organism follows the strategy we examine here.

To formulate the maximum efficiency property, we assume the cost (in moles per unit mole of initial substrate) of foraging is a constant value  $C_f$ , and the cost of digesting the food is proportional to the residence time  $T$ , i.e.  $C_d T$ , where  $C_d$  is a constant in moles per unit mole of initial substrate, per unit time. It has been noted (McWilliams and Karasov, 1998a,b;

Jumars and Martínez del Rio, 1999) that misidentifying foraging costs can lead to incorrect predictions because over several feedings, an organism may have different costs due to changes in environment. The cost in this study is lumped in a single constant  $C_f$ , which could vary over different feeding time intervals. Therefore, in our model, the cost of foraging and digestion is  $C_f + C_d T$ . Then, in terms of the digestibility  $D(T)$ , the average rate of energy gain, per unit mole of initial substrate, during the residence period is

$$E(T) = \frac{D(T) - (C_f + C_d T)}{T}.$$

We use  $E$  as the performance criterion or objective function. To maximize  $E$  we take its derivative with respect to  $T$  and set it equal to 0. After reorganizing the terms, we obtain an equation for the optimum residence time  $T_m$ ,

$$D'(T_m) = \frac{D(T_m) - C_f}{T_m}. \tag{12}$$

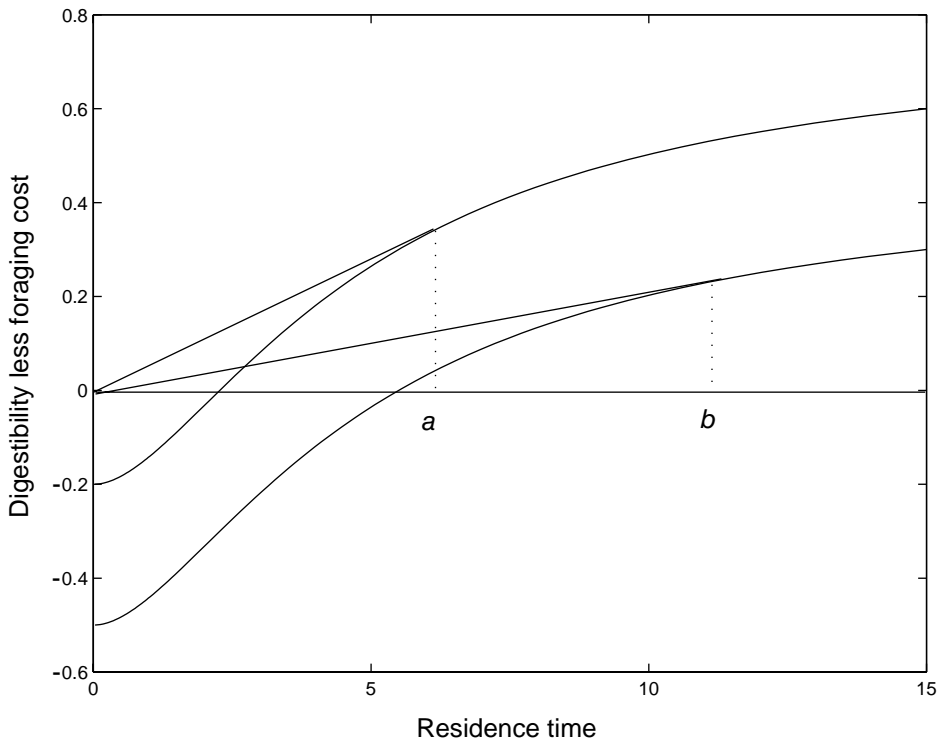


Fig. 4. Geometrical meaning of the optimization condition (12). Shown are two curves  $D(T) - C_f$  with  $C_f = 0.2$  (upper curve) and  $C_f = 0.5$  (lower curve). In each case the optimal residence times  $T_m = a$  and  $T_m = b$  are determined from the tangency condition.

