Effects of Enrichment on Three-Level Food Chains with Omnivory

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ABSTRACT: Although omnivory (the consumption of resources from more than one trophic level) is widespread, this fundamental limitation to the applicability of food chain theory to real communities has received only limited treatment. We investigated effects of enrichment (increasing carrying capacity, K, of the resource) on a system consisting of a resource (R), an intermediate consumer (N), and an omnivore (P) using a general mathematical model and tested the relevance of some of its predictions to a laboratory system of mixed bacteria ($=R$) and the ciliates *Tetrahymena* ($=N$) and *Blepharisma* ($=P$). The model produced six major predictions. First, N may facilitate or inhibit P. Enrichment may revert the net effect of N on P from facilitation to inhibition. Second, along a gradient of K, up to four regions of invasibility and stable coexistence of N and P may exist. At the lowest K, only R is present. At somewhat higher K, N can coexist with R. At intermediate K, either N and P coexist, or either consumer excludes the other depending on initial conditions. At the highest K, N may be excluded through apparent competition and only R and P can coexist. The pattern of persistence of *Tetrahymena* and *Blepharisma* along an enrichment gradient conformed fairly well to the scenario allowing coexistence at intermediate K. Third, for stable equilibria of the omnivory system, R always increases and N always decreases with K. The abundances of bacteria and *Tetrahymena* were suggestive of such a pattern but did not allow a strict test because coexistence occurred at only one level of enrichment. Fourth, an omnivore can invade an R-N system at a lower K than an otherwise identical specialist predator of N. Fifth, an omnivore can always invade a food chain with such a specialist predator. Sixth, over ranges of K where both omnivory systems and otherwise identical three-level food chains are feasible, N is always less abundant in the omnivory system, whereas the relative abundances of R and P in omnivory systems compared to food chains may change with K. It is thus possible that total community biomass at a given K is lower in an omnivory system than in a food chain. Both the model and the experimental results caution that patterns of trophic-level abundances in response to enrichment predicted by food chain theory are not to be expected in systems with significant omnivory.

The study of enrichment effects on community structure and ecosystem functioning is a central theme of ecology (DeAngelis 1992; Polis and Winemiller 1996). Of particular recent interest has been the study of enrichment effects on the abundances of trophic guilds (producers, herbivores, detritivores, etc.), which are often referred to as trophic levels (Leibold et al. 1997). Much of this interest was stimulated by an equilibrium theory of food chain dynamics (Smith 1969; Oksanen et al. 1981; DeAngelis et al. 1996). Assuming a closed, well-mixed system and purely exploitative competition within consumer trophic levels, the theory makes two major predictions: first, the number of trophic levels in a food chain is positively related to enrichment; and second, for a food chain of given length, enrichment translates into increased equilibrium biomasses at the top trophic level and even-numbered levels below it, whereas the equilibrium biomasses at odd-numbered trophic levels below the top level do not change. With its simplifying assumptions, this theory is directly applicable only to a limited number of systems, such as microorganisms in well-mixed, liquid media (Grover 1997). Nevertheless, numerous empirical studies have tested the applicability of this food chain theory to a wide range of natural systems (McNaughton et al. 1989; Hansson 1992; Persson et al. 1992; Wootton and Power 1993; Mazumder 1994; Schmitz 1994; Mikola and Setälä 1998). The mixed evidence from these studies has fueled a controversy over the roles of resource limitation and consumer control in community regulation (reviewed by Leibold et al. 1997).

In recent years, many realistic features of natural systems (e.g., flexible consumer behavior, unstable coexistence, or the presence of more than one species per trophic level) have been incorporated into food chain models (Leibold 1989, 1996; Abrams 1992, 1993; Abrams and Roth 1994*a*;

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Holt et al. 1994; Nisbet et al. 1997; Murdoch et al. 1998; Huisman et al. 1999). Many of these extensions to the basic model have proven capable of producing phenomena that are not predicted by standard food chain theory but are frequently observed in natural systems, such as positive effects of enrichment on the abundances of adjacent trophic levels (reviews in Diehl et al. 1993; Leibold et al. 1997). Still, the potentially most fundamental limitation to the general applicability of food chain theory, that is, omnivory (Cousins 1987), has received only limited formal treatment to date.

"Omnivory" is defined as the feeding on nonadjacent trophic levels, either simultaneously or during different life-history stages (Pimm 1982; Pimm and Rice 1987). Omnivory is widespread in natural communities and links the dynamics of interacting species through a multitude of direct and indirect pathways (Polis et al. 1989; Diehl 1993). Theoretical work on the population dynamical effects of omnivory has been sparse and has focused mainly on issues of coexistence and stability (Pimm and Lawton 1978; Matsuda et al. 1986; Law and Blackford 1992; Thingstad et al. 1996; Holt and Polis 1997). A detailed treatment of enrichment effects on omnivory systems is so far lacking.

In this article, we investigate the effects of enrichment on a system consisting of a basal resource, an intermediate consumer, and an omnivore, using a twofold approach. First, we develop and analyze a general mathematical model to answer the following questions: How does enrichment (increasing carrying capacity of the resource) affect the possibilities for coexistence of the three species? When coexistence of all three species is possible, how do their equilibrium densities change with enrichment? At any given level of enrichment, how do the densities of resources, intermediate consumers, and top consumers in an omnivory system compare to their corresponding densities in systems from which either the omnivorous feeding link is dropped (linear food chain) or one of the two consumers is absent? How does enrichment affect the invasibility of one-consumer/one-resource systems by the respective other consumer?

Second, we confront some of the model predictions with the results of a microcosm experiment in which we studied effects of enrichment on coexistence and abundance of a bacterivorous protist and an omnivorous protist and their shared bacterial resource. To our knowledge, only one other study of enrichment effects on an omnivory system has been published to date (Morin 1999). We performed this experiment with a protist community because the behaviors and life histories of the two protist species in our experiment match the assumptions of the model reasonably well. Furthermore, many of the predictions concern equilibrium situations, which require many generations to

be expressed. Most experimental studies of omnivory systems have been performed on timescales shorter than, at most, a few generations of the top consumer (reviewed in Diehl 1993, 1995). The study of long-term population dynamics is tractable in systems of microorganisms, and the use of simple protist communities as test systems for the applicability of population dynamical theory has a long tradition in ecology (Gause 1934; Vandermeer 1969; Luckinbill 1973; Holyoak and Lawler 1996). In recent years, the study of protist communities involving omnivores has received increasing attention (Lawler and Morin 1993; Morin and Lawler 1996; Weatherby et al. 1998; Morin 1999), but so far very little is known about the effects of enrichment on the long-term behavior of such systems.

Model Formulation

The general model is described by equations (1)–(3) and summarized in table 1.

$$\frac{dR}{dt} = rR\rho(R, K) - a(R)N - f(R, N)P, \quad (1)$$

$$\frac{dN}{dt} = g(R)N - c(R, N)P - mN, \quad (2)$$

$$\frac{dP}{dt} = h(R, N)P - m'P. \quad (3)$$

The state variables are the densities of resources (R), intermediate consumers (N), and omnivores (P). The equations involve functions describing the growth of resources and consumers and the feeding and mortality of consumers. For maximum generality, we do not specify these functions but assume that they obey the inequalities listed under "Assumptions" in table 1 and described below.

Resources grow in a density-dependent manner and attain their maximum specific growth rate (r) only when R is close to 0. The actual specific growth rate is a fraction $\rho(R, K)$ of r, which is a decreasing function of R and an increasing function of K, the carrying capacity of resources in the absence of consumers. Intermediate consumers and omnivores die at density-independent per capita rates m and m', respectively. Resources die through consumption by intermediate consumers and omnivores. The functional response ($a(R)$) and the growth rate ($g(R)$) of the intermediate consumer are both increasing functions of resource density (e.g., Holling Type I, II, or III). The densities of resources (R) and intermediate consumers (N) are substitutable food sources of the omnivore; that is, either R or N alone, if present at sufficient densities, can support the omnivore. The functional responses of the omnivore when feeding on resources ($f(R, N)$) and intermediate

Table 1: The general model

	Definition
Populations:	
$R(t)$	Density of resources at time t
$N(t)$	Density of intermediate consumers at time t
$P(t)$	Density of omnivores at time t
Feeding and growth:	
$\rho(R, K)$	Proportion of maximum specific growth rate of resources
$a(R)$	Functional response of intermediate consumers
$g(R)$	Growth rate of intermediate consumers
$f(R, N)$	Functional response of omnivores with respect to resources
$c(R, N)$	Functional response of omnivores with respect to intermediate consumers
$h(R, N)$	Growth rate of omnivores
Parameters:	
r	Maximum specific growth rate of resources
K	Resource-carrying capacity (defined by $\rho(K, K) = 0$)
m	Density-independent mortality rate of intermediate consumers
m'	Density-independent mortality rate of omnivores
Assumptions:	
$(\partial\rho/\partial R) < 0$ and $(\partial\rho/\partial K) > 0$ for all $R, K > 0$	Growth of resources
$(\partial a/\partial R) > 0$; $(\partial f/\partial R) > 0$; $(\partial f/\partial N) \le 0$; $(\partial c/\partial N) > 0$; $(\partial c/\partial R) \le 0$	Functional responses
$(\partial g/\partial R) > 0$	Growth of intermediate consumers
$(\partial h/\partial R) > 0$; $(\partial h/\partial N) > 0$	Growth of omnivores

Dynamic equations	
$(dR/dt) = rR\rho(R, K) - a(R)N - f(R, N)P$	(1)
$(dN/dt) = g(R)N - c(R, N)P - mN$	(2)
$(dP/dt) = h(R, N)P - m'P$	(3)

consumers ($c(R, N)$) are assumed to be increasing functions of the densities of resources and intermediate consumers, respectively, but may be negatively affected by the density of the respective alternative prey (e.g., if handling one prey reduces the feeding rate on the other prey). If the two prey differ strongly in their nutritional value, the latter implies that increases in the density of the less profitable prey may actually decrease the growth rate ($h(R, N)$) of the omnivore because time spent handling the less profitable prey may decrease total food intake (Holt 1983; Abrams 1987). We assume that, under such circumstances, the top consumer drops the less profitable prey from its diet; in which case it is no longer an omnivore. In this article, we explore effects of enrichment on systems in which omnivory is a structurally stable component. We therefore consider only situations for which the growth rate of the omnivore is an increasing function of the densities of both prey.

