

Resource–consumer models and the biomass conversion principle

Rodrigo Ramos-Jiliberto*

*Mathematical Ecology Group, Instituto de Matemáticas, Universidad Católica de Valparaíso,
Casilla 4059 Valparaíso, Chile*

Abstract

In the search for a unified basis for constructing food-web models, the long-standing discrepancy between biomass conversion (BC) and individual survival (IS) modeling has been revitalized by Ginzburg (J. Anim. Ecol. 67 (1998) 325) and Berryman (J. Anim. Ecol. 68 (1999) 1263) in the context of resource–consumer interactions. In this work, the principles underlying the confronting approaches are summarized and the criticisms addressed against each. Also, it is argued that the achievement of a single theory of resource–consumer ecology could benefit from this debate by incorporating key elements of both approaches. A logical procedure is suggested to build simple continuous resource–consumer models that follow the principle of biomass conversion, possess structural homogeneity, and distinguish the effects of depletable and fixed resource availability. Additionally, a new conversion function and a general Holling type extraction function (functional response) are introduced. Finally, it is shown that some well known IS models can be obtained as special cases of a general BC model.

Keywords: Prey–predator models; Food chain models; Predation; Biomass conversion; Functional response

1. Introduction

Consumer–resource interactions constitute a fundamental process to be understood in order to construct a consistent food-web theory. From a theoretical standpoint, there is little agreement about which is the most appropriate strategic model to describe the essence of the consumer–resource interaction. If such a general agreement could be reached, ecologists would have a baseline to derive more realistic and detailed models.

In the last decade there has been a rich controversy about the biologically correct structure of resource–consumer (prey–predator) systems. Among the most conspicuous recent debates are the ratio-dependent vs.

prey-dependent functional response models. In contrast to the traditional prey-dependent models, ratio-dependent models were popularized by [Arditi and Ginzburg \(1989\)](#) although [Getz \(1984\)](#) presented the first approach to finding a unified methodology to modeling trophic interactions using a ratio-dependent paradigm. Later on, the debate was continued by [Berryman \(1992\)](#), [Abrams \(1994\)](#), [Gleeson \(1994\)](#), [Sarnelle \(1994\)](#), [Berryman et al. \(1995\)](#), and [Abrams and Ginzburg \(2000\)](#) among others. Another controversy exists between the adherents and biomass conversion (BC) vs. individual survival (IS) models ([Ginzburg, 1998](#); [Berryman, 1999](#)). I will concentrate on the last divergence, allowing for the use of either prey-dependent or ratio-dependent approach.

The aim of this paper is to show that, in the frame of ordinary differential equation models, it is possible to adopt a single approach that solves most of the criticisms presented against each of competing schemes.

* Present address: Departamento de Ciencias Ecológicas, Facultad de Ciencias, Universidad de Chile, Las Palmeras 3425, Ñuñoa, Santiago, Chile.

E-mail address: roramos@uchile.cl.

2. Two modeling approaches

In the context of one resource and one consumer, IS continuous models can be written in the following general form:

$$\frac{dx_1}{dt} = G_1x_1 - Hx_2 \quad (1)$$

$$\frac{dx_2}{dt} = G_2x_2 \quad (2)$$

where x_1 and x_2 are the resource and consumer population densities, respectively. In the above equations, $G_i = g_i(x_{i-1})$ or $G_i = g_i(x_{i-1}, x_i)$ ($i = 1, 2$) is the per capita growth function of population i in the absence of interaction with the upper trophic level, and $H = h(x_1)$ or $H = h(x_1, x_2)$ is the per unit-consumer extraction rate of resource, often called functional response. A structural requisite of this model is that the function G_2 must contain the variable x_1 to connect the two equations. The IS model represented by Eqs. (1) and (2) can be generalized for any population of trophic level i , as:

$$\frac{dx_i}{dt} = G_ix_i - H_{i+1}x_{i+1} \quad (3)$$

On the other hand, BC models usually exhibit the following general structure:

$$\frac{dx_1}{dt} = G_1x_1 - Hx_2 \quad (4)$$

$$\frac{dx_2}{dt} = f(H)x_2 \quad (5)$$

where x_i , G_i and H should be interpreted as before. The key attribute of this model is that the consumer equation (5) contains a conversion function from the per capita consumption rate H to the per capita population growth. The structural requisite of this model is that H must contain x_1 . A general BC model can be written for any population of trophic level i as:

$$\frac{dx_i}{dt} = f_i(H_i)x_i - H_{i+1}x_{i+1} \quad (6)$$

The main logical distinction between IS and BC models is revealed by the formal expression of the per capita growth rate of consumers in the absence of interaction with the upper trophic level. More specifically, both approaches differentiate in the functional dependence between that rate and the abundance of resources. In IS models this expression (G_i in Eq. (3)) is based on the per capita intrinsic rate of increase (a constant parameter), minus some terms representing restrictions to growth in dependence on the interaction

with the resource. For BC models, on the other hand, the per capita growth rate in the absence of predation is an explicit function of the per capita consumption rate of resources, which depends itself on the abundance of the resource or on the ratio resource/consumer. This implies that a single process—resource extraction—explains both the decrease in resource density and the increase of consumer biomass. This idea is based on energetic considerations of biomass flux through the food chain (Berryman and Gutierrez, 1999).

A non-exhaustive list of monotonic functional forms of G_i is provided in Table 1. Although in principle any of the listed functions is a plausible choice for the per capita rate of growth of any population, the IS philosophy needs at least one subtracting term from the maximal constant rate in the consumer equation. Thus, only functions (1.2–1.4) are useful for IS models and the term b_i should be a function $b_i(x_{i-1})$ in order to relate the growth rate of the consumer to the availability of resources.

Table 2 shows a list of functional forms for H , including linear functions (2.1–2.4) and the most common non-decreasing saturating forms (2.5–2.13), both with prey-dependency and ratio-dependency (see Gutierrez, 1996; Getz, 1999; Jeschke et al., 2002 for some other equation not listed here). Function (2.9) is a generalization of both Holling types I ($\delta \rightarrow \infty$) and II ($\delta = 1$, see Getz, 1999 for details). The last function (2.14) allows for nonmonotonic (Holling type IV) responses with $\psi > \lambda$. I propose this function, which also includes all the listed functions except (2.5–2.7), as the most general of its type. I will not provide definitions of the terms used in Tables 1 and 2 since they are easily found in any serious ecology textbook or in the cited literature.

Table 3 shows three alternative conversion functions with some desirable properties; and the graphical representation of each is shown in Fig. 1. Since BC models are mostly known for having a linear conversion (see for example the review of Berryman and Gutierrez, 1999), I will provide a deeper description of these functions. The linear function in Table 3 is the most commonly used, and it has been the prototype among the BC models. The intercept w represents the per capita growth rate (usually negative) as consumption tends to

Table 1

Forms for the per capita population growth rate in the absence of interaction with an upper trophic level, G_i

	Model	Type
(1.1)	a_i	Exponential, no self-limitation
(1.2)	$a_i - b_ix_i$	Logistic, linear self-limitation
(1.3)	$a_i - b_i \ln x_i$	Gompertz, non-linear self-limitation
(1.4)	$a_i - b_ix_i^{\beta_i}$	Logistic, non-linear self-limitation with $\beta_i \neq 1$ (Rosenzweig, 1971; Gilpin and Ayala, 1973)