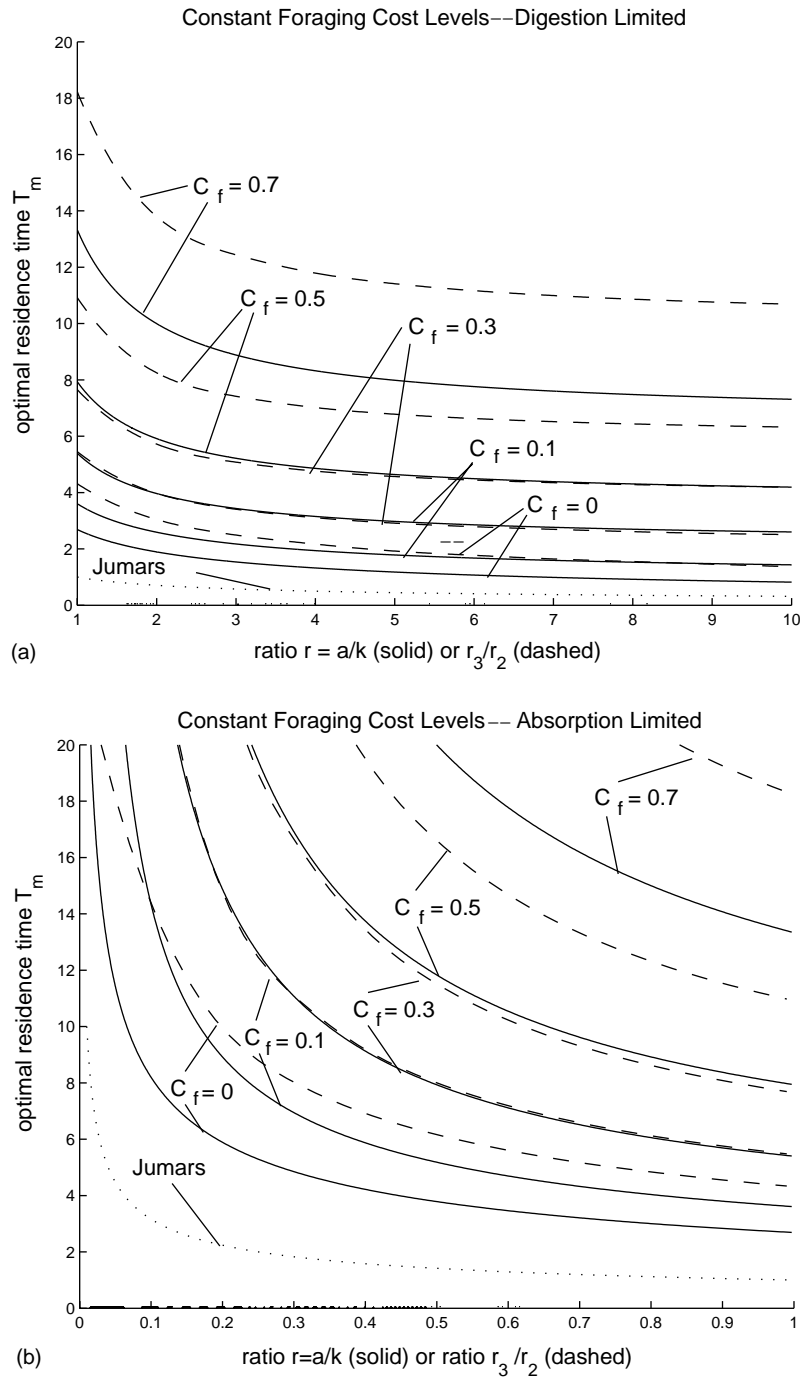


Fig. 5. The solid curves show how  $T_m$  and  $r$  vary with constant values of the foraging cost  $C_f$  ( $C_f = 0, 0.1, 0.3, 0.5, 0.7$ ) in: (a) the digestion limited case and (b) the absorption limited case. The dashed curves show how  $T_m$  and  $r_3/r_2$  vary with constant values of  $C_f$ , with  $r_1 = 1$ , in the Michaelis–Menten case. The Jumars curve  $1/\sqrt{r}$  is also shown.

Notice that this expression depends upon the foraging cost, but in this model is independent of the cost of digesting the food. Geometrically, (12) has an interesting interpretation: the value  $T_m$  is the  $T$  coordinate of the point of tangency of the straight line emanating from the origin and the graph of  $D(T) - C_f$  (Fig. 4). An important implication is that the larger the foraging cost, the longer the organism retains the food.

