



Location, Time, and Temperature Dependence of Digestion in Simple Animal Tracts

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In this paper, we develop plug flow reactor models that simultaneously investigate how reaction and absorption, morphological differences, and temperature influence nutrient acquisition rates in simple, tubular animal guts. We present analytical solutions to the resulting reaction–advection equations that model these processes, and we obtain formulas giving the throughflow speed that maximizes the absorption rate. The model predicts that the optimal digestion speed increases as the ratio of the rate of enzyme breakdown to the rate of absorption increases.

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1. Introduction

Digestion is often neglected in foraging studies that are predicated on understanding food selection while optimizing nutrient intake. However, digestion can be a limiting bottleneck, or it can provide compensatory mechanisms that accommodate variable diets and environments. Chemical reactor theory provides a framework to incorporate digestion into foraging models in ways that appropriately simplify the complex biochemical and physiological processes.

Food gathering and processing are fundamental problems faced by all consumers (Stephens & Krebs, 1986). While early efforts aimed primarily to understand the adaptive nature of diet selection (Stephens & Krebs, 1986; Sih & Christiansen, 2001), it is increasingly clear that adaptive digestion responses can be equally important for understanding energy and nutrient

acquisition (Sibly, 1981; Karasov & Diamond, 1983, 1988; Penry, 1983; Karasov *et al.*, 1986; Cochran, 1987; Hirakawa, 1997; Kingsolver & Woods, 1997; Jumars & Martínez del Río, 1999; Frazier *et al.*, 2000; Secor & Diamond, 1973; Whelen *et al.*, 2000; Whelen, 2002).

Modeling digestion using chemical reactor theory provides a nice compromise between mechanistic detail (specific biochemical interactions and cellular processes) and whole-organism responses (understanding overall nutrient breakdown and transport coupled to energetic relationships in the context of diet input) (Penry & Jumars, 1986, 1987; Karasov & Hume, 1997; McWilliams & Karasov, 1998a,b). Sacular organs, like stomachs or crops, can be modeled as continuously stirred tank reactors (CSTRs) or batch reactors (BRs). Tubular organs, like intestines or midguts, can be modeled as plug flow reactors (PFRs). Some guts, such as that found in many insects (Terra, 1990), can be

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modeled as a CSTR (the crop) coupled in series to a PFR (the midgut). The flow-through properties and reactions of a CSTR lead to a system of ordinary differential equations for the chemical species, which in turn become algebraic relations in the steady state; the latter have been the basis of many studies in the biological literature. PFRs, on the other hand, lead to coupled systems of reaction–advection equations, which are partial differential equations for the chemical species involved; in steady state they reduce to a system of ordinary differential equations.

There are several cases where analytic solutions are not available in the existing literature, and providing these is one of the goals of this paper. Our aim is to show how PFR theory can be applied to investigate simultaneous reaction and absorption, morphological differences in the gut, location-dependent reaction and absorption, and external thermal influences, and we derive analytic solutions to the resulting reaction–advection equations that describe these processes. These model solutions can motivate further experimental work on digestive processes and parameter identification, and they can benchmark numerical algorithms on systems of reaction–advection equations. Further, we find the flow rate in a PFR that maximizes the rate of absorption for simple substrate–enzyme–nutrient kinetics, and derive an analytic solution. Our discussion focuses on the PFR model and ignores the presence of other portions of the digestive tract, for example, the crop or hindgut, which can be modeled as BRs or CSTRs. These contributions provide a rigorous analytical framework to focus much needed efforts on the role of digestion in the general problem of foraging.

The original application of reactor theory to digestion, based on the principles of chemical engineering reactor design, can be found in Penry & Jumars (1986, 1987). Much research has been done on this subject, particularly with regard to analysing and comparing the performance of different types of reactor models for various organisms and determining which reactor provides the best model for a particular digestive strategy. (For example, see Dade *et al.*, 1990, or Martínez del Río & Karasov, 1990.) We refer to Jumars (2000a, b) for additional references.

2. The Reaction–Advection Equation

In a PFR, or tubular reactor, digesta moves in the axial direction through a tube where reaction and absorption occur as it proceeds; it is perfectly mixed at each instant and concentrations are assumed not to vary in the radial direction, i.e. in each cross-section. Axial mixing along a tubular gut is known in some situations, particularly with regard to particulate vs. fluid fractions (Levey & Martínez del Río, 1999; Caton *et al.*, 2000). In insect guts, a wide range of countercurrent paths direct digestive enzymes from the posterior toward the anterior portion of the midgut, spatially compartmentalized by the peritrophic membrane (Terra, 1990). However, in our simple model we assume that mixing in the axial direction is negligible, and we ignore diffusion in the axial direction.

Foods eaten by an organism are complex nutritional combinations of carbohydrates, proteins and lipids. During digestion, resulting products from the same food item may result in constituent components with different reactive and absorptive kinetics (Karasov & Diamond, 1983; Johnson & Felton, 1996; Caton *et al.*, 2000; Harrison, 2001), and the primary sites of reactions and absorption may occur in different parts of the gut (Chapman, 1985a, b; Turunen, 1985; Terra, 1990). Moreover, transport of final digestion products across gut membranes relies on several factors, including the number and nature of transporter sites varying in response to species, feeding habits, temperature, and recent diet quality (Karasov & Diamond, 1983, 1988; Karasov & Cork, 1994; Ferraris & Diamond, 1997; Karasov & Hume, 1997; Wright & Ahearn, 1997; Karasov & Pinshow, 2000). These issues are important because kinetic responses in digestion are ultimately determined by specific reaction and transport dynamics.