Frequently, we will support our conclusions with numerical examples of a specific case of the general model, which we call the Lotka-Volterra omnivory model. The model assumes logistic resource growth ($\rho = 1 - R/K$),

linear functional responses ($a(R) = aR$, $f(R, N) = a'R$, and $c(R, N) = \alpha N$), and constant conversion efficiencies (b for conversion of R into N, b' for conversion of R into P, and β for conversion of N into P). The model has been analyzed by Stoecker and Evans (1985) and in greater detail by Holt and Polis (1997). To facilitate cross-referencing, we follow the latter authors' notation. The model thus takes the form

$$\frac{dR}{dt} = R\left[r\left(1 - \frac{R}{K}\right) - aN - a'P\right], \quad (4)$$

$$\frac{dN}{dt} = N(abR - \alpha P - m), \quad (5)$$

$$\frac{dP}{dt} = P(a'b'R + \alpha\beta N - m'). \quad (6)$$

At several instances, we compare equilibrium solutions of the system with omnivory to systems without omnivory (food chain) or to systems lacking one of the two con-

sumers. Whenever we use examples, we compare the system described by equations (4)–(6) to the corresponding Lotka-Volterra models of a food chain (in which $-a'P$ is dropped from eq. [4] and $b'a'R$ from eq. [6]), an R-N system (in which eq. [6] and all terms involving P are dropped), and an R-P system (in which eq. [5] and all terms involving N are dropped).

Model Predictions

Holt and Polis (1997) have shown that a three-species omnivory system may exhibit complex behavior, such as unstable coexistence of all three populations when there is no locally stable equilibrium. Unstable coexistence of all three populations is generally characterized by violent oscillations (e.g., Holt 1997, fig. 17.3), which in practice should lead to extinctions during population lows. We therefore restrict our theoretical investigation to the subset of situations in which the omnivory system has a unique, locally stable equilibrium over certain ranges of K.

In spite of the general nature of the model assumptions (table 1), answers to many of the questions listed in the introduction of this article can be found without further specification of the population gain and loss rates. Below, seven major conclusions are derived from the general model in table 1. To help the reader through the somewhat cumbersome, but unavoidable, mathematical notation, frequently used symbols are summarized in table 2.

Conclusion 1

Beyond a threshold level of enrichment, omnivores may exclude intermediate consumers.

For a general model essentially similar to the one in table 1, Polis and Holt (1992) have shown that a stable three-species omnivory system is only feasible if the intermediate consumer is the superior competitor for the shared resource, that is, if

$$R_N^* < R_O^* < R_P^*, \tag{7}$$

where R_i^* is the density of the resource at equilibrium with either the intermediate consumer ($i = N$), the omnivore ($i = P$), or both ($i = O$). Equation (7) is equivalent to

$$K_N < K_P, \tag{8}$$

where K_i is the threshold level of enrichment above which consumer i can invade a system from which the other consumer is absent.

If resources and omnivores are at equilibrium in the absence of intermediate consumers, resource density is fixed at R_P^* and any increase in K increases the density P_P^* of omnivores (fig. 1). With increasing K, the per capita growth rate of an invading intermediate consumer $g(R_P^*)$ thus stays constant, whereas its per capita loss rate ($\{[c(R_P^*, N)P_P^*]/N\} + m$) increases. Because intermediate consumers have a positive growth rate at R_P^* in the absence

Table 2: Definitions of frequently used symbols

Symbol	Definition
K_C	Resource-carrying capacity above which a specialist (top) consumer of the intermediate consumer can invade an R-N system at equilibrium
K_N	Resource-carrying capacity above which an intermediate consumer can invade in the absence of top consumers
K_{N-P}	Resource-carrying capacity below which an omnivore cannot invade an R-N system at equilibrium
K_P	Resource-carrying capacity above which an omnivore can invade in the absence of intermediate consumers
K_{P-N}	Resource-carrying capacity above which an intermediate consumer cannot invade an R-P system at equilibrium
N_C^*	Equilibrium density of the intermediate consumer in a linear food chain
N_N^*	Equilibrium density of the intermediate consumer in an R-N system
N_O^*	Equilibrium density of the intermediate consumer in a three-species omnivory system
P_C^*	Equilibrium density of the top consumer in a linear food chain
P_O^*	Equilibrium density of the top consumer (=omnivore) in a three-species omnivory system
P_P^*	Equilibrium density of the top consumer in an R-P system
R_C^*	Equilibrium density of the resource in a linear food chain
R_N^*	Equilibrium density of the resource in an R-N system
R_O^*	Equilibrium density of the resource in a three-species omnivory system
R_P^*	Equilibrium density of the resource in an R-P system
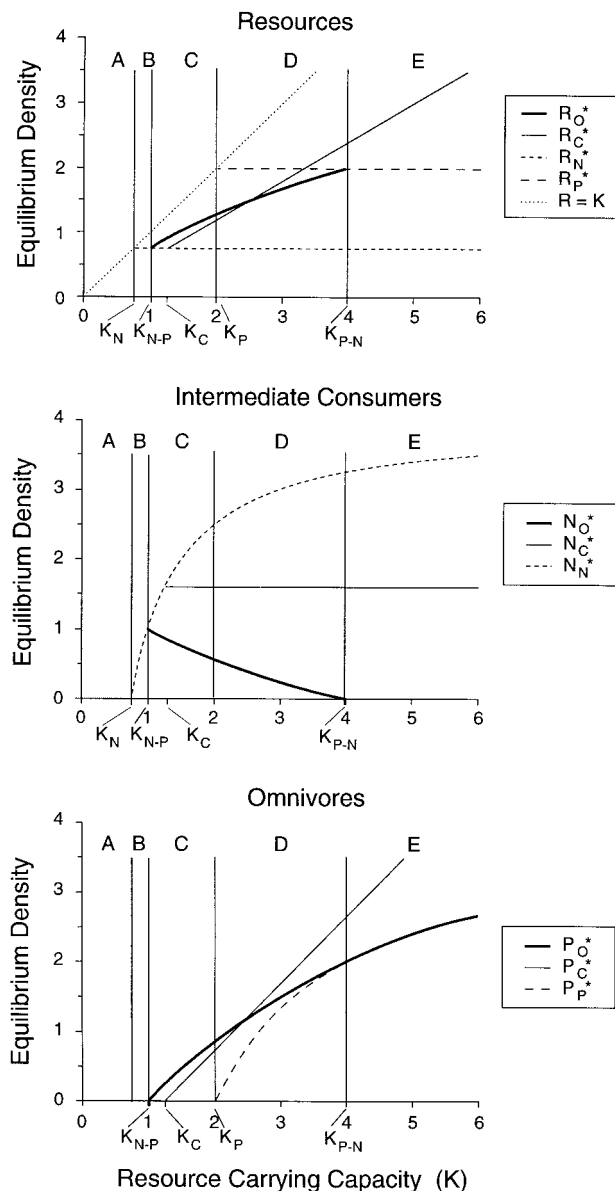
Figure 1: Equilibrium densities of resources, intermediate consumers, and top consumers as functions of resource-carrying capacity for the Lotka-Volterra omnivory model and its subsets of trophic configurations. Shown is an example of facilitation of the omnivore by the intermediate consumer (case 1, eq. [10]). Vertical lines crossing the abscissae at values K_i separate invasibility and coexistence regions A–E (see table 3). Also shown is K_C, the level of K above which a top consumer that does not feed on the resource ($a' = 0$) can invade an R-N system. For explanation of symbols, see table 2. Parameter values are $r = 0.4$, $a = 0.1$, $a' = 0.1$, $\alpha = 0.05$, $b = 0.8$, $b' = 0.2$, $\beta = 0.5$, $m = 0.06$, $m' = 0.04$.

of omnivores (eq. [7]), they will always be able to invade an R-P system (eq. [2] is positive) if P_P^* is small, that is, if K is equal or slightly larger than K_P. Beyond a threshold level of enrichment (K_{P-N}), however, P_P^* will be large enough to prevent the invasion of intermediate consumers (eq. [2] turns negative). The enrichment threshold K_{P-N} may not always exist because P_P^* may level off with increasing K at a density too low to turn the growth rate of an invading intermediate consumer negative. Whenever K_{P-N} exists, the following condition will be fulfilled:

$$K_N < K_P < K_{P-N}. \tag{9}$$

Conclusion 2

Intermediate consumers may facilitate or inhibit omnivores. Enrichment may revert the net effect of intermediate consumers from facilitation to inhibition.