In the case  $r \neq 1$ , Eq. (12) becomes

$$\left(T_m + \frac{2}{r}\right) e^{-rT_m} - r(2 + T_m) e^{-T_m} + T_m[1 - r + C_f(r - 1)] - \frac{2}{r} + 2r = 0. \quad (13)$$

For  $r = 1$  we have

$$(T_m^2 + 3T_m + 4) e^{-T_m} + (1 - C_f)T_m = 4. \quad (14)$$

For a given value of  $r$ , Eqs. (10) and (11) are non-linear transcendental equations and must be solved numerically to determine  $T_m$ . One efficient way to present the results is to solve (13) and (14) for  $C_f$  in terms of  $r$  and  $T_m$ , i.e.  $C_f = C_f(r, T_m)$ , and then plot the level curves of  $C_f$ . Fig. 5a and b show how the optimal residence time  $T_m$  varies with values of the ratio  $r$  at constant values of the foraging cost in the digestion-limited case and the absorption-limited case. The solid curves correspond to first-order kinetics and the dashed curves correspond to Michaelis–Menten kinetics, discussed in Section 3. To obtain the dimensioned optimal residence time, divide the dimensionless time by the substrate breakdown rate constant  $k$ . It is interesting to compare the values to those of Jumars (2000a), computed under nontransient, or steady-state conditions. For continuous processing in a reactor of volume  $V_0$  operating at steady state, he gives the (dimensional) formula

$$q_{\text{opt}} = \sqrt{ka}V_0.$$

Using this value in the formula for dimensionless residence time, we obtain a residence time

$$T_j = \frac{kV_0}{q_{\text{opt}}} = \frac{kV_0}{\sqrt{ka}V_0} = \frac{1}{\sqrt{r}}.$$

From Fig. 5a and b we observe that with no foraging costs, the time of residence in our BR model is about 2.5 times the value obtained by Jumars in a CSTR model. This is reasonable because an organism with a

sacular gut that is egesting substrate, along with some of the nutrients produced, would eject slower in order to obtain the maximum efficiency.

We can also interpret the relation between the ratio  $r$  and optimal residence time  $T_m$  in terms of food quality. A food that is low in nutrient quality or that is difficult to extract the nutrient corresponds to a high value of  $r$  (digestion limited), and therefore a short residence time. A high food quality corresponds to a long residence time or slow throughput rate. Yang and Joern (1994b) observed this behavior in grasshoppers, i.e. poor quality food is ejected quickly while high quality food is retained.

#### 4. Michaelis–Menten uptake

In some cases substrate breakdown is limited by enzyme concentrations and the nutrient products from the lumen are passed through the epithelium by facilitated transport. In this case the chemistry is modeled by Michaelis–Menten kinetics, and we replace (1) and (2) by

$$R_{S \rightarrow P} = \frac{k_3 S}{k_4 + S}, \quad R_{P \rightarrow \text{absorp}} = \frac{k_1 P}{k_2 + P}.$$

Whereupon, using the same nondimensionalization (5), but with  $\tau = k_3 t / s_0$  as dimensionless time, the governing dynamics are

$$s' = -\frac{s}{r_1 + s}, \quad p' = \frac{s}{r_1 + s} - \frac{r_3 p}{r_2 + p}, \quad (15)$$

$$s(0) = 1, \quad p(0) = 0.$$

Now there are three dimensionless parameters:

$$r_1 = \frac{k_4}{s_0}, \quad r_2 = \frac{k_2}{s_0}, \quad r_3 = \frac{k_1}{k_3}. \quad (16)$$

The two equations in (15), which replace (3), are not solvable in analytic form and a solution must be found numerically. In this case the fraction absorbed, or digestibility, during residence time  $T$  is

$$D = \frac{1}{s_0 V_0} \int_0^{V_0/q} \frac{k_1 P(t)}{k_2 + P(t)} V(t) dt$$

$$= \frac{1}{T} \int_0^T \frac{r_3 p(\tau)}{r_2 + p(\tau)} (T - \tau) d\tau.$$

Now we compute the optimal residence time using criterion (12). Using the Leibniz rule (e.g. see Neuhauser, 2000), the derivative of  $D$  is

$$D'(T) = \int_0^T \frac{r_3 p(\tau)}{r_2 + p(\tau)} \frac{\tau}{T^2} d\tau.$$

Therefore, upon writing down (12) and rearranging, we obtain an equation whose solution is the optimal residence time  $T_m$ :

$$\int_0^{T_m} \frac{r_3 p(\tau)}{r_2 + p(\tau)} (T_m - 2\tau) d\tau - C_f T_m = 0. \quad (17)$$

The unknown  $T_m$  appears in the limit of integration, and a numerical procedure is required. One can adapt Newton's method to solve for  $T_m$  in only a few iterations. Letting  $G(T_m)$  denote the left side of (17), we set up the iterative scheme

$$T_m^{(n+1)} = T_m^n - \frac{G(T_m^n)}{G'(T_m^n)}, \quad n = 0, 1, 2, \dots$$

where  $T_m^n$  is the  $n$ th approximation to  $T_m$ . At each step the integrals are computed using the trapezoidal rule and the differential Eq. (15) are solved by a fourth order Runge-Kutta method.