Many organisms have tubular guts, and PFR models approximate a variety of known digestive systems (Karasov & Hume, 1997). For example, the basic grasshopper gut is a simple compartmented tube in which different digestive functions occur. While typically divided into three main regions (crop, midgut and hindgut), each with important functions, the main digestive reactions and absorption occur in the

midgut, which can be modeled as a plug flow reactor. Digestive enzymes are released and products of digestion are absorbed into the haemolymph in this region. Similarly, guts of vertebrates such as insectivorous and frugivorous birds are generally characterized by modified plug flow reactor models with mixed success (Karasov & Hume, 1997).

In the simplest model a single substance, substrate, nutrient, or any limiting quantity such as energy, enters the gut and is consumed by chemical reaction, or by direct absorption. Such mechanisms associated with direct consumption and absorption of hexoses are known for nectarivorous and frugivorous birds, for example (Karasov *et al.*, 1986; Dade *et al.*, 1990; Levey & Duke, 1992; Karasov & Cork, 1994). For example, in a PFR-intestine the digestion of a monosaccharide such as glucose can be modeled as the rate at which the monosaccharide is absorbed.

We model a tubular gut as a plug flow reactor (PFR) of length L and cross-sectional area $A(x)$, $0 < x < L$ (Fig. 1). Let $n = n(x, t)$ denote the concentration of a substance, e.g. a nutrient, in the gut measured in moles per unit volume, and let $J = J(x, t)$ denote the nutrient flux, that is, the number of moles per unit area per unit time traversing the cross-section at x at time t . Finally, let $r = r(x, t)$ denote the local rate per unit volume that the nutrient is consumed by reaction or absorption at x at time t . The flux and the consumption rate may depend on x and t explicitly, or through their dependence on the nutrient concentration n itself, or its gradient. In the general case $J(x, t) = J(x, t, n, \partial n / \partial x)$ and $r(x, t) = r(x, t, n)$. These dependencies are expressed in terms of constitutive relations, which are in turn empirically based. As noted above, the nutrient in this discussion could be an

elemental concentration like nitrogen, carbon, or phosphorous, or it could be a substrate concentration containing some other nutrient.

In a small section (Fig. 1) of the gut between $x = a$ and b we can balance the number of moles and obtain a partial differential equation relating n , J , and r , and the cross-sectional area $A(x)$. Mass balance dictates that the time rate of change of the total mass of the nutrient in the section must equal the rate that it flows in at $x = a$, minus the rate that it flows out at $x = b$, minus the rate that it is consumed by reaction or by absorption:

$$\begin{aligned} \frac{\partial}{\partial t} \int_a^b A(x)n(x, t) dx &= J(a, t)A(a) \\ &- J(b, t)A(b) - \int_a^b r(x, t, n)A(x) dx. \end{aligned}$$

This integral form of the conservation law holds even when the various quantities are piecewise smooth with discontinuities. If the functions are continuously differentiable, then the time derivative may be pulled inside the integral on the left and the fundamental theorem of calculus can be applied to rewrite the flux difference as an integral (e.g. Logan, 1997):

$$\begin{aligned} \int_a^b A(x) \frac{\partial}{\partial t} n(x, t) dx &= - \int_a^b \frac{\partial}{\partial x} (J(x, t)A(x)) dx \\ &- \int_a^b r(x, t)A(x) dx. \end{aligned}$$

The arbitrariness of the section allows us to remove the integrals and we get

$$\frac{\partial n}{\partial t} = - \frac{1}{A(x)} \frac{\partial}{\partial x} (A(x)J) - r, \quad (1)$$

which is the local form of the mass balance law. This partial differential equation relates temporal changes in the nutrient concentration to spatial changes in the flux and to the consumption rate. Consistent with the one-dimensional assumption, it is assumed that the area does not vary significantly over the length of the gut. If the area is a constant A_0 , that is, $A(x) = A_0$, then it cancels out:

$$\frac{\partial n}{\partial t} = - \frac{\partial J}{\partial x} - r. \quad (2)$$

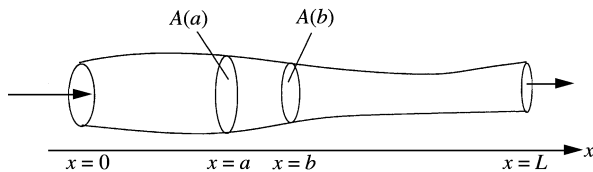


FIG. 1. A tubular gut of length L modeled as a plug flow reactor. $A(x)$ is the variable cross-sectional area; $x = 0$ represents the inlet (mouth). The nutrient concentration does not vary radially. Shown in the figure is an arbitrary section of the gut over which mass is balanced.

This single balance law, eqn (1) or (2), contains three unknown quantities (n , J , and r), and therefore two additional assumptions are required: specifying the form of the flux J and the form of the consumption rate r . We assume that there is a single mechanism that contributes to the flux, namely the bulk movement of the nutrient through the gut at constant speed v . This speed is called the gut speed, digestion speed, or through-flow. Thus, we postulate the constitutive relation

$$J = vn, \quad (3)$$

which is merely a statement that the flux equals the flow rate times the concentration. We are ignoring a diffusive contribution to the flux in this model because diffusion occurs on a much longer time-scale than the bulk movement of the nutrient. In case (1) where the cross-sectional area varies, the hypothesis (3) is inconsistent for constant v ; we examine this case further in Section 5.