If resources and intermediate consumers are at equilibrium in the absence of omnivores, resource density is fixed at R_N^*, and any increase in K increases the density N_N^* of intermediate consumers. Thus, the per capita growth rate of an invading omnivore $h(R_N^*, N_N^*)$ increases with increasing K. Because omnivores have a negative growth rate at R_N^* in the absence of intermediate consumers (eq. [7]), they will be unable to invade an R-N system (eq. [3] is negative) if N_N^* is small, that is, if K is only slightly larger than K_N. Only at a sufficiently high level of enrichment (K_{N-P}) can N_N^* become large enough to allow the invasion of omnivores (eq. [3] turns positive). Because N_N^* may level off with increasing K at a density insufficient to raise the growth rate of an invading omnivore above 0, K_{N-P} may not always exist.

Because intermediate consumers interact with omnivores both as prey and resource competitors, the net effect on omnivores may be facilitation or inhibition. Net inhibition occurs, for example, if intermediate consumers prevent omnivores from invading a stable R-N system at a level of enrichment where omnivores would otherwise be able to coexist with the resource alone (figs. 2, 3). This requires $K_P < K < K_{N-P}$ (table 3). In the opposite case ($K_{N-P} < K < K_P$), intermediate consumers facilitate omnivores; that is, omnivores can invade a system at a lower level of enrichment when intermediate consumers are present than when they are absent (table 3; fig. 1).

Whether the net effect of intermediate consumers on omnivores is positive or negative may, however, depend on enrichment. For example, omnivores can be facilitated (i.e., reach higher densities in the presence than in the absence of intermediate consumers) at one level of K but be inhibited at a different level of K (fig. 4).
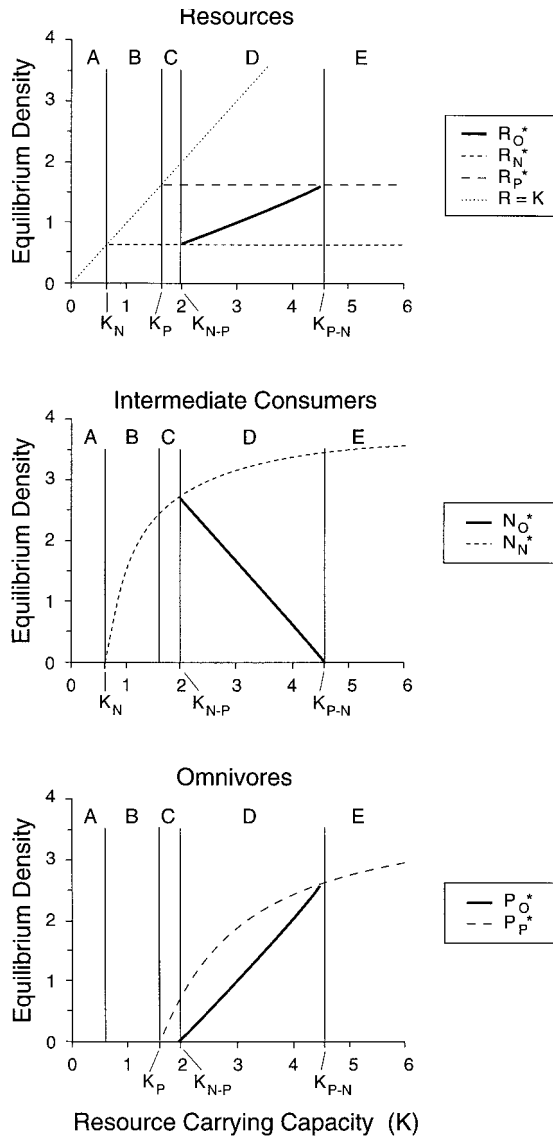
Figure 2: Equilibrium densities of resources, intermediate consumers, and top consumers as functions of resource-carrying capacity for the Lotka-Volterra omnivory model and its subsets of trophic configurations. Shown is an example of inhibition of the omnivore by the intermediate consumer (case 2, eq. [11]). Vertical lines crossing the abscissae at values K_i separate invasibility and coexistence regions A–E (see table 3). For explanation of symbols, see table 2. Parameter values are $r = 0.4$, $a = 0.1$, $a' = 0.1$, $\alpha = 0.03$, $b = 0.8$, $b' = 0.25$, $\beta = 0.3$, $m = 0.05$, $m' = 0.04$.

Conclusion 3

With enrichment, the system may go through up to four regions of invasibility and coexistence: at the lowest K, only R is present. At somewhat higher K, R and N can coexist. At intermediate K, either all three species coexist

or one consumer excludes the other. At the highest K, only R and P can coexist.

If all the above-threshold levels of K exist, we can distinguish three cases, which differ with respect to the ranking of K_{N-P} in equation (9):

$$\text{case 1:} \qquad K_N < K_{N-P} < K_P < K_{P-N}, \qquad (10)$$

$$\text{case 2:} \qquad K_N < K_P < K_{N-P} < K_{P-N}, \qquad (11)$$

$$\text{case 3:} \qquad K_N < K_P < K_{P-N} < K_{N-P}. \qquad (12)$$

In each of these cases, the four threshold levels of K separate five regions of enrichment (labeled A–E in table 3), which differ with respect to the invasibility of stable R-N and R-P systems by the respective other consumers and with respect to the species combinations that can co-
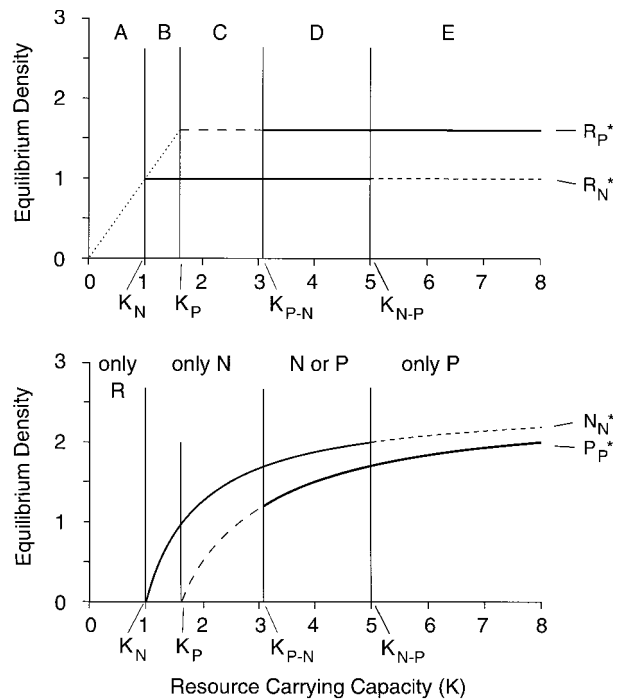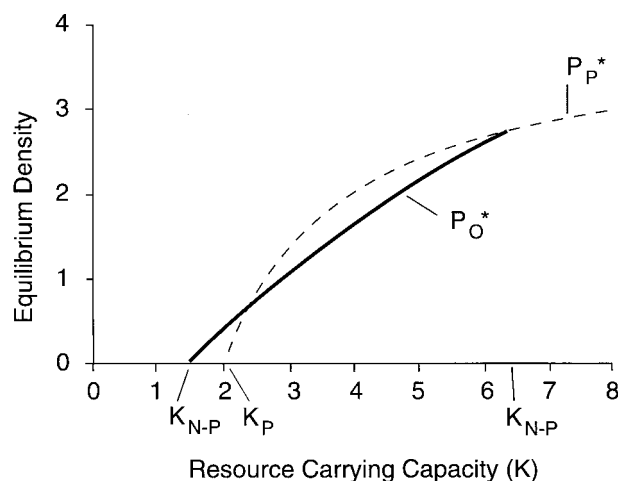

Figure 3: Equilibrium densities of resources, intermediate consumers, and top consumers as functions of resource-carrying capacity for the Lotka-Volterra omnivory model. Shown is an example of mutual inhibition of the intermediate consumer and the omnivore (case 3, eq. [12]). Vertical lines crossing the abscissae at values K_i separate invasibility and coexistence regions A–E (see table 3). Uninvasible states are indicated by solid lines. Note that stable coexistence of all three species is impossible and that mutually uninvasible states (either R-N or R-P) arise in the region D ($K_P < K < K_N$). For explanation of symbols, see table 2. Parameter values are $r = 0.25$, $a = 0.1$, $a' = 0.1$, $\alpha = 0.025$, $b = 0.5$, $b' = 0.25$, $\beta = 0.3$, $m = 0.05$, $m' = 0.04$.

exist stably. Regions A, B, and E have identical properties in all cases. In region A, enrichment is too low to sustain consumers and only the resource is present. In region B, enrichment is high enough to support intermediate consumers but still too low to support omnivores. In region E, enrichment is high enough to support omnivores on the resource alone at a sufficient density to exclude an invading intermediate consumer. Thus, an important result derived by Holt and Polis (1997) for the limited assumptions of the Lotka-Volterra omnivory model proves to be robust to the inclusion of nonlinear functional and numerical responses: the superior resource competitor (the intermediate consumer) may exclusively persist at low enrichment (region B) but may be excluded by apparent competition from the resource at high enrichment (region E).