Table 2
Forms for the per unit-consumer extraction rate of resource H_i

	Model	Type
(2.1)	ϕ	Constant (Berryman et al., 1995)
(2.2)	ϕx_{i-1}	Linear prey-dependent or Lotka–Volterra mass-action
(2.3)	$\phi x_{i-1}/x_i$	Linear ratio-dependent
(2.4)	$\begin{cases} \phi x_{i-1} & \text{for } x_{i-1} < \alpha \\ q & \text{else} \end{cases}$	Standard Holling type I (Holling, 1959)
(2.5)	$\phi(1 - \exp[kx_{i-1}])$	Standard Watt–Ivlev–Gause
(2.6)	$\phi\left(1 - \exp\left[\frac{kx_{i-1}}{x_i}\right]\right)$	Ratio-dependent Watt–Ivlev–Gause
(2.7)	$\phi\left(1 - \exp\left[\frac{kx_{i-1}}{n+qx_i}\right]\right)$	Generalized Watt–Ivlev–Gause
(2.8)	$\frac{\phi x_{i-1}}{s+x_{i-1}}$	Standard Holling type II–Michaelis–Menten–Monod
(2.9)	$\frac{\phi x_{i-1}}{(s^\delta + x_{i-1}^\delta)^{1/\delta}}$	Holling types I–II (Getz, 1999)
(2.10)	$\frac{\phi x_{i-1}^\lambda}{s+x_{i-1}^\lambda}$	Standard Holling type III, with $\lambda > 1$
(2.11)	$\frac{\phi x_{i-1}}{x_i s + x_{i-1}}$	Ratio-dependent type II
(2.12)	$\frac{\phi x_{i-1}}{u+x_i+x_{i-1}\phi}$	Ratio-dependent type II (DeAngelis et al., 1975)
(2.13)	$\frac{\phi x_{i-1}^\lambda}{u+x_i^\delta s+x_{i-1}^\lambda\phi}$	Generalized Beddington–DeAngelis
(2.14)	$\frac{\phi x_{i-1}^\lambda}{u+x_i^\delta s+x_{i-1}^\psi\phi}$	Generalized Holling

zero; the coefficient m is the slope of the linear relation. In fact, the linear function in combination with (1.1 and 2.2) renders the familiar Lotka–Volterra prey–predator model. Function (3.2) is an increasing sigmoid curve where σ represents the asymptotic maximum growth when consumption is very high, ν is the minimum growth rate (usually negative) when consumption tends to zero, z is the abruptness of the curve, and γ is a shape parameter that indicates the inflexion point (when $z > 1$) on the consumption axis. Herein, I introduce this

Table 3
Forms for the conversion rate from per capita consumed biomass to per capita growth $f_i(H_i)$

	Model	Type
(3.1)	$mH_i + w$	Linear
(3.2)	$\frac{\sigma - \nu}{1 + \left(\frac{\gamma}{H_i}\right)^z} + \nu$	Sigmoid
(3.3)	$\rho\left(1 - \frac{\kappa}{H_i}\right)$	Hyperbolic with pole at zero