To compare the results for Michaelis–Menten kinetics with the first-order kinetics, we have put the results on Fig. 5a and b. The dashed curves show the variation of the optimal residence time  $T_m$  versus the dimensionless ratio  $r_3/r_2$ , with  $r_1 = 1$ . From (16) we observe that this ratio is  $r_3/r_2 = (k_1/k_2)/(k_3/k_4)$ , which is the ratio of the initial slopes of the Michaelis–Menten curves for absorption and substrate breakdown; thus it may be compared to  $r = a/k$  for first-order kinetics. It is clear that for a fixed foraging cost, Michaelis–Menten kinetics leads to longer optimal residence times than those calculated with first-order kinetics.

## 5. Tubular gut structure

Now we compare the optimal performance of a digestion structure that can be modeled as a tubular gut (PFR) of length  $L$  and cross-sectional area  $A$ .

The reaction–advection equations governing the unknown concentrations are (Woods and Kingsolver,

1999; Logan et al., 2002)

$$S_t = -VS_x - kS, \quad P_t = -VP_x + kS - aP, \quad (18)$$

where  $V$  is the constant speed of the digesta in the gut and  $S = S(x, t)$  and  $P = P(x, t)$  are the concentrations of the substrate and product at position  $0 < x < L$  and at time  $t$ . The first term on the right side of each equation is the term giving the rate that the chemical species advects through the gut, and the remaining terms are the rates of chemical reaction. The constant cross-sectional area  $A$  has been canceled from all the terms. We did not include a radial factor  $1/R$  in the rate terms as did Woods and Kingsolver (1999) to indicate a radial dependence in the rate of reaction (more reaction nearer the lateral gut boundary). Thus, our results will give greater absorption rates than if such a factor were included because we assume uniform reaction in the radial direction. Our results cannot really be compared with Woods and Kingsolver because they consider a steady-state situation. The boundary conditions at the mouth are

$$S(0, t) = P(0, t) = 0, \quad t > 0,$$

and the initial conditions are

$$S(x, 0) = S_0(x), \quad P(x, 0) = 0, \quad 0 < x < L,$$

where  $S_0(x)$  is the initial substrate concentration in the gut, which at present, could be nonuniform. As in the case of the batch reactor, we scale time by  $k^{-1}$  and  $P$  and  $S$  by  $s_m$ , the maximum concentration of the substrate in the gut at time  $t = 0$ , i.e.  $s_m = \max S_0(x)$ . The spatial variable is scaled by the gut length  $L$ . Then (18) becomes, with dimensionless independent variables  $y = x/L$  and  $\tau = kt$ ,

$$s_\tau = -vs_y - s, \quad p_\tau = -vp_y + s - rp, \quad (19)$$

where

$$v = \frac{V}{kL}$$

is the dimensionless throughput speed and, as before,  $r = a/k$ . The dimensionless boundary and initial conditions are

$$s(0, \tau) = p(0, \tau) = 0$$

and

$$s(y, 0) = f(y), \quad p(y, 0) = 0, \quad 0 < y < 1,$$

where

$$f = \frac{S_0}{s_m}$$

The system (19) can be solved by the method of characteristics (e.g. Logan, 1994, 1997) to obtain exact formulas for the unknown concentrations:

$$s(y, t) = f(y - v\tau) e^{-\tau},$$

$$p(y, \tau) = \frac{1}{1-r} f(y - v\tau)(e^{-r\tau} - e^{-\tau}), \quad r \neq 1$$

and

$$s(y, t) = f(y - v\tau) e^{-\tau},$$

$$p(y, \tau) = f(y - v\tau)\tau e^{-\tau}, \quad r = 1.$$

To compare the performance of the tubular gut (PFR) to a sacular gut (BR), at time  $t = 0$  we

load a bolus of food (substrate) of concentration  $s_0$  over the length  $0 < x < V_0/A$ , where for comparison,  $V_0$  is the volume of the batch reactor examined in Section 2. Thus, the initial condition on  $S$  becomes

$$S_0(x) = \begin{cases} s_0, & 0 < x < V_0/A, \\ 0, & V_0/A < x < L, \end{cases}$$

or, in dimensionless terms,

$$f(y) = \begin{cases} 1, & 0 < y < Y, \\ 0, & Y < y < 1, \end{cases}$$

where  $Y = V_0/AL$  is the fraction of the gut that is loaded with substrate. It is a dimensionless constant that contains the relative geometry of the gut; different geometries will give the same result (i.e. constant values of  $AL$ ). Therefore, the digestibility, or total amount absorbed per unit mole of substrate, is the double