The invasion and coexistence properties at intermediate levels of enrichment (regions C and D) depend on the net effect of intermediate consumers on the omnivore. If intermediate consumers facilitate omnivores (case 1, fig. 1), omnivores can invade an R-N system, and stable coexistence of all three species is possible in region C, in spite of the omnivore being unable to persist in this region with the resource alone. In region D, both consumers can mutually invade systems with the other consumer and the resource at equilibrium, and stable coexistence of all three species is again possible.

If intermediate consumers inhibit omnivores (cases 2 and 3), omnivores can persist in region C when alone, but intermediate consumers can always invade. In contrast, omnivores cannot invade a stable R-N system in region

Figure 4: Equilibrium densities of omnivores in the presence (P_O^*) and absence (P_P^*) of intermediate consumers as functions of resource-carrying capacity for the Lotka-Volterra omnivory model. Shown is an example of case 1, in which the intermediate consumer facilitates the omnivore at low K ($P_O^* > P_P^*$) but inhibits the omnivore at intermediate K ($P_O^* < P_P^*$). Above K_{P-N} the intermediate consumer is unable to coexist with the omnivore. Parameter values are $r = 0.4$, $a = 0.1$, $a' = 0.1$, $\alpha = 0.04$, $b = 0.8$, $b' = 0.2$, $\beta = 0.3$, $m = 0.05$, $m' = 0.04$.

C. If intermediate consumers inhibit omnivores only up to moderate levels of enrichment ($K_{N-P} < K_{P-N}$; case 2, fig. 2), both consumers can invade systems with the other consumer at equilibrium, and stable three-species coexistence is possible in region D. Conversely, if inhibition of the omnivore by the intermediate consumer is strong also

Table 3: Invasibility and stable coexistence regions of intermediate consumers (N) and omnivores (P) along a gradient of increasing carrying capacity (K) of the shared resource (R) for the three different cases defined by the rank order of four threshold levels of K (eqq. [8]–[10])

	Region A	Region B	Region C	Region D	Region E
Case 1	$K < K_N$	$K_N < K < K_{N-P}$	$K_{N-P} < K < K_P$	$K_P < K < K_{P-N}$	$K_{P-N} < K$
R-N system	Not possible	P cannot invade	P can invade	P can invade	P can invade
R-P system	Not possible	Not possible	Not possible	N can invade	N cannot invade
Noninvasible system[a]	R	R-N	R-N-P	R-N-P	R-P[b]
Case 2	$K < K_N$	$K_N < K < K_P$	$K_P < K < K_{N-P}$	$K_{N-P} < K < K_{P-N}$	$K_{P-N} < K$
R-N system	Not possible	P cannot invade	P cannot invade	P can invade	P can invade
R-P system	Not possible	Not possible	N can invade	N can invade	N cannot invade
Noninvasible system[a]	R	R-N	R-N[b]	R-N-P	R-P[b]
Case 3	$K < K_N$	$K_N < K < K_P$	$K_P < K < K_{P-N}$	$K_{P-N} < K < K_{N-P}$	$K_{N-P} < K$
R-N system	Not possible	P cannot invade	P cannot invade	P cannot invade	P can invade
R-P system	Not possible	Not possible	N can invade	N cannot invade	N cannot invade
Noninvasible system[a]	R	R-N	R-N[b]	R-N or R-P[b]	R-P[b]

[a] Nontrivial equilibrium states, which, if locally stable, are noninvasible by a missing consumer species at low density. These are the only feasible noninvasible, stable equilibrium states of the Lotka-Volterra model (eqq. [1]–[3]).

[b] The possibility that an additional stable R-N-P equilibrium exists under the assumptions of the general model (table 1) cannot be ruled out.

at high levels of enrichment ($K_{P-N} < K_{N-P}$; case 3, fig. 3), mutual invasibility is not possible, and two alternative, noninvasible stable states (R-N and R-P) arise in region D, which depend on initial conditions.

A cautionary note is needed here. Although mutual invasibility of equilibria with only one consumer by the other consumer is a necessary condition for stable three-species coexistence in the Lotka-Volterra model (Holt and Polis 1997), this condition may not always hold under the more general assumptions of the model in table 1; that is, three-species equilibria might be feasible in situations where only one of the consumers can invade a system with the other consumer at equilibrium (see footnotes to table 3).

Table 3 suggests an empirical research agenda. By first establishing (or failing to establish) R-N and R-P systems at various levels of enrichment and then introducing the respective missing consumer, questions can be answered, such as, Which consumer is the superior resource competitor? Is three-species coexistence possible? Does the omnivore exclude the intermediate consumer at high levels of enrichment? Does the intermediate consumer facilitate the omnivore? If not, is inhibition by the intermediate consumer strong enough to cause mutual consumer exclusion at high enrichment?

Conclusion 4

For stable equilibria of the omnivory system, resources always increase and intermediate consumers always decrease with enrichment.

Appendix B gives the equilibrium expressions for resources, intermediate consumers, and omnivores for the Lotka-Volterra omnivory model. A three-dimensional isocline graph illustrating the effects of enrichment on these equilibria is given in Diehl and Kornijow (1998). Rearrangement of equation (B1) yields

$$R_O^* = \frac{r\alpha\beta + a'm\beta - am'}{[(r\alpha\beta)/K] + a'a(b\beta - b')}. \tag{13}$$

Holt and Polis (1997) have shown that local stability of the Lotka-Volterra omnivory model with all three species present requires that the denominator in equation (13) be positive. From equations (13) and (B2), it can be seen that equilibrium densities of resources and intermediate consumers respond in opposite ways to increases in K; that is, resources increase and intermediate consumers decrease with increasing K (app. B; figs. 1, 2). In appendix A, we prove that these results are robust to the inclusion of nonlinear functional and numerical responses, that is, extend to the general model in table 1.

Inspection of equation (B3) reveals, furthermore, that the equilibrium density of the omnivore increases with increasing K in the case of Lotka-Volterra dynamics (app. B; figs. 1, 2). This result may not, however, always extend to the general model in table 1. As shown in appendix A, there is a chance that the omnivore might decrease with K if its functional response with respect to N is saturating. We have yet not verified the existence of this possibility nor explored the parameter space in which it might occur.

Conclusion 5

An omnivore can invade an R-N system at a lower K than an otherwise identical specialist predator on the intermediate consumer.

It is well known that invasibility of a consumer-resource system by a third trophic level requires a threshold level of enrichment (Oksanen et al. 1981; Gurney and Nisbet 1998). To see whether this threshold is lowered when the top consumer is an omnivore, we split the growth term of the omnivore, $h(R, N)$, in equation (3) into two components:

$$h(R, N) = [h_N(N) + h_R(R, N)]. \tag{14}$$

Here, h_N is the omnivore's growth rate when feeding exclusively on intermediate consumers, and h_R is the net benefit derived from feeding on resources, including costs of reduced feeding on intermediate consumers. Our assumption that inclusion of the resource in the omnivore's diet is adaptive ($\partial h(R, N)/\partial R > 0$) implies that this net benefit must be positive. With the resource at nonzero density, an omnivore would thus always attain a higher growth rate than an otherwise identical specialist predator of the intermediate consumer. Because intermediate consumers increase with enrichment in a stable R-N system, it is obvious that an omnivore would invade an R-N system at a lower level of enrichment (and a lower N_N^*) than a specialist predator on N (i.e., $K_{N-P} < K_C$; fig. 1).

Conclusion 6

An omnivore can always invade a linear food chain with an otherwise identical top consumer.

This follows directly from our assumption that $\partial h(R, N)/\partial R > 0$. Substituting the equilibrium density of the intermediate consumer in a food chain, N_C^*, for N in equation (14) shows that an omnivore will always have positive net population growth at the density of the intermediate consumer at which a specialist top consumer would be at equilibrium.

Conclusion 7

Intermediate consumers are always less abundant in omnivory systems than in corresponding food chains. At relatively low levels of enrichment, resources and top consumers are always more abundant in omnivory systems than in corresponding food chains. Further enrichment may reverse these relationships.

We have shown that an omnivore can invade an *R-N* system at a lower density N_N^* of the intermediate consumer than an otherwise identical specialist predator of *N*. Because the equilibrium density of the intermediate consumer is independent of *K* in a three-level food chain (e.g., eq. [B5]) but a decreasing function of *K* in an omnivory system (app. A), it follows that the equilibrium density of the intermediate consumer is always lower in the omnivory system than in the corresponding linear food chain ($N_O^* < N_C^*$; fig. 1).

Because an omnivore can invade an *R-N* system at a lower *K* than an otherwise identical specialist on *N*, at low *K* the density of the top consumer will always be higher in an omnivory system than in the corresponding food chain ($P_O^* > P_C^*$; fig. 1). At low *K*, the density of the resource will also be higher in the omnivory system than in the food chain ($R_O^* > R_C^*$; fig. 1). This follows from equation (7) and the fact that $R_C^* = R_N^*$ at the threshold level of *K* for invasion of the specialist predator on *N* (Oksanen et al. 1981).