The consumption rate r is the uptake rate via chemical reaction or adsorption. If uptake through absorption or digestion is localized in one portion of the gut, r could depend on the location x . Or, it could depend on time, t , explicitly through a known, *external* temperature dependence.

When reactions and absorption are involved, then r depends on the nutrient concentration n through the kinetics of the reaction. For example,

$$r = kn \text{ (first-order kinetics),} \quad (4)$$

where k is the rate constant, or

$$r = \frac{k_1 n}{n + k_2} \text{ (Michaelis–Menten kinetics),} \quad (5)$$

where k_1 and k_2 are positive constants. The constant k_1 is the maximal rate of absorption/reaction at saturation, and k_2 is the half-saturation. Another model is

$$r = \frac{k_1 n^2}{n^2 + k_2} \text{ (sigmoid kinetics).}$$

First-order kinetics model facilitated uptake, e.g. direct passage across the gut wall. Michaelis–Menten, or hyperbolic kinetics, model processes

in animals with rapid uptake systems and that feed on simple substrates (monosaccharides), or that have carrier-mediated processes where reaction occurs at sites on the gut wall before absorption takes place. Sigmoid kinetics, where the uptake is slow initially, followed by a rapid increase, is characteristic of animals that absorb or digest more complex materials, perhaps through several reactions in parallel (Edelstein-Keshet, 1988; Murray, 1994). Note that the rate constants could depend on x and t ; for example, the rate of adsorption or reaction could depend on the location in the gut. Even when it varies, we shall still use the term “rate constant”.

When eqn (3) is substituted, the balance law (2) is

$$\frac{\partial n}{\partial t} = -v \frac{\partial n}{\partial x} - r(x, t, n), \quad (6)$$

which is the reaction–advection equation, the governing equation for the transport (advection) and reaction of the quantity n in the gut. For the present we do not specify the actual form of r .

A well-posed mathematical, and physical, problem requires specifying an initial concentration $n_0(x)$ of the nutrient in the gut at time $t = 0$ and a boundary condition at $x = 0$ that gives the concentration of the nutrient $n_b(t)$ at the entry point. For example, $n_b(t)$ could be the nutrient concentration at the mouth or at the entry point from the crop. These conditions are

$$n(x, 0) = n_0(x), \quad 0 < x < L, \quad (7)$$

$$n(0, t) = n_b(t), \quad t > 0. \quad (8)$$

Therefore, the nutrient density n is determined by solving the problem defined by the partial differential equation (6), supplemented by the auxiliary conditions (7) and (8). Because the flux is vn , a flux boundary condition at $x = 0$, namely $vn(0, t) = g(t)$, is tantamount to eqn (8). In order to have a well-posed mathematical problem, we may not specify concentrations at the outlet, or right boundary $x = L$.

3. First-order Kinetics

We first consider first-order kinetics (4) where the rate constant depends on time and location,

and the rate is linear in concentration. In many cases the morphology and absorptive properties of the digestive tract are not constant, and the rate of digestion, both enzyme activity and absorption, is localized in one or more sections. Variation in digestive function in the axial direction can be treated in two ways. A common chemical engineering device is to consider the inhomogeneous PFR reactor as a series of coupled CSTRs, each differing in its reaction and absorption capabilities as defined by the reaction kinetics and the rate constants. This discrete model leads to a system of ordinary differential equations for the concentrations in each CSTR, as each CSTR feeds the next, and so on. In steady state, the system reduces to a system of algebraic equations for the steady concentrations (Jumars, 2000b). Another way to treat variation over the length of the gut in a continuous manner is to permit the reaction rate r to depend on the location x , which is the approach that we adopt. The time dependence can come from external temperature conditions, again affecting the magnitude of the rate constant. This kind of external temperature dependence is different from the case of endothermic and exothermic reaction kinetics; the latter would require energy balances and the consideration of heat flow.

Thus, we consider the equation

$$\frac{\partial n}{\partial t} = -v \frac{\partial n}{\partial x} - k(x, t)n, \quad (9)$$

subject to the conditions (7) and (8). A special case is $k(x, t) = k = \text{constant}$. The standard method for solving reaction–advection equations is the *method of characteristics* (Taubes, 2001; Logan, 2001). We replace x by a new “moving” spatial coordinate y that advects with speed v . This transformation turns the partial differential equation into an integrable, ordinary differential equation whose solution, in principle, can be found. To this end, define the change of variables

$$y = x - vt, \quad \tau = t. \quad (10)$$

Then the chain rule in calculus relates the partial derivatives of n with respect to x and t to

partials with respect to y and τ :

$$\frac{\partial n}{\partial t} = \frac{\partial n}{\partial \tau} - v \frac{\partial n}{\partial y}, \quad \frac{\partial n}{\partial x} = \frac{\partial n}{\partial y}.$$

There should be no confusion in adhering to the common convention of using the same symbol n to denote both a function of x and t and of the transformed variables y and τ . Consequently, eqn (9) becomes

$$\frac{\partial n}{\partial \tau} = -k(y + v\tau, \tau)n,$$

where $n = n(y, \tau)$. Separating variables and integrating gives

$$\ln n = - \int_0^\tau k(y + vs, s) ds + C_1(y),$$

where $C_1(y)$ is an arbitrary function. Therefore,

$$\begin{aligned} n(x, t) &= C(y) e^{- \int_0^\tau k(y + vs, s) ds} \\ &= C(x - vt) e^{- \int_0^\tau k(x - vt + vs, s) ds}, \end{aligned}$$

which is the general solution of the reaction–advection equation (9). Here $C = e^{C_1}$ is an arbitrary function of a single argument.