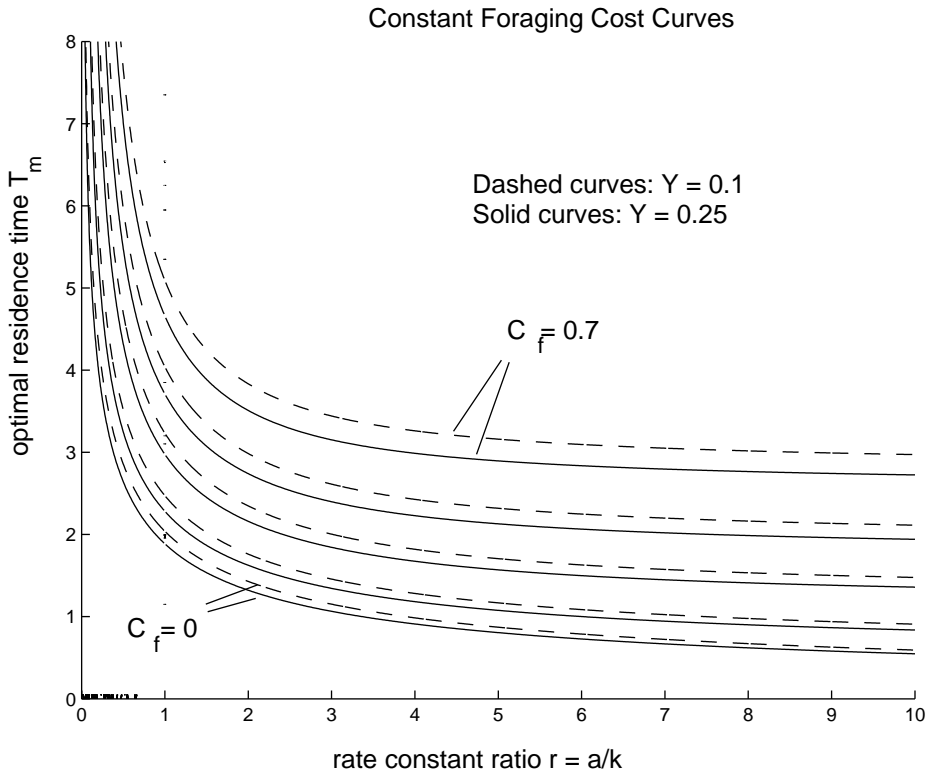


Fig. 6. Plots showing how  $T_m$  and  $r$  vary along a level curves of  $C_f = C_f(T_m, r)$  in the PFR case.

integral

$$D = \frac{1}{s_0 V_0} \int_0^L \int_0^L AaP(x, t) dx dt$$

$$= \frac{r}{y_0} \int_0^T \int_0^1 p(y, \tau) dy d\tau,$$

where  $T = v^{-1}$  is the scaled residence time.

To find the optimal residence time we can apply the criterion (12). Because the integrand is defined piecewise, we calculated the double integral  $D(T)$  and its derivative  $D'(T)$  on a computer algebra package (Maple, version 5). The results are shown in Fig. 6 where variations of  $T_m$  with  $r$  are shown for constant values of the foraging cost  $C_f$ . The PFR model gives shorter optimal residence times than the BR model. As foraging costs increase, this difference is magnified. For example, when  $r = 10$  and  $C_f = 0.3$ , then  $T_m = 1.3$  for the PFR compared to  $T_m = 4.1$  for the BR. If an organism with high foraging costs has a choice, then it may have an advantage with a tubular gut because it is much less sensitive to these costs.

A full, direct comparison between a tubular and sacular gut morphologies is not possible in this model because in the sacular gut the volume changes as digesta is excreted throughout the process; in the tubular gut model, the volume of digesta remains constant as it passes through the entire length of the gut before finally exiting.