These relationships may, however, be reversed with enrichment. For example, with increasing *K*, equilibrium resource and top consumer densities level off in the Lotka-Volterra omnivory system but increase linearly in the corresponding food chain (app. B; fig. 1). Thus, at sufficiently high *K*, the densities of all three populations may be lower in an omnivory system than in the corresponding food chain. The latter has an intriguing implication: invasion of a food chain by an omnivorous mutant of the top consumer (which derives a fitness benefit from being an omnivore) may lead to a decrease in population density at all trophic levels, that is, to a decrease in the efficiency with which productive capacity (as expressed by *K*) is converted into total community biomass.

Description of the Experiment

Study Organisms and Questions

The two ciliates *Tetrahymena pyriformis* (which feeds on bacteria) and *Blepharisma* (which feeds on bacteria and *Tetrahymena*) can coexist in microcosms with heterotrophic bacteria reared in an organic medium (Morin and Lawler 1996). Because of this potential for coexistence, we selected a *Blepharisma-Tetrahymena*-bacteria system to investigate whether the theory developed so far could qualitatively describe the effects of enrichment on a simple three-trophic level community with omnivory. We established communities of mixed bacteria and *Tetrahymena* in bottles containing differently enriched organic media and introduced *Blepharisma* in low numbers after *Tetrahymena* had reached their carrying capacities. This represents a first step of the research agenda suggested by table 3.

On the basis of model expectations, we asked the following specific questions. First, over a large range of enrichment, do we find one of the sequences of invasibility and coexistence regions listed in table 3? Second, if different coexistence regions occur, does *Tetrahymena* when alone depress bacteria to lower levels than does *Blepharisma* when alone? Are bacterial densities in communities with both protists intermediate to bacterial densities in communities with either protist alone? Third, over ranges of enrichment where all three species coexist, does the density of bacteria increase and the density of *Tetrahymena* decrease with enrichment? Fourth, if communities with only one of the two protists represent the persistent community state at several levels of enrichment, do the densities of that protist increase with enrichment, whereas the densities of bacteria stay constant?

Methods

Experimental microcosms were 100-mL Erlenmeyer flasks containing two wheat seeds and 50 mL of medium. Vessels, wheat seeds, and media were autoclaved before use. Lids of aluminum foil allowed some air circulation while restricting evaporation and contamination. We manipulated productivity by varying the concentration of the medium, using 0.1, one, three, five or seven "protozoan pellets" (Carolina Biological Supply, Burlington, N.C.; mass per pellet = 0.56 g) per liter of water (an equal mix of well water and distilled water). Media were prepared by suspension of seven ground pellets in 1 L of water. When particles had settled, the supernatant was removed and diluted to final concentrations.

We replicated each treatment four times. To each of the 20 microcosms, we added approximately 450 *Tetrahymena* with a mix of bacteria in 1 mL of medium from a stock culture and let them grow close to their carrying capacity (which is usually reached within 4–6 d). On day 4, we introduced approximately 100 *Blepharisma* with 1 mL of medium from another stock culture to each microcosm. Stock cultures were well mixed to ensure that all microcosms received the same bacterial inoculum. Microcosms were kept at room temperature on a shaded bench. On days 8, 14, 22, 29, 35, 42, 50, and 55, we removed 5 mL

of medium from each microcosm and replaced it with 6 mL of fresh medium.

Between days 4 and 61, we sampled protists two to three times per week. Because population dynamics had not yet stabilized on day 61 and replacement of medium seemed to perturb the microcosms, we stopped replacing medium and interrupted sampling until day 102. Between days 102 and 144, we sampled protists one to two times per week. We added 5 mL of fresh medium to each microcosm on days 132 and 140 to replace sampling and evaporation losses. Samples for bacterial counts were taken on days 132 and 139.

To count *Tetrahymena*, we took samples of 20–200 μL of medium and added a dilute Lugol's acid iodine solution to a volume of 220 μL. We counted all *Tetrahymena* in single or duplicate subsamples of 50 μL in a Nageotte chamber at $100\times$ magnification. To count *Blepharisma* (and *Tetrahymena* when it was rare), we took single or duplicate samples of 100–400 μL of medium and counted all protists under a dissecting microscope. To count bacteria, we removed samples of 100 μL of medium and preserved them with 200 μL of a 0.2-μm filtered 4% formaldehyde solution. Samples were stored in the dark at 4°C and treated with ultrasound to destroy bacterial aggregations before staining with the fluorochrome DAPI (4'6-diamidino-2-phenylindole; Porter and Feig 1980) and collection of the particulate fraction on a 0.2-μm black polycarbonate filter. Filters were stored in the dark at 4°C, and bacteria were counted by epifluorescence microscopy within 48 h.

Results

Establishment of both protists was successful in all microcosms; that is, *Tetrahymena* and *Blepharisma* increased initially. Peak densities of *Tetrahymena* (reached on days 4–8) ranged between 1,080 and 1,760; 1,800 and 2,700; 5,900 and 6,900; 9,900 and 11,100; and 17,000 and 20,400 individuals/mL in the 0.1-, one-, three-, five-, and seven-pellet treatments, respectively (fig. 5). Both peak densities and densities of *Tetrahymena* on day 4 (before *Blepahrisma* were added) were strongly related to enrichment (linear regressions of log peak density and log day-4 density vs. treatment, $R^2 = 0.94$, $P < .001$). Thus, enrichment of the organic medium appeared to produce the desired range of bacterial productivities and carrying capacities.

Initial dynamics were highly unstable (fig. 5). Introduction of *Blepharisma* was followed by an increase in *Blepharisma* and a decrease in *Tetrahymena* in all microcosms. Peak densities of *Blepharisma* (reached on days 8–46) ranged between three and eight, 70 and 140, 450 and 630, 650 and 860, and 670 and 870 individuals/mL in the 0.1-, one-, three-, five-, and seven-pellet treat-
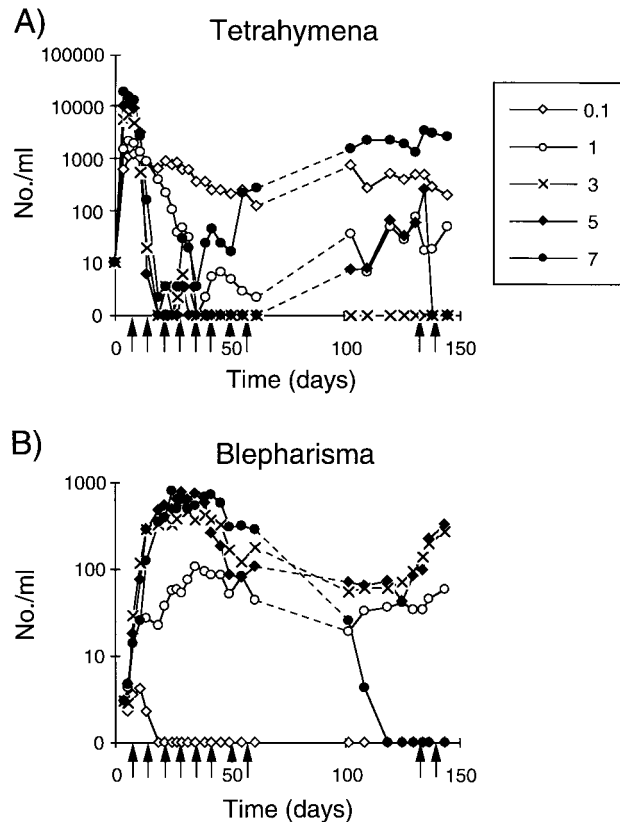
Figure 5: Time course of the densities of *Tetrahymena* and *Blepharisma* at various levels of enrichment of the organic medium (0.1, one, three, five, and seven pellets/L). Each data point is the average of four replicate microcosms. Vertical arrows denote days on which 10% of the medium was replaced with fresh medium. Note that no population counts were made between days 61 and 102.

ments, respectively. Peak densities were strongly related to enrichment (linear regression, $R^2 = 0.88$, $P < .001$) but leveled off between the five- and seven-pellet treatments.

Long-term community composition depended strongly on enrichment and was highly consistent among replicates. The four replicates of each treatment always settled to the same final community state with respect to the presence/absence of *Tetrahymena* and *Blepharisma*. Bacteria were, however, morphologically diverse, and replicate microcosms sometimes developed different microbial assemblages over the course of the experiment.

In the 0.1-pellet treatment, only *Tetrahymena* persisted (fig. 5). *Blepharisma* increased only marginally and then went rapidly extinct. No *Blepharisma* were found after day 19, and *Tetrahymena* settled to densities somewhat below initial peak densities.

The one-pellet treatment was the only one in which *Tetrahymena* and *Blepharisma* coexisted throughout the

experiment (fig. 5). Following the increase of *Blepharisma*, *Tetrahymena* declined below detection level on day 35, reappeared sporadically, and finally settled to densities in the range of five to 140 individuals/mL after day 102. After the initial peak, *Blepharisma* settled to slightly lower densities of five to 60 individuals/mL during days 102–130 to increase slightly after the addition of fresh medium on day 132.