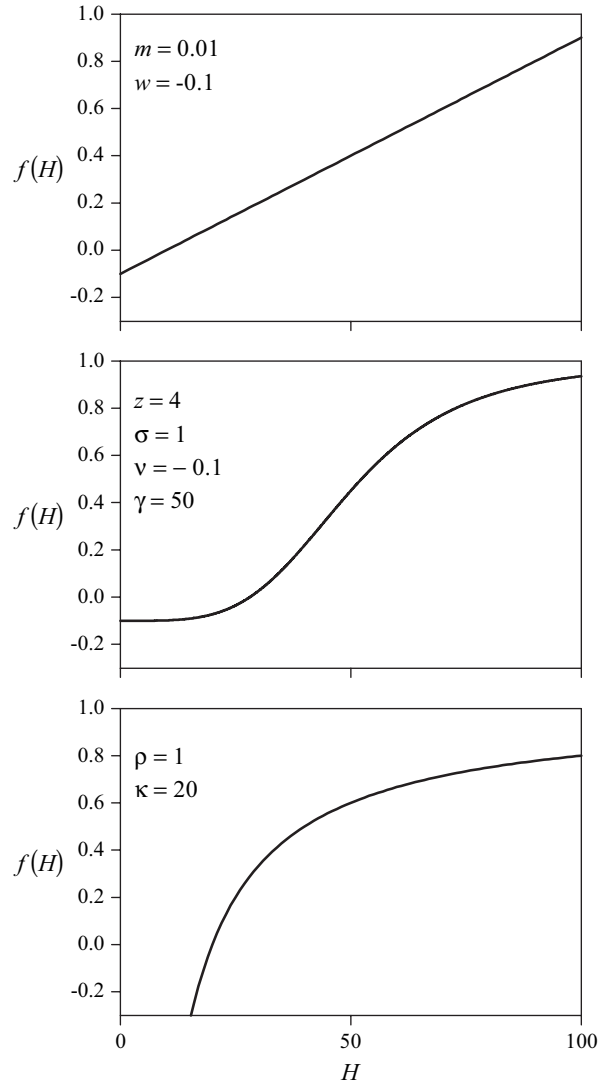


Fig. 1. Graphical display of the conversion functions listed in Table 3. Top: linear conversion, middle: sigmoid conversion, bottom: hyperbolic conversion with pole at zero. Parameter values are shown inside each graph.

formula as an alternative conversion function, which possesses some convenient properties. First, the maximum growth rate is asymptotically approached at high levels of consumption, assuming an intrinsic upper bound to the per capita growth rate under conditions of unlimited consumption. Nevertheless, the consumption rate defined by the extraction rate function is more often asymptotic itself, which imposes a bound on the conversion rate. Second, functions (3.1 and 3.2) share the property of having a finite lower limit that might be reasonably set to negative, but whose magnitude should depend on the ability of the consumers to maintain a certain level of growth in the absence of the explicitly considered resource. It is hypothetically possible to still have a positive growth rate in the absence of the modeled resource if other sources of biomass input exist (e.g. alternative preys, external or internal food

storing, etc.). On the other hand, the sigmoid shape of function (3.2) accounts for an accelerating increase in growth as consumption rises from very low to moderate levels, and for a decelerating increase of per capita growth as consumption raises towards the maximum attainable level. Under no evidence for a sigmoid conversion shape, setting $z = 1$ turns the function (3.2) into hyperbolic. The conversion form (3.3) proposed by Getz (1991, 1994) has the distinct property of approaching $-\infty$ as consumption tends to zero, which does not allow for alternative resource inputs. With only two parameters (like function (3.1)), the function (3.3) has an upper bound (like function (3.2)) defined by ρ . Parameter κ is the consumption level needed to maintain a zero growth, e.g. a maintenance requirement.

3. Shortcomings addressed for IS and BC approaches

Historically, both IS and BC models have a long tradition in theoretical ecology and they have been and still are being used in continuous as well as discrete versions, that include different currencies to measure the state variables. The almost octogenarian Lotka–Volterra model for the resource–consumer (prey–predator) interaction is founded on the biomass conversion principle. Although Vito Volterra’s logistic competition model is an IS model that is easily applicable to the prey–predator interaction, he considered that the biomass flux across trophic levels is best described by its BC model. On the other hand, Leslie (1948) introduced the IS model approach in the context of the resource–consumer interaction by coupling a pair of equations in which the density of predators negatively affects the per capita population growth of prey (accounting for predation losses), and the prey density directly determines the carrying capacity of consumers. These models have been modified throughout the years by means of introducing a saturating per capita predation function, linear or non-linear self-limited growth in the absence of interaction, and so on (May, 1974; Wangersky, 1978). Different static and dynamic properties arise once these modifications are made.

Several criticisms have been made against IS and BC models that apply for any kind of population modeling approach. One such criticism refers to the lack of realism or oversimplification of nature. For example, the simplest Lotka–Volterra prey–predator models are criticized because they assume a geometric growth of populations (positive for the prey and negative for the predator) in the absence of interaction. They are also criticized because they lack satiation in the resource extraction process, although the use of a linear functional response could provide an acceptable approximation for some purposes. These assumptions probably seem unacceptable by today’s population ecologists since

they have been empirically and convincingly refuted, and because alternative assumptions give rise to important qualitative differences in the dynamic properties of the model systems (see Berryman, 1992). Further assumptions, such as linearity in the dependence of the per capita rate of increase on the population density, are more tolerable for simple models. These criticisms have been raised against some prototypes of BC or IS models and do not reveal an inadequacy of the model building logic itself, but of the particular functions utilized to assemble the models. Tables 1 and 2 show several alternatives that easily avoid these criticisms.