## 6. Conclusions

Time-dependent chemical reactor models like the one developed here will help provide a foundational, analytical, framework to assess the entire food acquisition process. We have analyzed a simple, mathematically tractable model where quantitative predictions are fully determined and correspond to qualitative expectations based on empirical evidence and intuition. Like previous efforts (Penry and Jumars, 1986, 1987; Karasov and Hume, 1997; Woods and Kingsolver, 1999; Jumars, 2000a,b; Logan et al., 2002), our extended model makes simplifying assumptions to facilitate mathematical development. Quantitatively, we can compare retention times for different foraging costs, different reaction and absorption rates (that may also be temperature dependent), different chemical ki-

netics for absorption (linear versus saturating), and for different morphology (sacular versus tubular guts). To examine optimal digestion, costs are treated in a general manner in these models, rather than incorporating specific mechanisms. For example, absorption is treated simply as nutrient transport across the gut wall into the body; it does not distinguish between alternate underlying physiological and biochemical mechanisms such as the importance of potential limiting transport across the brush border membrane resulting from limited number of transport sites, compared with limitation from incomplete radial mixing in delivering products to absorption sites for subsequent transport (Woods and Kingsolver, 1999). However, in each of these modeling decisions, the outcome of the model analysis will point to key limiting points for which alternate mechanisms can then be incorporated and evaluated.

The important implications of the model include: (a) the larger the foraging cost, the longer the time an organism retains the food; (b) the residence time for our time-dependent model is about 2.5 times the residence time computed with steady-state models; (c) this optimization model indicates conditions for digestion limitation versus absorption limitation based on the absorption-to-substrate-breakdown ratio  $r$ . If  $r \gg 1$ , then the residence time  $T_m$  is small and there is digestion limitation based on either low food quality, difficulty in extracting the nutrient, or rapid absorption capability. (In the latter case, “free transporters” are always available relative to the rate of nutrient production formation.) If  $r \ll 1$ , then  $T_m$  is longer and there is limited absorption, resulting either from absorption mechanisms, or high food quality that overwhelms structural capacity to absorb available nutrients in a given amount of time. In this case, it is better to digest what you have rather than search for more food; (d) the plots in Figs. 5a, b and 6 show that tubular guts are less sensitive to dramatic variations in foraging costs than are sacular guts, suggesting that an organism with a tubular gut would do better in a variable environment compared to an organism with a sacular gut. The plots also show that for either gut type there is a threshold range of  $r$  (around 2 or 3) beyond which large increases in the low quality of food have little effect on the optimum residence time.

Additionally, is it sufficient to examine regulation of the digestion and absorption without considering the

role of post-ingestive events on consumption. Feedbacks between hemolymph nutrient concentrations, residence time of digesta in the gut, and initiation of feeding, including compensating consumption are well documented for insect herbivores (Simpson and Raubenheimer, 1993; Yang and Joern, 1994a,b,c). The capability to regulate food input based on metabolic need may make finely regulated digestive systems unnecessary without sacrificing much in terms of the costs of excess capacity. Based on a chemical reactor model of digestion, Woods and Kingsolver (1999) reject consumption limitation, digestion limitation or matched process hypotheses for larval *Manduca sexta* while finding equivocal support for absorption limitation or post-ingestive limitation hypotheses. Additional study is required to further reconcile feedbacks and limitation in food acquisition and digestion.

Our results also enable us to consider temperature variations using the  $Q_{10}$  rule. For example, if for every 10 °C increase in temperature the absorption rate doubles, then in the first-order model in Section 2 the ratio  $r$  will double, giving an appropriate decrease in residence time (Fig. 5a and b). For Michaelis–Menten uptake, increasing  $k_1$  and  $k_2$  by a factor of 2 will increase both  $r_2$  and  $r_3$  by a factor of 2, but will leave  $r_1$  unchanged.

Time-dependent chemical reactor models may ultimately play an important role in addressing key issues in the evolution of digestion systems. One view of an optimal digestive and absorptive system predicts a finely tuned system, where the physiological capacities of consumption, digestion, absorption and post-absorptive metabolic use of transported products in the animal should be roughly matched (Woods and Kingsolver, 1999). If one or more steps exhibit excess capacity or severe limitation, biosynthesis costs would be incurred without offsetting benefits (Woods and Kingsolver, 1999). Mechanistic reactor models may help frame alternate testable hypotheses and address some of these issues.

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