In the three- and five-pellet treatments, only *Blepharisma* persisted in the long run (fig. 5). *Tetrahymena* declined below detection level on day 19 and was never found again in the three-pellet treatment and two replicates of the five-pellet treatment after day 32. In the two remaining replicates of the five-pellet treatment, *Tetrahymena* and *Blepharisma* coexisted over a long period without disturbance. After the addition of fresh medium on day 132, *Tetrahymena* went extinct also in those microcosms. After the initial peaks, densities of *Blepharisma* settled to levels of 25–140 individuals/mL during days 102–130 in both the three- and five-pellet treatments to increase slightly after the addition of fresh medium on day 132.

In the seven-pellet treatment, only *Tetrahymena* persisted in the long run (fig. 5). *Tetrahymena* declined below detection level on day 19. Past day 35, it slowly increased, settled to densities of 900–2,500 individuals/mL during days 102–130, to increase slightly again after fresh medium was added on day 132. *Blepharisma* started to decline on day 50. It persisted in two replicates until day 102 but was not found after day 109.

Comparison of Experimental Data to Model Predictions

To compare our experimental results to model predictions, we used data from days 102–144 of the experiment when the microcosms had settled to relatively stable states. For each microcosm, we calculated average densities of *Tetrahymena* and *Blepharisma*, unless an extinction occurred during that period. In that case, the extinct species was counted as zero. The remaining species' density was still averaged over days 102–144 because extinctions never led to conspicuous shifts in abundance of a remaining species. Bacterial counts were made on days 133 and 139 and averaged for each microcosm. To support the test of a priori hypotheses derived from model predictions with statistical evidence, we performed (after one-way ANOVA) correlations and pairwise comparisons for selected combinations of treatment and response variables. Because the assumptions of parametric statistics were not met in a few cases, we consistently used nonparametric tests.

Enrichment had strong and statistically highly significant effects on the densities of bacteria, *Tetrahymena*, and *Blepharisma* (fig. 6; table 4). Below, we discuss the results
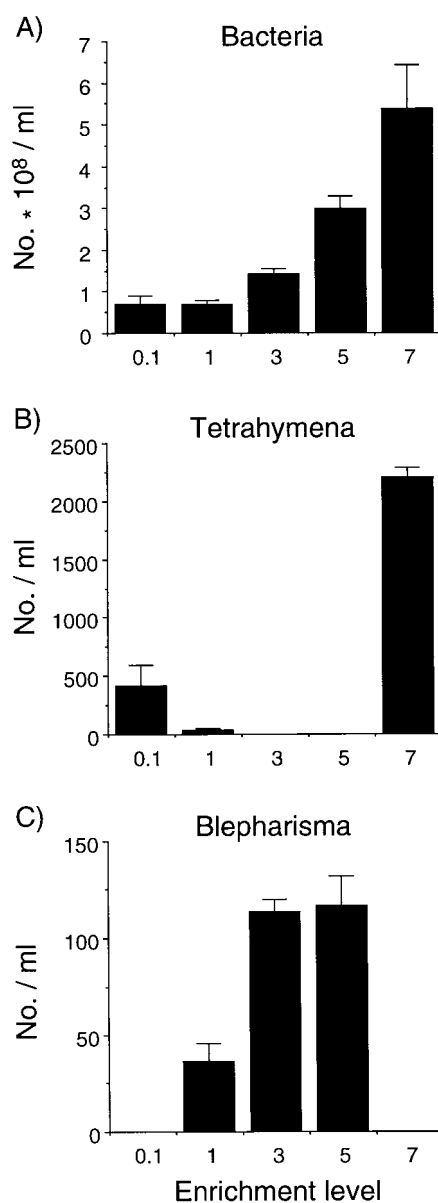
Figure 6: Average densities (± 1 SE) of (*A*) bacteria, (*B*) *Tetrahymena*, and (*C*) *Blepharisma* as functions of enrichment (0.1, one, three, five, and seven pellets/L) after microcosms had settled to their long-term community states. Densities of bacteria are averages of days 132 and 139. Densities of *Tetrahymena* and *Blepharisma* are averaged over days 102–144; $N = 4$ replicate microcosms for each enrichment level.

in the context of the four specific questions raised above (see "Study Organisms and Questions").

First, we found a sequence of coexistence regions that would be largely compatible with the patterns predicted for cases 1 and 2 in table 3 (fig. 6). At low enrichment, only *Tetrahymena* persisted, whereas both protists coexisted at the next higher enrichment level. This is consistent

Table 4: Summary of statistics of enrichment effects on the densities of bacteria, *Tetrahymena*, and *Blepharisma*

Population	ANOVA P value[a]	Spearman rank correlation[b] R_s	P value	Mann-Whitney U-test Pairwise comparison	P value
Bacteria	<.001	.68	<.02	.1 versus 1 pellet	NS[c, d]
				.1 versus 3 pellets	.05[d]
				.1 versus 7 pellets	.05[e]
				1 versus 3 pellets	.025[d]
				3 versus 5 pellets	.05[e]
Tetrahymena	<.001	−.93	<.001	.1 versus 7 pellets	.025[d]
Blepharisma	<.001	.96	<.001	3 versus 5 pellets	NS[c, d]

[a] Kruskal-Wallis one-way ANOVAs on all data.
[b] Treatment range in all three populations = 0.1–3 pellets.
[c] NS = not significant, $P > .1$.
[d] One-tailed test (models predict positive effect of enrichment on abundance).
[e] Two-tailed test (models predict no effect of enrichment on abundance).

with the predictions that the intermediate consumer must be the superior resource competitor to be able to coexist with the omnivore and that a threshold level of enrichment must be reached before the omnivore can invade. At intermediate to high enrichment levels, *Blepharisma* persisted alone. This is consistent with the prediction that, beyond a threshold of enrichment, the shared resource may support a level of predation by the omnivore on the intermediate consumer that leads to the exclusion of the latter through apparent competition. The observation that, at the highest enrichment level, *Blepharisma* went extinct while *Tetrahymena* persisted alone is, however, inconsistent with this latter prediction.

Second, consistent with expectations, bacterial densities were lower in both the persistent omnivory system (one pellet) and the 0.1-pellet system with *Tetrahymena* alone than in the systems with *Blepharisma* alone (three and five pellets; fig. 6*A*; table 4). In contrast to expectations, bacterial densities did not differ between the persistent omnivory system and the 0.1-pellet system with *Tetrahymena* alone (fig. 6*A*; table 4).

Third, because long-term coexistence of both protists occurred only at one enrichment level, we could not fully address the question of how population densities are affected by enrichment when all three trophic levels coexist. Instead, we correlated the densities of bacteria, *Tetrahymena*, and *Blepharisma* with enrichment across the range of treatments that bounded the coexistence region. Consistent with expectations, those correlations were positive for bacteria (and *Blepharisma*) and negative for *Tetrahymena* (table 4).

Fourth, consistent with expectations, densities of *Tetrahymena* when alone increased with enrichment (0.1- vs. seven-pellet treatments; fig. 6*B*, table 4). In contrast, en-

richment did not affect the densities of *Blepharisma*, when alone (three- vs. five-pellet treatments; fig. 6*C*, table 4). While the model predicts that the abundance of the resource should not be affected by enrichment in a two-trophic-level system, bacteria increased with enrichment in both *Tetrahymena*-bacteria systems and *Blepharisma*-bacteria systems (0.1- vs. seven-pellet treatments and three- vs. five-pellet treatments; fig. 6*A*; table 4).

Discussion

Effects of Enrichment on Trophic-Level Abundances

The theoretical analysis of enrichment effects on the abundances of resources, intermediate consumers, and omnivores produced three nonintuitive results. First, the sign of the net effect of intermediate consumers on the density of omnivores may depend on enrichment. This possibility arises even under the limited assumptions of the Lotka-Volterra model, suggesting that such enrichment effects may be even more likely under the broader assumptions of the general model in table 1.

Second, omnivory, although beneficial to individual top consumers, may lower the densities of all trophic levels compared to a food chain (e.g., beyond $K = 2.5$; fig. 1). This seems to contradict the conventional wisdom that feeding lower in the food chain increases transfer efficiency of energy and matter to a given trophic level (Begon et al. 1996). However, in figure 1, parameters were chosen such that $b\beta - b' > 0$, which implies that resources are more efficiently converted into omnivores if consumed indirectly in the form of intermediate consumers rather than directly. In this case, enrichment decreases transfer efficiency from resources to omnivores because interme-

diate consumers become increasingly rare. Simulations indicate that in the opposite case ($b\beta - b' < 0$), the Lotka-Volterra omnivory system becomes unstable at levels of K where omnivores would reach lower densities than top consumers in the corresponding food chain (S. Diehl, unpublished data).

The possibility of lower total community biomass in an omnivory system compared to an otherwise identical food chain can only arise if the resource is a living organism whose production depends on its own density. The phenomenon cannot occur in Thingstad et al.'s (1996) model of an aomnivory system consisting of a nutrient (resource), a bacterium (intermediate consumer), and a mixotrophic flagellate (omnivore) because of a mass balance constraint. Thingstad et al. expressed the abundances of mixotrophs and bacteria in units of the nutrient. Consequently, free nutrients and nutrients bound up in consumers (the sum of which corresponds to total community biomass in our model) must always add up to the (constant) total amount of nutrients in the system, irrespective of trophic structure.