To determine the function C we must divide the problem into two regions: the region $x > vt$, which is ahead of the leading signal $x = vt$, and the region $0 < x < vt$, which is behind the leading signal. The initial condition affects the region $x > vt$ and the boundary condition affects the region $x < vt$. The leading signal is the position $x = vt$ of an initial bolus of food eaten at $t = 0$ in the gut (Fig. 2). In the region $x > vt$, we apply the initial condition (7) to get

$$n(x, 0) = n_0(x) = C(x).$$

Therefore, ahead of the leading signal the solution is

$$n = n_0(x - vt) e^{- \int_0^t k(x - vt + vs, s) ds}, \quad \text{when } x > vt. \quad (11)$$

In the region $x < vt$ we write the general solution as

$$n(x, t) = C(t - x/v) e^{- \int_0^t k(x - vt + vs, s) ds},$$

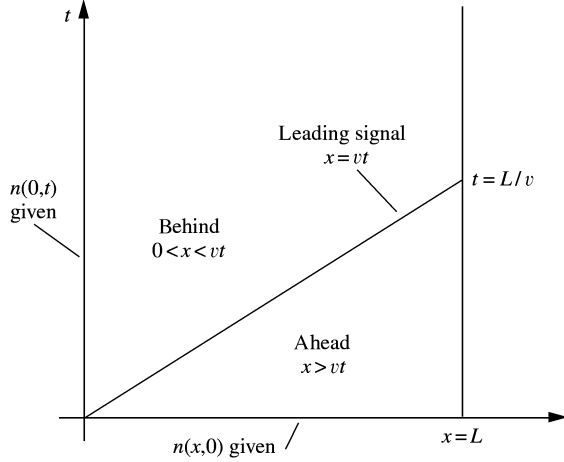


FIG. 2. The xt -space, or spacetime, diagram, showing the leading signal, the regions ahead and behind, and the initial and boundary conditions. The leading signal shows the position of an initial bite as it passes through the gut.

where we have represented the arbitrary function C as a function of $t - x/v$ rather than $x - vt$, which is equivalent. Then, applying the boundary condition (8), we obtain

$$n(0, t) = n_b(t) = C(t)e^{-\int_0^t k(-vt+vs, s) ds},$$

which determines C . Substituting back into the general solution and simplifying gives

$$n(x, t) = n_b(t - x/v)e^{-\int_{t-x/v}^t k(x-vt+vs, s) ds}, \quad (12)$$

when $x < vt$.

In summary, eqns (11) and (12) give analytic formulas for the solution to the partial differential equation (9) subject to eqns (7) and (8). If $n_b(0) \neq n_0(0)$, then the solution is discontinuous along the line $x = vt$. Here, the function $k(x, t)$ is a user-supplied function that specifies how the reaction rate depends on time and location in the gut.

Example 1 (Constant k). In the special case that $k(x, t) = k = \text{constant}$, formulas (11) and (12) simplify to

$$n(x, t) = \begin{cases} n_b(t - x/v)e^{-kx/v}, & x < vt, \\ n_0(x - v/t)e^{-kt}, & x > vt. \end{cases} \quad (13)$$

Thus, the initial nutrient in the gut moves through at constant speed v , decaying at rate k as

it goes. Nutrients entering the mouth advect through at constant speed v , decaying along the length of the gut with spatial decay rate k/v . At any time t , the total amount of nutrient $N(t)$ in the gut is the integral

$$\begin{aligned} N(t) &= A_0 \int_0^L n(x, t) dx \\ &= A_0 \int_0^{vt} n_b(t - x/v)e^{-kx/v} dx + A_0 e^{-kt} \\ &\quad + \int_{vt}^L n_0(x - vt) dx \end{aligned}$$

where $vt < L$. For the general problem (7)–(9) the rate of uptake at any time t is defined by

$$U(t) = A_0 \int_0^L k(x, t)n(x, t) dx,$$

and the total uptake over a time interval $0 \leq t \leq T$ is the integral of the uptake rate, or

$$\text{Total uptake} = A_0 \int_0^T \int_0^L k(x, t)n(x, t) dx dt.$$

To illustrate how time dependence can enter the problem through the reaction rate, consider the case of a grasshopper that feeds during the day. Foraging will occur only over certain temperature ranges (Yang & Joern, 1994a, b). To model the effects of variable temperature on digestion, we could postulate first-order kinetics (uptake) with a piecewise, 24-hr, periodic rate constant of the form

$$k = k(t) = \begin{cases} k_0 + a \sin \omega t, & 0 < t < 12, \\ k_0 & 12 < t < 24, \end{cases}$$

where $\omega = \pi/12$. Here, time $t = 0$ corresponds to the time when feeding begins. Thus, the rate of uptake increases during time of feeding and then drops off to a constant, ambient level. If the gut is initially empty we have $n_0(x) = 0$; the food intake caused by foraging defines the boundary concentration $n_b(t)$. In this case the reaction–advection equation for the concentration is

$$\frac{\partial n}{\partial t} = -v \frac{\partial n}{\partial x} - k(t)n,$$

and a closed-form solution can be obtained as above. We emphasize that this model is only speculative, but it illustrates how time dependence can enter the rate constant through temperature-dependent absorption rates and feeding habits. Analytic solutions to these types of problems, coupled with appropriate experiments, can lead to a better understanding of external temperature effects on digestion.

