On the hyperbolic functional response in DEB theory

J.A. Ferreira
Department of Theoretical Biology
Faculty of Earth and Life Sciences
de Boelelaan 1085, 1081 HV Amsterdam, The Netherlands
http://www.bio.vu.nl/vakgroepen/thb/

1 Introduction

In the context of DEB theory, the feeding rate of an organism as a function of *food density* X is usually given in $C-$moles per surface area or volume by

$$\dot{J}_X = f_{\dot{J}_{Xm},X_K}(X), \tag{1.1}$$

where for each $\alpha, \beta > 0$

$$f_{\alpha,\beta}(x) = \frac{\alpha x}{x+\beta}, \quad x \geq 0, \tag{1.2}$$

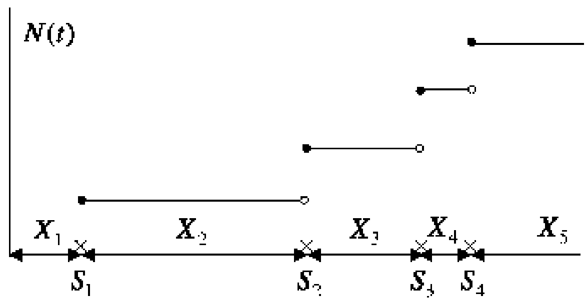
and $\dot{J}_{Xm}$ and X_K are constants (respectively the maximum ingestion rate and the saturation coefficient); see p. 73 of Kooijman (2000). In connection with biological quantities such as $\dot{J}_X$, a function of X is known as a *functional response*, and the particular class of functions defined by (1.2) is called a *hyperbolic* (or type II, or Holling type II) functional response.

Experimental data shows that the hyperbolic functional response provides a good approximation to a variety of phenomena that conceptually reduce to that of the ingestion of a substrate by an organism; see p. 74, and in particular Figure 3.6, of Kooijman (2000) for examples. The main theoretical explanation for this success is based on a feeding model in which 'meals' appear in time as points of a Poisson process, a meal is accepted by the organism if and only if the organism is not busy 'processing' a previous meal, and the processing times are independent exponential random variables; see p. 74 of Kooijman (2000). This same model, possibly with some variations, is used elsewhere in DEB theory, for instance in specifying the behaviour of Synthesizing Units (SU) and in studying the variability of growth at the population level in terms of feeding behaviour (cf. Kooijman (2000), pp. 43-48 and pp. 221-222); it is a special case of the well-known Type I counter model from renewal theory (eg. Karlin and Taylor (1975)).

In this essay we study very briefly the problem of whether the assumption that the meal arrivals form a renewal process rather than a Poisson process still allows a hyperbolic functional response. This question could be of some interest in connection with the closure property of the class of hyperbolic functional responses with respect to composition.

2 Renewal processes

Let $X_1, X_2, \ldots$ be a sequence of non-negative, independent and identically distributed (i.i.d.) random variables with distribution function (d.f.) F. The *renewal process* associated with this sequence is the sequence of partial sums $S_n = X_1 + \cdots + X_n$, $n \in \mathbb{N}$, and the corresponding *counting renewal process* is the process defined by $N_t = \min\{n \in \mathbb{N} : S_n \leq t\}$ for $t \geq 0$. A renewal process is best visualized as a random sequence of points on a horizontal 'time' axis; relative to an origin specifying the beginning of time, the first point occurs at time S_1, the second at time S_2, and so on, the distances between successive points being X_1, X_2,, etc. To this picture we can add a vertical axis in which the values of N_t are represented as a function of t: since by definition N_t counts the number of points lying in the portion $[0, t]$ of the horizontal axis—the number of points occurring up to and including time t—, we see that the counting renewal function $t \to N_t$ is a right-continuous step function increasing from 0 to ∞ by integer steps at the renewal points $S_1, S_2, \ldots$



Among the various results about renewal processes we need to mention two. Let $\lambda^{-1} := E(X_1)$ and define the *renewal function* by $m(t) = E(N_t)$ $(t \geq 0)$; then under very general conditions

$$\lim_{t\to\infty} \frac{N_t}{t} = \lambda \quad \text{with probability 1,} \quad \text{and} \quad \lim_{t\to\infty} (m(t+h) - m(t)) = \lambda h. \tag{2.1}$$

A Poisson process is a renewal process in which $X_1, X_2, \ldots$ are exponentially distributed random variables, i.e., such that $F(x) = 1 - e^{-x/\lambda}$, $x \geq 0$, for some $\lambda > 0$. In the case of a Poisson process the renewal function is given by $m(t) = \lambda t$, so that the second result in (2.1) can be strengthened to $m(t + h) - m(t) = \lambda h$ for all $t, h \geq 0$.

3 The feeding model in terms of renewal processes

To describe the feeding model in terms of renewal processes let us suppose that $X_1, X_2, \ldots$ represent the intervals between successive arrivals of meals (substrates, nutrients...). Then, with λ as above, the first statement in (2.1) says that with high probability we have, for large t, $N_t/t \approx \lambda$, i.e., that the density of meal arrivals in the interval $[0, t]$ is approximately λ; and the second statement says that, after the organism has been feeding for a while, the expected number of meal arrivals in the interval $(t, t + h]$ is about λh.