A different kind of objection also applies to IS and BC models. Given that any population in nature may act either as consumer, resource, or both, it is desirable to use the same general equation for any population, regardless of the trophic level it occupies in the trophic stack (Getz, 1994; Berryman et al., 1995). The desired property is known as structural homogeneity, and it should be naturally fulfilled if the same ecological principles are used to derive the population dynamic model of any species.

A number of criticisms have been directed against IS models that apparently do not apply to BC models, and vice versa. The most serious weakness reported for IS models is that they do not assume reproduction of consumers to depend on resource consumption (Ginzburg, 1998). In IS models, consumers have a positive rate of growth on their own that could be restricted by a number of factors. This major criticism reveals that there is no explicit mechanism or conditions under which consumers could attain their intrinsic growth rate.

One of the recognized shortcomings of *some* BC models is the assumption of an exponential decay or “graceful anabolism” of consumers in the absence of resources (Getz, 1991, 1994; Berryman, 1999). This property is a by-product of BC models containing a conversion function with a finite limit as the extraction rate tends to zero. However, conversion functions that overtake this situation have been introduced (e.g. function (3.3) in Table 3).

The IS modeling approach introduced by Berryman et al. (1995) emphasizes the basic distinction between fixed vs. depletable resources and the appropriateness of considering separately the effects of the availability of the different kinds of resources in population dynamics equations. It could be argued that BC models do not incorporate such distinction, but the criticism does not apply when using (1.2) or (1.3) instead of (1.1) as the growth function (see below).

4. A proposal

From a theoretical perspective, the biomass conversion principle is an essential component of trophic chain

models when a mechanistic consideration of the underlying biological process is preferred (Yodzis, 1989). However, more realistic BC models can be constructed as a natural extension of the most simple single-population models.

There seems to be little arguments for using G_i and H functions other than those listed in Tables 1 and 2 in the context of simple lumped continuous models. An exception is the use of nonmonotonic forms of self-limitation (e.g. Allee effect) that are not considered here. Conversion functions listed in Table 3, on the other hand, cover only the most simple and plausible theoretical assumptions. A simple and versatile procedure for assembling theoretical resource–consumers models is: (1) decide the basic growth and extraction functions for the resource population, on the basis of the underlying biological assumptions. Since Eqs. (1) and (3) are identical there is no basic distinction between IS and BC models with respect to the equation for the lowest trophic level. (2) On the basis of the underlying biological assumptions decide the basic growth function for the consumer population (a G_2 function such as in Eq. (2)) assuming *unlimited* renewable-resource availability. Should it be logistic? Should it exhibit non-linear density dependence? This step is congruent with the procedure of building IS models, but is opposite to the classical BC model building strategy, since the latter asks for the consumer dynamics in the *absence* of resources, and then adds a conversion function, usually linear. (3) Identify the maximum of G_2 , which corresponds to parameter a_2 for the cases listed in Table 1, and makes it a function f (e.g. one of the Eqs. (3.1–3.3)) of the extraction function H previously chosen for the resource equation. The underlying logic is that the flux of biomass from resources to consumers defines the renewable-resource-dependent constraints to growth, but not other potential constraints such as space-limitation. Therefore I suggest a simple wide-ranging form for a BC model:

$$\frac{dx_i}{dt} = [f_i(H_i) - b_i x_i^{\beta_i}] x_i - H_{i+1} x_{i+1} \quad (7)$$

where the first term within square brackets is the per capita resource-dependent growth (in the absence of other restrictions to growth). The second term within square brackets accounts for the self-limitation due to competition for fixed *essential* resources, whereas the last term of the right hand is the extraction function from the upper trophic level. Model (7) can be considered a generalization of the Bazykin model (Turchin, 2003, p. 98), due to the inclusion of both the logistic term and a biomass conversion function. When the population exhibit competition for several resources which are *perfectly substitutable*, model (7) reduces to