Third, for stable three-species systems, intermediate consumers decrease with enrichment in spite of a simultaneous increase in their food. Here, enrichment sustains an increasing predation pressure from the omnivore on the intermediate consumer that outweighs the positive effect of increasing resource density on the intermediate consumer's growth rate. A similar increase in importance of apparent competition with enrichment is also observed in models of two or more consumers who compete for a shared resource and also share a predator (Holt et al. 1994; Leibold 1996; Chase 1999).

The predicted negative response of intermediate consumers to enrichment questions the applicability of food chain theory to communities with omnivores. If a three-species omnivory system is simplified to a food chain, the intermediate species may be assigned a separate trophic level, it may be ignored, or it may be combined with either its resource or its predator into a single trophic level. In neither case would the responses of equilibrium trophic level abundances to enrichment conform to the predictions of standard food chain theory. In the first case, the intermediate trophic level would decrease with enrichment instead of remaining constant. In the other cases, "adjacent" trophic levels (R vs. P, $R + N$ vs. P, or R vs. $N + P$) would frequently show positive (and, in some cases, negative) correlations instead of no correlations along enrichment gradients. In food chain analyses, species are routinely aggregated into trophic levels. The frequent finding of positive correlations of adjacent trophic levels with enrichment (e.g., Hansson 1992; Mazumder 1994) may, in part, be related to the widespread occurrence of omnivory.

Sufficient data to address any of the nonintuitive enrichment effects in protist systems discussed here are not yet available. We could not strictly test the prediction that intermediate consumers decrease with enrichment in stable three-species omnivory systems because the two protists coexisted only in one treatment. Interpolation across the two adjacent treatments suggests, however, that *Tetrahymena* is likely to decrease with enrichment over the narrow range that permits coexistence with *Blepharisma*. In the only other enrichment study of an omnivory system of which we are aware, the omnivore *Blepharisma americanum* coexisted with the bacterivorous ciliate *Colpidium striatum* only at one enrichment level, again precluding a test of enrichment effects on the intermediate consumer's abundance across a range of persistent omnivory systems (Morin 1999).

Coexistence Regions

Our model analysis corroborates three important theoretical results concerning the coexistence of omnivores and intermediate consumers (Polis and Holt 1992; Thingstad et al. 1996; Holt and Polis 1997). First, stable coexistence of omnivores and intermediate consumers occurs only over limited parameter space. Second, coexistence requires that the intermediate consumer is able to exclude the omnivore at lower levels of enrichment. Third, the omnivore may exclude the intermediate consumer at high levels of enrichment.

Our experimental data and data from other protist studies are in fairly good agreement with these predictions. *Blepharisma* and *Tetrahymena* coexisted only in the one-pellet treatment, suggesting that coexistence regions may be narrow (or nonexistent) for other species pairs, too. At the lowest level of enrichment, only *Tetrahymena* persisted, whereas exclusive persistence of *Blepharisma* only occurred at higher enrichment levels. Similarly, *Colpidium striatum* excluded *B. americanum* at low enrichment (0.5 protozoan pellets/L), whereas coexistence was still observed after 62 d in some replicates at intermediate enrichment (two pellets/L; Morin 1999). Weatherby et al. (1998) found that *Blepharisma japonicum* always excluded *Tetrahymena pyriformis*, whereas *Colpidium striatum* was excluded in two out of six microcosms after 101 d. It is not known how the medium used by Weatherby et al. compares to protozoan pellets.

In our experiment, the observed coexistence pattern of the two protists may have been affected by transient dynamics. Stable omnivory systems frequently approach their equilibria in an oscillatory manner (S. Diehl, unpublished data), and transient periods of low density may lead to stochastic extinctions in real world systems. In models of unstable food chains, enrichment tends to increase the amplitudes of population oscillations (Abrams and Roth

1994*a*). In our experiment, the amplitudes of population fluctuations during transient dynamics were correlated with enrichment. *Tetrahymena* repeatedly recovered from population densities below detection level, but *Blepharisma* always went extinct once it had become that rare. It is thus possible that the unpredicted extinction of *Blepharisma* at the highest enrichment level was a consequence of transient population fluctuations and a limited ability to recover from low-population densities. Addressing the issue of deterministic versus stochastic extinction requires experiments in which consumers are repeatedly reintroduced following their extinction.

Alternative Explanations

In contrast to the consumer trophic levels, the resource level in our experiment was a mix of taxa. Bacterial taxa may vary with respect to their abilities to compete for food and to withstand predation from protists (Sinclair and Alexander 1989; Cochran-Safira and von Ende 1998). Our results on bacteria are thus open to alternative explanations. For example, the bacterial increase over most of the enrichment gradient could be related to shifts toward more predation resistant taxa. We could not assess predation resistance of bacteria, but the data indicate that compositional changes within the bacterial trophic level occurred with enrichment. Bacterial densities were, in the exclusive presence of either *Tetrahymena* or *Blepharisma*, always higher at higher enrichment levels. This conflicts with expectations from one-resource/one-consumer models but would be predicted by models including a second, less edible resource (Leibold 1989; Kretzschmar et al. 1993; Grover 1995). How changes in resource edibility might affect higher trophic levels in models of omnivory system is presently not known.

An ideal empirical evaluation of our omnivory model would require the use of axenic protist cultures along with a single bacterial species. Still, Kaunzinger and Morin (1998) found unpredicted (weak) positive enrichment effects on bacterial abundances in a bacteria-*Colpidium* system even when bacteria were from a single, edible strain. This suggests that protist microcosms, even if stocked with mobile, well-mixing taxa such as *Colpidium*, *Tetrahymena*, or *Blepharisma*, may not entirely conform to the assumptions on which the model predictions were based. For example, instabilities in the consumer-resource interactions (cf. weak population fluctuations during days 102–144) or spatial heterogeneity (e.g., aggregation of bacteria on particles) can produce correlations of enrichment and mean resource abundance in consumer-resource systems (Abrams and Roth 1994*b*; Scheffer and de Boer 1995).

Other possible mechanisms producing such positive correlations in protist microcosms include interference among bacteria and consumers via build up of waste products. The latter mechanism might be an alternative explanation for the unpredicted extinction of *Blepharisma* in the seven-pellet treatment. We stopped replacing medium after day 55, and waste products may subsequently have reached inhibitory levels.

Benefits and Trade-Offs of Omnivory

The intuitive notion that omnivory is beneficial to a consumer is supported by our model analyses in two ways. First, all other feeding, conversion, and mortality rates being equal, an omnivore can only do better than a specialist consumer of the resource because the latter could always be displaced by a competitively superior intermediate consumer. Also, omnivores will attain higher population densities in the presence than in the absence of intermediate consumers if the net effects of intermediate consumers on omnivores are positive. So far, these expectations cannot be evaluated for bacteria-protist systems. Bacterial densities are rarely monitored, and we are unaware of studies in which equilibrium bacterial densities (and thus competitive consumer rankings) were determined for intermediate consumers and omnivores in the absence of each other. There is, however, an example of an omnivore benefiting from an intermediate consumer. In a one-pellet medium, *B. americanum* was on average 2.75 times more abundant when grown with *T. pyriformis* than when grown with only bacteria (Lawler and Morin 1993).

Second, with all other rates being equal, an omnivore is also superior to a specialist consumer of the intermediate resource. Such an omnivore can always invade a food chain with the specialist and can furthermore invade a two-trophic level system at a lower level of enrichment than the specialist. These predictions have some empirical support. When two omnivorous and six specialist protists were cultured separately with ciliate prey, both omnivores attained higher densities than any of the specialists (Morin and Lawler 1996). The mixotrophic flagellate *Ochromonas* grew, at given bacterial densities, always better in the light (when it consumed both bacteria and a shared limiting nutrient) than in the dark (when it consumed only bacteria; Rothhaupt 1996*b*). The *Ochromonas*-bacteria system may best meet the assumption of "all other rates being equal" because the functional response of *Ochromonas* with respect to bacteria was identical in the light and in the dark.

The double advantage of omnivores over specialist consumers can only play out fully, if the "all other rates being equal" assumption is met. Yet, the benefits of the omnivorous strategy must be balanced by inherent costs, otherwise omnivory would be even more widespread than it

already is. Empirical data do indeed indicate that omnivores face trade-offs in their resource use efficiencies. We have already cited evidence that the specialists *Tetrahymena* and *Colpidium* seem to be more efficient users of bacteria than the omnivore *Blepharisma*. Similarly, some of the specialist consumers of ciliates studied by Morin and Lawler (1996) depressed ciliate prey to lower levels than did the two omnivores, indicating a competitive advantage of these specialists over the omnivores. Finally, when cultured in the dark (when only phagotrophy was possible), *Ochromonas* was competitively displaced by the specialist bacterivore *Bodo* (Rothhaupt 1996a).

Better knowledge of the costs and trade-offs inherent to the omnivorous strategy should provide a base for the study of further interesting issues, such as the potential for coexistence of omnivores with specialist consumers (as pioneered by Thingstad et al. 1996) or of optimal strategies for the allocation of (morphological, physiological, behavioral, etc.) effort to the consumption of resources and intermediate consumers by omnivores in given environments.