It seems reasonable to assume that an organism needs time to process (eat, digest,...) meals, and that while busy processing a meal it may reject arriving meals. Thus let us assume that the sequence of processing times is a sequence of i.i.d. random variables $Y_1, Y_2, \ldots$, independent of $X_1, X_2, \ldots$, with d.f. G and mean $\mu^{-1} := E(Y_1)$. Moreover, let us assume that feeding begins at the origin with the processing of one meal that lasts for Y_1 time units. Then any meal arriving in the interval $(0, Y_1]$ is rejected, and the first meal to be accepted and processed is the first meal that arrives after Y_1, which occurs at time

$$Z_1 = S_{N_{Y_1}+1}.$$

At time Z_1 a new cycle begins: during the Y_2 time units taken to process the first accepted meal, i.e., during the interval $(Z_1, Z_1 + Y_2]$, all arriving meals are rejected, and the second meal to be accepted and processed is the first meal that arrives after $Z_1 + Y_2$, which occurs at time

$$Z_1 + Z_2 = S_{N_{Z_1+Y_2}+1}.$$

The cycle proceeds at time $Z_1 + Z_2$ with the processing of the second accepted meal; in general, the $n-$th accepted meal arrives at time

$$\tilde{S}_n := Z_1 + Z_2 + \cdots + Z_n = S_{N_{Z_1+\ldots+Z_{n-1}+Y_n}+1}, \quad n = 1, 2, \ldots$$

It can be seen that $Z_1, Z_2, \ldots$, the sequence of intervals between *ingested* meals, is also i.i.d., so that *the sequence* $\tilde{S}_1, \tilde{S}_2, \ldots$ *of accepted meals is also a renewal process.*

Writing

$$\frac{1}{\mu_{F,G}} := E\left(S_{N_{Y_1}+1} - Y_1\right) \quad \text{and} \quad \frac{1}{\nu} := E(Z_1) = \frac{1}{\mu} + \frac{1}{\mu_{F,G}}$$

and applying (2.1) we can conclude that the density of ingested meals during the interval $(0, t]$ is with probability 1 approximately equal to

$$\nu = \frac{\mu\, \mu_{F,G}}{\mu + \mu_{F,G}} \equiv f_{\mu,\mu}(\mu_{F,G}), \tag{3.1}$$

a hyperbolic functional response in $\mu_{F,G}$, and that the expected number of ingested meals during the interval $(t, t+h]$ is approximately

$$\nu h = f_{\mu,\mu}(\mu_{F,G})h. \tag{3.2}$$

If the arrivals form a Poisson process then the random variable $S_{N_{Y_1}+1} - Y_1$ has the same distribution as X_1—the exponential distribution with parameter $1/\lambda$—, so that $\mu_{F,G} = \lambda$ and the quantities in (3.1) and (3.2) reduce to

$$f_{\mu,\mu}(\lambda) \quad \text{and} \quad f_{\mu,\mu}(\lambda)h,$$

which lead to (1.1).

The fact that the class of hyperbolic functional responses is closed under composition (i.e., that $f_{\alpha,\beta}\left(f_{\alpha',\beta'}(x)\right) = f_{\alpha'',\beta''}(x)$ with α'', β'' determined from α, β and α', β') is regarded as important for explaining the regulation of metabolic pathways (Kooijman (2000), p. 75). If in the feeding model now described meals are replaced by substrates, processing of meals is regarded as ‘production’, and ‘products’ take the place of ingested meals, then what we get is a model for a SU. In a metabolic pathway, the products originating from a SU are not regarded as final products but rather as ingredients to be processed by other SU’s, in which case it is important to be able to make statements such as (1.1) at each step of the pathway. Unless the d.f. G of the processing time is of a very special form (a mixture of an exponential d.f. and a d.f. concentrated at 0), the *output* process of a SU (the process of ingested meals in a feeding model) with Poisson arrivals will not form a Poisson process, but merely a renewal process. Since one would also like to state something like (1.1) for the next SU in the metabolic pathway, it may seem desirable, at least in some situations, to consider not just Poisson but more general renewal processes as arrival processes. The idea is thus to see whether by requiring only the arrival and production mechanisms to have the same struture—that of renewal processes—the approximate density of ingested meals/transformed products can still be given in the form of a hyperbolic response of the arrival rate.

Of course, in general $\mu_{F,G}$ is not just a function of λ, but we can argue heuristically to get an approximation for it in terms of λ and of $\sigma^2 := \mathrm{Var}(X_1)$. For large t,

$$E\left(S_{N_t+1} - t\right) \approx \frac{\lambda^{-1} + \lambda\sigma^2}{2},$$

so if the processing times are typically not too small then

$$\frac{1}{\mu_{F,G}} = E\left(S_{N_{Y_1}+1} - Y_1\right) \approx \frac{\lambda^{-1} + \lambda\sigma^2}{2} = \frac{1 + (\lambda\sigma)^2}{2\lambda},$$

whence

$$\nu \approx \frac{\mu\lambda}{\lambda + \mu\left(1 + (\lambda\sigma)^2\right)/2}.$$

In terms of the feeding model, this gives us an approximate formula for the functional response as a function of the food density and of the variability of the intervals between meal arrivals. If the coefficient of variation of the intervals between meal arrivals does not vary much as a function of λ, say $\lambda\sigma \approx c$ for a range of values of λ and a constant c, we have the further approximation

$$\nu \approx \frac{\mu\lambda}{\lambda + \mu(1 + c^2)/2} = f_{\mu,\mu(1+c^2)/2}(\lambda),$$

yielding an approximately hyperbolic response function.

References

Karlin, S., and Taylor, H. (1975). *A First Course in Stochastic Processes* (2 ed.). Academic Press.

Kooijman, S. (2000). *Dynamic Energy and Mass Budgets in Biological Systems.* Cambridge University Press.