4. Nonlinear Reaction Rates

Analysis of reaction–advection equations does not change substantially when the reaction rate is $r = k(x, t)R(n)$, where R is a given nonlinear function of the nutrient concentration n (like Michaelis–Menten or sigmoid). The difference is that integrals of functions of n appear, which may not be resolvable in analytic form. We consider the reaction–advection equation

$$\frac{\partial n}{\partial t} = -v \frac{\partial n}{\partial x} - k(t)R(n),$$

where, for simplicity, we have taken the rate constant to be dependent only on t . Spatial dependence can be easily accommodated as in the last section. We also assume that the gut is empty initially, that is, $n(x, 0) = n_0(x) = 0$. Then, clearly, $n(x, t) = 0$ for the entire region $x > vt$ ahead of the leading signal. Non-zero initial conditions can also be treated simply as in the last section. To determine the solution behind the leading signal, in $0 < x < vt$, we use the same change of variables to characteristic coordinates τ and y . We obtain, after simplification,

$$\frac{1}{R(n)} \frac{\partial n}{\partial \tau} = -k(\tau),$$

where $n = n(y, \tau)$. Therefore,

$$\begin{aligned} \int_{n(x, t_0)}^{n(x, t)} \frac{dw}{R(w)} &= \tilde{C}(x - vt) - \int_{t_0}^t k(s) ds \\ &= C(t - x/v) - \int_{t_0}^t k(s) ds, \end{aligned}$$

where C is an arbitrary function and t_0 is any constant. Setting $x = 0$ gives

$$\int_{n_b(t_0)}^{n_b(t)} \frac{dw}{R(w)} = C(t) - \int_{t_0}^t k(s) ds,$$

which determines C . Therefore

$$\begin{aligned} \int_{n(x, t_0)}^{n(x, t)} \frac{dw}{R(w)} &= \int_{n_b(t_0)}^{n_b(t-x/v)} \frac{dw}{R(w)} \\ &\quad + \int_{t_0}^{t-x/v} k(s) ds - \int_{t_0}^t k(s) ds, \end{aligned}$$

which, after combining integrals, yields

$$\int_{n_b(t-x/v)}^{n(x, t)} \frac{dw}{R(w)} = - \int_{t-x/v}^t k(s) ds, \quad 0 < x < vt. \quad (14)$$

Equation (14) defines the solution implicitly. In principle, the left-hand side can be integrated and then solved to determine the nutrient concentration $n(x, t)$ explicitly.

Example 2 (*Michaelis–Menten kinetics*). When

$$R(n) = \frac{k_1 n}{n + k_2}$$

the integral on the left-hand side of eqn (14) becomes

$$\int \frac{w + k_2}{k_1 w} dw = \frac{1}{k_1} w + \frac{k_2}{k_1} \ln w.$$

Therefore, the nutrient concentration in $0 < x < vt$ is given implicitly by

$$\begin{aligned} n + k_2 \ln n &= n_b(t - x/v) + k_2 \ln(n_b(t - x/v)) \\ &\quad - k_1 \int_{t-x/v}^t k(s) ds. \end{aligned} \quad (15)$$

For each value of x and t the right-hand side is a numerical value and we are left with a nonlinear algebraic relation for the nutrient concentration $n = n(x, t)$. This nonlinear equation for n will have a unique solution (which must be determined numerically) since the left-hand side of eqn (15) is a strictly increasing function of n with range $(-\infty, \infty)$.

Example 3 (Sigmoid kinetics). *For sigmoid kinetics* or

$$R(n) = \frac{k_1 n^2}{n^2 + k_2}.$$

Then eqn (14) gives

$$\int \frac{dw}{R(w)} = \int \frac{w^2 + k_2}{k_1 w^2} dw = \frac{1}{k_1} w - \frac{k_2}{k_1 w}.$$

Therefore,

$$\begin{aligned} \frac{1}{k_1} n - \frac{k_2}{k_1 n} &= \frac{1}{k_1} n_b(t - x/v) - \frac{k_2}{k_1 n_b(t - x/v)} \\ &\quad - \int_{t-x/v}^t k(s) ds, \quad 0 < x < vt. \end{aligned}$$

This equation can be written as a quadratic equation for n , namely

$$\begin{aligned} n^2 - \left(n_b(t - x/v) - \frac{k_2}{n_b(t - x/v)} - k_1 \int_{t-x/v}^t k(s) ds \right) \\ \times n - k_2 = 0, \quad 0 < x < vt. \end{aligned}$$

Because the discriminant is positive for each x and t , it is clear that there is a unique, positive solution $n = n(x, t)$, provided n_b is a positive function. In the case of sigmoid kinetics, therefore, an explicit formula for the nutrient concentration can be determined.