APPENDIX A

Changes in Equilibrium Densities with Increasing K

The full model takes the form

$$\frac{dR}{dt} = rR\rho(R, K) - a(R)N - f(R, N)P, \quad \text{(A1)}$$

$$\frac{dN}{dt} = g(R)N - c(R, N)P - mN, \quad \text{(A2)}$$

$$\frac{dP}{dt} = h(R, N)P - m'P. \quad \text{(A3)}$$

If we define

$$\theta_1(R, N, P, K) = rR\rho(R, K) - a(R)N - f(R, N)P,$$
$$\theta_2(R, N, P) = g(R)N - c(R, N)P - mN, \quad \text{(A4)}$$
$$\theta_3(R, N, P) = h(R, N)P - m'P,$$

then at equilibrium, $\theta_1(R^*, N^*, P^*, K) = 0$, $\theta_2(R^*, N^*, P^*) = 0$, and $\theta_3(R^*, N^*, P^*) = 0$.

We want to know whether the equilibrium values of R, N, and P increase or decrease as K increases. Consider a small change δK in K. The corresponding changes δR^*, δN^*, and δP^* can be calculated as

$$0 = \delta\theta_1 = \frac{\partial\theta_1}{\partial R}\delta R^* + \frac{\partial\theta_1}{\partial N}\delta N^* + \frac{\partial\theta_1}{\partial P}\delta P^* + \frac{\partial\theta_1}{\partial K}\delta K,$$

$$0 = \delta\theta_2 = \frac{\partial\theta_2}{\partial R}\delta R^* + \frac{\partial\theta_2}{\partial N}\delta N^* + \frac{\partial\theta_2}{\partial P}\delta P^*, \quad \text{(A5)}$$

$$0 = \delta\theta_3 = \frac{\partial\theta_3}{\partial R}\delta R^* + \frac{\partial\theta_3}{\partial N}\delta N^* + \frac{\partial\theta_3}{\partial P}\delta P^*,$$

that is,

$$\mathbf{J}_3\begin{bmatrix}\delta R^*\\\delta N^*\\\delta P^*\end{bmatrix} = -\frac{\partial\theta_1}{\partial K}\begin{bmatrix}\delta K\\0\\0\end{bmatrix}, \quad \text{(A6)}$$

where

$$\mathbf{J}_3 = \begin{bmatrix}\frac{\partial\theta_1}{\partial R} & \frac{\partial\theta_1}{\partial N} & \frac{\partial\theta_1}{\partial P}\\\frac{\partial\theta_2}{\partial R} & \frac{\partial\theta_2}{\partial N} & \frac{\partial\theta_2}{\partial P}\\\frac{\partial\theta_3}{\partial R} & \frac{\partial\theta_3}{\partial N} & \frac{\partial\theta_3}{\partial P}\end{bmatrix}. \quad \text{(A7)}$$

Note that the (Jacobian) matrix $\mathbf{J}_3$ on the left-hand side of equation (A6) is the matrix that appears in routine local stability analyses. The signs of most matrix elements can be determined from the inequalities in table 1, the result being

$$\mathbf{J}_3 = \begin{bmatrix}? & ? & -\\+ & ? & -\\+ & + & 0\end{bmatrix}. \quad \text{(A8)}$$

If we are describing a locally stable equilibrium, the determinant

$$\Gamma \equiv \frac{\partial\theta_1}{\partial N}\frac{\partial\theta_2}{\partial P}\frac{\partial\theta_3}{\partial R} + \frac{\partial\theta_1}{\partial P}\frac{\partial\theta_2}{\partial R}\frac{\partial\theta_3}{\partial N} - \frac{\partial\theta_1}{\partial R}\frac{\partial\theta_2}{\partial P}\frac{\partial\theta_3}{\partial N} - \frac{\partial\theta_1}{\partial P}\frac{\partial\theta_2}{\partial N}\frac{\partial\theta_3}{\partial R}$$

(A9)

must be negative. From this point on, we assume $\Gamma < 0$, which implies that $\mathbf{J}_3$ has an inverse. Equation (A6) can thus be solved to give

$$\begin{bmatrix} \delta R^* \\ \delta N^* \\ \delta P^* \end{bmatrix} = -\frac{\partial\theta_1}{\partial K}\mathbf{J}_3^{-1}\begin{bmatrix} \delta K \\ 0 \\ 0 \end{bmatrix},$$

(A10)

with

$$\mathbf{J}_3^{-1} =$$

$$\Gamma^{-1}\begin{bmatrix} -\dfrac{\partial\theta_2}{\partial P}\dfrac{\partial\theta_3}{\partial N} & \dfrac{\partial\theta_1}{\partial P}\dfrac{\partial\theta_3}{\partial N} & \dfrac{\partial\theta_1}{\partial N}\dfrac{\partial\theta_2}{\partial P} - \dfrac{\partial\theta_1}{\partial P}\dfrac{\partial\theta_2}{\partial N} \\[2ex] \dfrac{\partial\theta_2}{\partial P}\dfrac{\partial\theta_3}{\partial R} & -\dfrac{\partial\theta_1}{\partial P}\dfrac{\partial\theta_3}{\partial R} & \dfrac{\partial\theta_1}{\partial P}\dfrac{\partial\theta_2}{\partial R} - \dfrac{\partial\theta_1}{\partial R}\dfrac{\partial\theta_2}{\partial P} \\[2ex] \dfrac{\partial\theta_2}{\partial R}\dfrac{\partial\theta_3}{\partial N} - \dfrac{\partial\theta_2}{\partial N}\dfrac{\partial\theta_3}{\partial R} & \dfrac{\partial\theta_1}{\partial N}\dfrac{\partial\theta_3}{\partial R} - \dfrac{\partial\theta_1}{\partial R}\dfrac{\partial\theta_3}{\partial N} & \dfrac{\partial\theta_1}{\partial R}\dfrac{\partial\theta_2}{\partial N} - \dfrac{\partial\theta_1}{\partial N}\dfrac{\partial\theta_2}{\partial R} \end{bmatrix}.$$

(A11)

It follows that

$$\delta R^* = -\Gamma^{-1}\frac{\partial\theta_1}{\partial K}\left(-\frac{\partial\theta_2}{\partial P}\frac{\partial\theta_3}{\partial N}\right)\delta K,$$

(A12)

$$\delta N^* = -\Gamma^{-1}\frac{\partial\theta_1}{\partial K}\frac{\partial\theta_2}{\partial P}\frac{\partial\theta_3}{\partial R}\delta K,$$

(A13)

$$\delta P^* = -\Gamma^{-1}\frac{\partial\theta_1}{\partial K}\left(\frac{\partial\theta_2}{\partial R}\frac{\partial\theta_3}{\partial N} - \frac{\partial\theta_2}{\partial N}\frac{\partial\theta_3}{\partial R}\right)\delta K.$$

(A14)

Using the signs in equation (A8) and noting that $\Gamma < 0$ and $\partial\theta_1/\partial K > 0$, we find

$$\frac{\delta R^*}{\delta K} > 0; \qquad \frac{\delta N^*}{\delta K} < 0; \qquad \frac{\delta P^*}{\delta K} = ?$$

Thus, we find that, for locally stable equilibria, an increase in K leads to an increase in R^* and a decrease in N^*. The sign of the effect of an increase in K on the density of the omnivore remains undetermined. A necessary (but not sufficient) condition for the omnivore to decrease with K is $\partial\theta_2/\partial N > 0$. The latter requires that the functional re- sponse of the omnivore with respect to N be decelerating (saturating) at equilibrium.

APPENDIX B

Steady State Solutions for the Lotka-Volterra Omnivory Model

The following are the steady state solutions for the densities of resources (R^*), intermediate consumers (N^*), and top consumers (P^*) for the Lotka-Volterra omnivory model (eqq. [4]–[6]) and its subsets of trophic configurations. Subscripts of equilibrium expressions denote trophic configurations (O = omnivory system; C = linear food chain; P = R-P system; and N = R-N system).

R-N-P Omnivory System

$$R_O^* = K\frac{r\alpha\beta + a'm\beta - am'}{r\alpha\beta + Ka'a(b\beta - b')},$$

(B1)

$$N_O^* = \frac{m' - a'b'R_O^*}{\alpha\beta},$$

(B2)

$$P_O^* = \frac{abR_O^* - m}{\alpha}.$$

(B3)

R-N-P Linear Food Chain

$$R_C^* = K\frac{r\alpha\beta - am'}{r\alpha\beta},$$

(B4)

$$N_C^* = \frac{m'}{\alpha\beta},$$

(B5)

$$P_C^* = \frac{abR_C^* - m}{\alpha}.$$

(B6)

R-P System

$$R_P^* = \frac{m'}{a'b'},$$

(B7)

$$P_P^* = \frac{r}{a'}\left(1 - \frac{R_P^*}{K}\right). \tag{B8}$$

R-N System

$$R_N^* = \frac{m}{ab}, \tag{B9}$$

$$N_N^* = \frac{r}{a}\left(1 - \frac{R_N^*}{K}\right). \tag{B10}$$

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