$$\frac{dx_i}{dt} = \left[f_i \left(\sum_j H_{ij} \right) \right] x_i - H_{i+1} x_{i+1} \quad (8)$$

following Getz (1991). As demonstrated by Getz (1991, 1993), this model reduces to the logistic one if only one fixed resource is available to the population, and conversion is governed by Eq. (3.3). Nevertheless, the alternative approach introduced here (Eq. (7)) is appropriate when considering an essential fixed resource (e.g. space) which limits the population growth independent on the limits imposed by food. On the other hand, model (7) can be easily extended to populations exploiting multiple substitutable resources and being victim of multiple predators, but the point here is to represent populations forming vertical food chains, as a starting place to model more complex structures.

Specific models of the general equation (7) are shown below for the three different conversion functions listed in Table 3 (linear, sigmoid, and hyperbolic with pole at zero), after using the more general functions (1.4) and (2.14) from Tables 1 and 2, respectively.

Linear conversion:

$$\begin{aligned} \frac{dx_i}{dt} = & \left[\frac{m_i \phi_i x_i^{\lambda_i}}{u_i + x_i^{\delta_i} s_i + \phi_i x_{i-1}^{\psi_i}} + w_i \right] x_i - b_i x_i^{\beta_i + 1} \\ & - \left(\frac{\phi_{i+1} x_i^{\lambda_{i+1}}}{u_{i+1} + x_{i+1}^{\delta_{i+1}} s_{i+1} + \phi_{i+1} x_i^{\psi_{i+1}}} \right) x_{i+1} \end{aligned} \quad (9)$$

Sigmoid conversion:

$$\begin{aligned} \frac{dx_i}{dt} = & \left[\frac{\sigma_i - v_i}{1 + \left(\frac{\gamma_i (u_i + x_i^{\delta_i} s_i + \phi_i x_{i-1}^{\psi_i})}{\phi_i x_{i-1}^{\lambda_i}} \right)^{z_i}} + v_i \right] x_i - b_i x_i^{\beta_i + 1} \\ & - \left(\frac{\phi_{i+1} x_i^{\lambda_{i+1}}}{u_{i+1} + x_{i+1}^{\delta_{i+1}} s_{i+1} + \phi_{i+1} x_i^{\psi_{i+1}}} \right) x_{i+1} \end{aligned} \quad (10)$$

Hyperbolic conversion with pole at zero:

$$\begin{aligned} \frac{dx_i}{dt} = & \left[1 - \frac{\kappa_i (u_i + x_i^{\delta_i} s_i + \phi_i x_{i-1}^{\psi_i})}{\phi_i x_{i-1}^{\lambda_i}} \right] x_i - b_i x_i^{\beta_i + 1} \\ & - \left(\frac{\phi_{i+1} x_i^{\lambda_{i+1}}}{u_{i+1} + x_{i+1}^{\delta_{i+1}} s_{i+1} + \phi_{i+1} x_i^{\psi_{i+1}}} \right) x_{i+1} \end{aligned} \quad (11)$$

The models introduced above can be simplified considerably if one assumes some particular properties of the system, including: $b = 0$ for unlimited growth function under unlimited resources, $\beta = 1$ for linear self-limitation, $\lambda = 1$ for simple hyperbolic extraction function (type II), $\delta = 0$ or $s = 0$ for prey-dependent predation (no self-interference in feeding among consumers), $z = 1$ for hyperbolic conversion when using the sigmoid conversion (3.2), $x_{i+1} = 0$ for top predators,

and $x_{i-1} = R(t)$ for lowest-level resources (autotrophs). For example, starting from Eq. (9) and setting $b = 0$, $\lambda = 1$, $s = 0$, and $\phi = 0$ we obtain the original Lotka–Volterra resource–consumer system. Furthermore, starting from Eq. (11) and setting $b = 0$, $\lambda = 1$, $\delta = 1$, $\psi = 1$, and $\phi = 1$ we obtain the Getz’s metaphysiological model (Getz, 1991, 1994).