5. Variable Area

If the cross-sectional area of the gut varies, it is inconsistent to assume a constant velocity v in the constitutive relation (3) for the nutrient flux. We must consider the mass balance of the digesta itself. To this end, let ρ be the constant density of the digesta and let $v = v(x)$ be the flow velocity. Here we are assuming that v depends only on x and not on t . Then the total mass in a section from x to $x + dx$ is $\rho A(x) dx$, which is constant in time. So the rate that mass enters this section at x must equal the rate that mass leaves at $x + dx$. That is, $\rho v(x) A(x) = \rho v(x + dx) A(x + dx)$. In other words,

$$\frac{\partial}{\partial x} (A(x)v(x)) = 0,$$

$$A(x)v(x) = A(0)v(0) \equiv a.$$

Therefore, there is a relation between the cross-sectional area and the velocity; the input velocity $v(0)$ must be specified. As the area of the gut constricts, the velocity must increase, and as it expands, the velocity must decrease. These conclusions are based on the assumption of constant density of the digesta. Therefore the flux is

$$J(x, t) = v(x)n,$$

and the mass balance eqn (1) for variable gut morphology simplifies to

$$\frac{\partial n}{\partial t} = -v(x) \frac{\partial n}{\partial x} - r, \quad v(x) = \frac{a}{A(x)}. \quad (16)$$

We now postulate an uptake rate of the form $r = k(x, t)R(n)$, and we append the auxiliary conditions

$$n(0, t) = n_b(t), \quad n(x, 0) = 0.$$

Again, a transformation to different coordinates can reduce eqn (16) to a simple equation that can be integrated directly. Let

$$\tau = t, \quad y = t - \int_0^x v(s)^{-1} ds.$$

Because $A(x)$, and hence $v(x)$, is positive, y is a decreasing function of x . Therefore, the transformation can be inverted to find $t = \tau$, $x = h(y, \tau)$. Then eqn (16) becomes

$$\frac{\partial n}{\partial \tau} = -k(h(y, \tau))R(n),$$

which separates and integrates into the general solution, given implicitly by

$$\int \frac{dn}{R(n)} = - \int k(h(y, \tau)) d\tau + C(y), \quad (17)$$

where C is an arbitrary function. Therefore, the problem is reduced to inversions and quadratures. As before, the arbitrary function is determined by the given concentration at $x = 0$.

Example 4. For first-order kinetics, $r = kn$ with k constant, eqn (17) becomes

$$\ln n = -kt + C(y),$$

which gives

$$n(x, t) = C(t - \int_0^x v(s)^{-1} ds) e^{-kt}.$$

Along $x = 0$ we get $C(t) = e^{kt} n_b(t)$. Therefore, behind the leading signal, the solution to $n_t = -v(x)u_x - ku$ is

$$n(x, t) = n_b(t - \int_0^x v(s)^{-1} ds) \exp(-k \int_0^x v(s)^{-1} ds),$$

$$0 < t < v(x),$$

where $\exp(x) = e^x$ is the exponential function. This solution allows the possibility of modeling animal guts where reaction or absorption is localized in some particular section or sections. Solutions in the case of other reaction-absorption rates can be obtained similarly.

6. Multiple Chemical Species

As substrate, or food, moves through the digestive tract, enzymatic action breaks down the substrate into products. In general, it may be desirable to keep track of both the substrate concentration and the concentrations of all reactants and products. If there are N substances $n_1, \dots, n_N$ (enzymes, substrates, products, and so on), then each has an associated flux $J_1, \dots, J_N$, and the reactions $r_1, \dots, r_N$ may depend upon all the constituent concentrations. Then each species will satisfy mass balance and we obtain N coupled, reaction-advection equations of the form

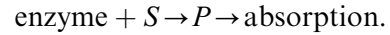
$$\begin{aligned} \frac{\partial n_1}{\partial t} &= -v \frac{\partial n_1}{\partial x} - r_1(x, t, n_1, \dots, n_N), \\ &\dots \\ \frac{\partial n_N}{\partial t} &= -v \frac{\partial n_N}{\partial x} - r_N(x, t, n_1, \dots, n_N). \end{aligned}$$

Initial conditions at $t = 0$ and boundary conditions at $x = 0$ must be imposed on each constituent. These equations can be modified appropriately if the area of the gut is variable.

6.1. ENZYME-SUBSTRATE KINETICS

We take up the case of substrate-enzyme kinetics where a third chemical species, a nutrient, is created and absorbed through the gut wall. For example, sucrose is not transported directly across the intestinal wall, but first has to be hydrolysed into its monosaccharide components, glucose and fructose; the enzyme sucrase, which is bound to the intestinal wall, is responsible for the sucrose hydrolysis.

We consider the specific model problem of an enzyme breaking down a substrate S , forming a product P , which is then absorbed through the intestinal wall. Symbolically,



We assume that the enzyme is abundant (non-limiting) and therefore has constant concentration (Karasov & Hume, 1997). For example, the enzyme could be sucrase and S could be sucrose; the products are glucose and fructose, which have collapsed together in P , a class called hexoses. Let us use the notation $n_1 = s$ and $n_2 = p$ for the concentrations of S and P . We assume first-order kinetics for both the breakdown and the absorption; that is,

$$-r_1 = -ks, \quad -r_2 = ks - ap,$$

where k and a are the rate constants. If the gut has non-uniform digestive properties, we infer that $a > k$ because we expect substrate breakdown to be slower than absorption; the best strategy is to absorb the nutrient products quickly, as they are produced, rather than have them advect down the gut away from absorption sites. If the gut is uniform, we still make this assumption. The assumption of first-order kinetics may be only an approximation. Sucrose hydrolysis generally follows Michaelis-Menten kinetics [eqn (5)], like many enzyme reactions. The kinetics of intestinal uptake, or absorption, are not well-documented, especially for fructose. For a carrier-mediated process the kinetics of absorption are usually modeled by Michaelis-Menten kinetics, while facilitated transport across the gut wall is usually assumed to be first order. In the case of first-order kinetics the reaction-advection

system becomes

$$\frac{\partial s}{\partial t} = -v \frac{\partial s}{\partial x} - ks, \quad (18)$$

$$\frac{\partial p}{\partial t} = -v \frac{\partial p}{\partial x} + ks - ap. \quad (19)$$

We assume initial starvation

$$s(x, 0) = p(x, 0) = 0 \quad (20)$$

and boundary conditions

$$s(0, t) = s_b(t), \quad p(0, t) = 0. \quad (21)$$

In this specific case the solution can be found analytically, whereas in the case of Michaelis–Menten kinetics the solution cannot be determined analytically. From eqn (13) the solution to eqn (18) is

$$s(x, t) = s_b(t - x/v)e^{-kx/v}, \quad 0 < x < vt. \quad (22)$$

Substituting into eqn (19) and using the method of characteristics, we then obtain a formula for the product concentration,

$$p(x, t) = \frac{k}{a - k} s_b(t - x/v) [e^{-kx/v} - e^{-ax/v}], \quad (23)$$

$$0 < x < vt.$$

Clearly, ahead of the leading signal $x = vt$ we have $s = p = 0$. The time-dependent absorption rate is

$$B(t) = A \int_0^L a p(x, t) dx$$

$$= \frac{kaA}{a - k} \int_0^{vt} s_b(t - x/v) [e^{-kx/v} - e^{-ax/v}] dx,$$

$$vt \leq L,$$

and the total absorption over a time interval $0 \leq t \leq T$ is $\int_0^T B(t) dt$. Observe that both these absorption quantities depend on the through flow rate v , the rate constants, the gut length, and the cross-sectional area. A question of interest, and answered by others in the context of batch and CSTRs, is to determine the maximum absorption rate as a function of the

flow rate v . The rationale is that an organism will move food through the gut at a speed that will maximize its rate of nutrient absorption. To determine the maximum absorption rate in a PFR we analyse the steady solution.

6.2. STEADY-STATE SOLUTIONS

One way to calculate the absorption rate easily is under equilibrium conditions. After a long time, if the boundary input concentration is constant ($s_b(t) = s_b$), the system reaches a steady state given by [see eqns (22) and (23)]

$$s(x) = s_b e^{-kx/v},$$

$$p(x) = \frac{k}{a - k} s_b [e^{-kx/v} - e^{-ax/v}].$$

The substrate concentration s decays exponentially from its value s_b at the inlet, while the product concentration p attains a maximum at $x_m = v(a - k)^{-1} \ln(a/k)$, and then decays. It is easy to see that the maximum value of the product concentration $p(x_m)$ depends only on the rate constants k and a , and upon the input s_b , but not on the speed of digestion v . It seems clear that an organism will adopt a strategy to have this maximum occur inside the gut, that is, so that $x_m \leq L$. This constraint on the gut speed v in terms of the rate constants and gut length is

$$v \leq \frac{(a - k)L}{\ln a - \ln k}.$$

Otherwise, digesta will move through the gut too fast, allowing little absorption. The absorption rate at steady state is

$$B = A \int_0^L a p(x) dx$$

$$= \frac{s_b A}{a - k} v (a - a e^{-kL/v} - k + k e^{-aL/v}). \quad (24)$$

Regarded as a function of the digestion speed v , i.e. $B = B(v)$, with a, k, A , and s_b fixed, B has a maximum value B_m at the speed $v = v_m$ for which $B'(v_m) = 0$, or

$$k \left(1 + \frac{aL}{v_m} \right) e^{-aL/v_m} - a \left(1 + \frac{kL}{v_m} \right) e^{-kL/v_m} = k - a.$$

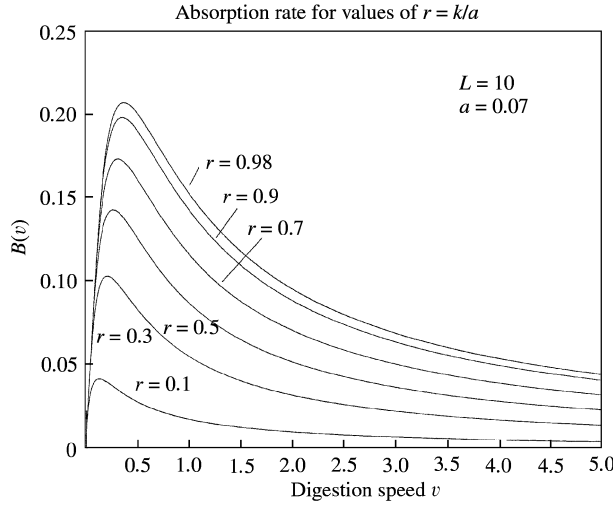


FIG. 3. Graphs of the absorption rate $B(v)$ (mol min⁻¹) in formula (24) for different ratios r of the rate constants k/a . Here $L = 10$ cm and $a = 0.07$ min⁻¹. The gut speed v is given in cm min⁻¹.

This transcendental algebraic equation for optimal digestion speed v_m can be solved numerically.

For illustrative purposes we consider a numerical example (Fig. 3). The value of a corresponds to data for a fructivore (see Martínez del Río *et al.*, 1990).

The gut length is $L = 10$ cm. The maximum gut speed B_m and the optimal speed v_m are determined by the local maximum on each curve. Observe that the optimal gut speed v_m increases as the ratio r of the rate constants increases, i.e. as the rate of enzyme breakdown to the rate of absorption increases. These values of v_m lead to residence or throughflow times from 25 to 100 min. The values of $x_m = v_m(a - k)^{-1} \ln(a/k)$, where the maximum product concentration occurs in the gut, for various ratios r , are near 4 cm, well inside the gut.