Finally, I will show that some paradigmatic IS models such as those attributed to Leslie (1948) and Berryman et al. (1995) can be understood as specific cases of the general BC model (7).

Specific case A: from Eq. (7) applied to a consumer population of trophic level $i \geq 2$, set $x_{i+1} = 0$ and $b_i = 0$, next choose the conversion function (3.3) and the resource extraction function (2.3). Then set $r_i = \rho$ and $n_i = \phi/\kappa$ and you obtain the well known Leslie equation for a consumer population:

$$\frac{dx_i}{dt} = x_i r_i \left(1 - \frac{x_i}{n_i x_{i-1}} \right) \quad (12)$$

This view offers us a mechanistic explanation to the meaning of parameters contained in the Leslie model e.g. the maximal per capita growth rate r is given by the upper bound of the conversion process; the coefficient n_i depends on the ratio between the rate of increment of resource extraction as a function of the amount of resource per consumer (ϕ), and the maintenance requirement of consumers (κ). Implicitly, this model assumes that intrapopulation competition is driven for food only, and that the extraction of resources is ratio-dependent. Moreover, the implicit conversion function of the Leslie model is hyperbolic with pole at zero, since the growth tends to $-\infty$ as the ratio resources/consumers tends to zero.

Specific case B: from Eq. (7) applied to any population of trophic level i , set $\beta_i = 1$, and use the same conversion function (3.3). Then choose function (2.3) for the extraction rate of resources and function (2.1) for the extraction rate from the upper trophic level. Next, set $a_i = \rho$, $c_i = \phi/\rho\kappa$, and $d_i = \Phi$ to obtain the model of Berryman et al. (1995):

$$\frac{dx_i}{dt} = x_i \left(a_i - b_i x_i - \frac{x_i}{c_i x_{i-1}} - \frac{d_i x_{i+1}}{x_i} \right) \quad (13)$$

The above derivation reveals an implicit conversion process whose form is the same as that of the former case (hyperbolic with pole at zero). On the other hand, the mechanistic definition of c_i shows that the detrimental effect of food competition is directly related to the per capita growth potential (ρ), to the maintenance requirement (κ), but inversely related to extraction efficiency (ϕ). Nevertheless, this analysis of the Berryman model shows that the extraction of resources of level $i - 1$ by consumers of level i is governed by rules other than those of the extraction from level $i + 1$ on level i , since the

former is linear ratio-dependent whereas the latter is merely a constant. Under this approach, e.g. considering the underlying biomass transfer from extracted resources to consumer growth, the model of Berryman et al. (1995) cannot be used for two populations of successive trophic levels, and therefore, the model lacks structural homogeneity, a property which Berryman himself (Berryman et al., 1995; Berryman, 1999) has stated as highly desirable.

The IS approach allows us to model populations in a phenomenological way, without considering the processes at a lower level of biological organization. In contrast, the BC approach offers us a more mechanistic view of population dynamics, taking into account some components of the population processes from which emergent properties arise. The philosophical differences between IS and BC models are not actually solved, but the purpose of this work is to present a model which is consistent with the BC approach and possesses a structure which avoids published criticisms against previous BC models. It should be noted that Eq. (7) can be considered to be a hybrid between IS and BC models since it rests on assumptions belonging to both traditions. Nevertheless, I do not see any philosophical conflict inherent to model (7), and it serves as a useful starting point to modeling intertrophic interactions.

Obeying the biomass conversion principle, distinguishing intraspecific competition for depletable and fixed resources, and ensuring structural homogeneity; the framework supported here provides a simple and consistent procedure to construct simple continuous models. At the same time, the modeler could choose among various particular details, such as prey- or ratio-dependent predation, exponential or abrupt decay of starved consumers, linear or non-linear self-limitation, etc., to incorporate in order to better represent the particular system under study. Furthermore, the structure of BC equations easily allows for the inclusion of physiological and behavioral traits in lumped population models (see for example Getz and Owen-Smith, 1999; Ramos-Jiliberto and González-Olivares, 2000; Ramos-Jiliberto, 2003) and thus represents a wide spectrum of biological scenarios.

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