It is difficult to compare these results to the results of other investigators because eqn (24) is an integrated value, and the values for the optimal throughflow are not known analytically. For a CSTR operating at steady state, Jumar (2000a, b) reports the formula $v_{opt} = a\sqrt{k/aG} = a\sqrt{k/aLA}$ for the optimal throughflow, where we have taken his reactor volume G to be the volume AL of the cylindrical gut in the present model. With $L = 10$ cm, $a = 0.07$ min⁻¹ and $r = k/a = 0.7$, this equation gives an optimum of

$v_{opt} = 0.59 A$, where A is the cross-sectional area. The corresponding value of the maximum gut speed, from Fig. 3, is $v_m = 0.17$ cm min⁻¹. Using this value as v_{opt} in the expression above leads to a cross-sectional area of about 0.28 cm², which is reasonable. Of course, the longer the gut length L , the greater difference between the PFR and the steady-state CSTR, and comparisons cannot be made.

6.3. SPATIALLY DEPENDENT RATES

For completeness, we give expressions for the solution s and p in the case that the rate constants are dependent on location in the digestive tract. Time dependence can be treated similarly. If the rate constants a and k have spatial dependence, i.e. $a = a(x)$ and $k = k(x)$, then the substrate-product equations, with first-order kinetics, become

$$\frac{\partial s}{\partial t} = -v \frac{\partial s}{\partial x} - k(x)s, \quad (25)$$

$$\frac{\partial p}{\partial t} = -v \frac{\partial p}{\partial x} + k(x)s - a(x)p. \quad (26)$$

Initial and boundary conditions are given by eqns (20) and (21). The first equation gives, as in Section 3, eqn (12),

$$s(x, t) = s_b(t - x/v)e^{-\int_{t-x/v}^t k(x-vt+vr) dr}, \quad (27)$$

$$0 < x < vt.$$

We can substitute this result into eqn (26), which gives a non-homogeneous partial differential equation for p . The method of characteristics can be used to solve this equation, but we omit the rather tedious calculation. We obtain

$$p(x, t) = \int_{t-x/v}^t F(x - vt + vr, r)e^{-\int_r^t a(x-vt+vz) dz} dr, \quad (28)$$

$$0 < x < vt,$$

where $F(x, t) \equiv k(x)s(x, t)$. In summary, the solution to eqns (25) and (26) with auxiliary conditions (20) and (21), is given by the formulas (27) and (28). These equations can be used to

compute absorption rates in the case of varying absorption and reaction kinetics through the gut.

7. Summary and Conclusions

Understanding digestion from a whole-animal perspective requires an integrative framework that builds on the extensive, detailed understanding of individual digestive and absorptive processes that are well studied. Cascades of loosely coordinated biochemical reactions break complex molecules into simple molecules that can be transported across the gut wall for metabolic use. Moreover, none of these processes is likely static, each varying with food composition and quality or rates of food intake, or physiological condition (Yang & Joern, 1994a,b; Karasov & Hume, 1997; Whelen, 2002; Whelen *et al.*, 2001). General interest in simplifying this problem at the whole-organism level exists, a goal facilitated by modeling the problem, using insights from optimality theory and chemical reactor theory (Sibly, 1981; Penry & Jumars, 1986, 1987; Karasov & Hume, 1997).

Without doubt, many different digestive approaches exist among animal consumers, reflecting the phylogenetic and ecological diversity of these species. Each species differs to some degree with regard to specific biochemical, physiological and nutritional details of the digestive process (Applebaum, 1985; Chapman, 1985b; Slansky & Scriber, 1985; Wright & Ahearn, 1997; Afik *et al.*, 1997), each influenced by diet selection. However, many strong reasons also exist to look for similarities in digestive processes, with the goal of abstracting general processes to facilitate the development of a general theory of digestion that links directly to both foraging theory (Bernays, 1985; Stephens & Krebs, 1986) as well as to the ultimate allocation of resources (dynamic energy budgets, Kooijman, 2000).

The principal use of plug flow reactor models for digestive processes is to encapsulate complex phenomena in a simple set of model equations that mirror the actual system. In some cases, we solve these models to provide analytical solutions that make it easy to understand how structural changes in the system might affect the outcome. For example, by varying the input

quantities we can compare different outputs. Analytical solutions are also useful for validating numerical procedures, like finite-difference procedures. Explicit formulas also enable researchers to calculate parameter values in the model using experimental data; at the present time the well-posedness of these parameter identification problems, or inverse problems, are at the forefront of mathematical research. Our results for plug flow reactor models extend those developed by Jumars (2000a, b). Moreover, our interest in understanding arthropod guts is facilitated by including temperature-dependence, which commonly influences insect digestion (Yang & Joern, 1994a, b). The primary issues that these models address are the calculation of retention time, extraction efficiency, and total nutrient gained, each of which is testable under experimental conditions.

Modifications of the models will eventually lead to a clearer theoretical picture of how foraging is interrelated with digestion, what portions of the digestive process most strongly affect nutrient intake, and ultimately how organisms budget the absorbed energy and nutrients obtained from digestion. Perhaps most profoundly, it is time to link foraging with digestion so that critical limiting feedbacks between these processes can be properly appreciated.

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