

Adaptive omnivory and species coexistence in tri-trophic food webs

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Abstract

The commonness of omnivory in natural communities is puzzling, because simple dynamic models of tri-trophic systems with omnivory are prone to species extinction. In particular, the intermediate consumer is frequently excluded by the omnivore at high levels of enrichment. It has been suggested that adaptive foraging by the omnivore may facilitate coexistence, because the intermediate consumer should persist more easily if it is occasionally dropped from the omnivore's diet. We explore theoretically how species permanence in tri-trophic systems is affected if the omnivore forages adaptively according to the "diet rule", i.e., feeds on the less profitable of its two prey species only if the more profitable one is sufficiently rare. We show that, compared to systems where omnivory is fixed, adaptive omnivory may indeed facilitate 3-species persistence. Counter to intuition, however, facilitation of 3-species coexistence requires that the intermediate consumer is a more profitable prey than the basal resource. Consequently, adaptive omnivory does not facilitate persistence of the intermediate consumer but enlarges the persistence region of the omnivore towards parameter space where a fixed omnivore would be excluded by the intermediate consumer. Overall, the positive effect of adaptive omnivory on 3-species persistence is, however, small. Generally, whether omnivory is fixed or adaptive, 3-species permanence is most likely when profitability (= conversion efficiency into omnivores) is low for basal resources and high for intermediate consumers.

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1. Introduction

Omnivory, the consumption of resources from more than one trophic level, is very common in natural communities (Polis et al., 1989; Diehl, 1993; Coll and Guershon, 2002). This empirical fact contrasts sharply with theoretical expectations, because stable persistence of omnivores and intermediate consumers is difficult to achieve in simple dynamical models (Pimm and Lawton, 1978). The two most consistent predictions from mathematical formulations of 3-species omnivory sys-

tems are: (i) stable coexistence of the omnivore and the intermediate consumer requires the intermediate consumer to be the superior competitor for the shared resource (Holt and Polis, 1997), and (ii) such coexistence is—if at all—only possible at intermediate levels of resource productivity (Holt and Polis, 1997; Diehl and Feissel, 2000; Mylius et al., 2001; Borer et al., 2003). A key component of the latter prediction is that high levels of resource productivity (usually modeled as resource renewal rate or carrying capacity) promote the exclusion of intermediate consumers by the omnivore.

Empirical tests of these model predictions are still rare but have only in part been consistent with expectations. In several studies, omnivores did not persist with intermediate consumers in low productivity environments but did so at higher levels of productivity (Morin,

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1999; Amarasekare, 2000; Diehl and Feissel, 2000). In contrast, only one study has documented the predicted exclusion of the intermediate consumer at yet higher levels of productivity (Diehl and Feissel, 2000). Two other well-studied tri-trophic omnivory systems [zooplankton-roach (*Rutilus rutilus*)-perch (*Perca fluviatilis*) and California red scale-*Encarsia perniciosis*-*Aphytis melinus*] conform to the assumption that the intermediate consumer is the superior competitor for the shared resource. Yet the 3-species systems persist over the entire ranges of naturally occurring resource productivities (Mylius et al., 2001; Borer et al., 2003). Clearly, there is a discrepancy between theory and data, which Holt and Polis (1997) termed “a puzzle in species coexistence: models with strong omnivory are prone to species exclusion, particularly in productive environments. Yet such systems are common in natural communities”.

Theoretical evidence suggests that the addition of a weak amount of omnivory can actually stabilize otherwise unstable food chains and that such weak interactions may be common in natural communities (McCann and Hastings, 1997; McCann et al., 1998; Montoya and Solé, 2003). More generally, however, the addition of omnivorous feeding links to model communities seems to decrease the overall parameter space in which these communities persist (Law and Blackford, 1992; Fussmann and Heber, 2002). Also, some of the more intensely studied natural omnivory systems appear to show rather tightly coupled dynamics (Amarasekare, 2000; Eubanks and Denno, 2000; Borer et al., 2003; Stibor et al., 2004). The search for robust mechanisms that can explain persistence of tightly linked omnivory systems therefore remains an important challenge (HilleRisLambers and Dieckmann, 2003).

Holt and Polis (1997) suggested that adaptive behaviors may facilitate coexistence. In particular, they proposed that, if adaptive foraging by the omnivore leads to switching between the basal resource and the intermediate consumer, the system should be stabilized. Using somewhat different model formulations, Gismervik and Andersen (1997) and Krivan (2000) have indeed shown that switching by the omnivore may greatly expand the region of stable coexistence towards higher resource productivities. Common to both of these models is the assumption that feeding by the omnivore on the basal resource and the intermediate consumer, respectively, requires mutually exclusive foraging modes (e.g., different morphologies, search modes or search in separate microhabitats). Search for alternative prey types is, however, frequently non-exclusive. In that case, an omnivore must decide upon each encounter with a resource or an intermediate consumer whether to feed on it or not. This is the familiar diet choice situation in classical optimal foraging theory, for which the “diet rule” predicts that inclusion of an encountered prey depends on its relative profitability (as determined by its

nutritional value per handling time) and the abundances of more profitable prey items (Werner and Hall, 1974; Stephens and Krebs, 1986).

According to the diet rule, a less profitable prey will be dropped from the diet whenever the densities of more profitable prey items exceed some threshold value. It thus seems plausible to hypothesize that optimal foraging according to the diet rule might facilitate persistence of the intermediate consumer in a 3-species omnivory system. Specifically, if the intermediate consumer is less profitable than the resource, it might occasionally be dropped from the omnivore’s diet and thus potentially recover from low densities. Whether this intuitive hypothesis is correct is, however, by no means obvious. In contrast to classical switching (sensu Murdoch and Oaten, 1975), consumption rates in the diet model do not necessarily approach zero when a prey item goes to low density. The decision whether to include a prey item in the diet is all or none (i.e., the prey is either always consumed or always ignored upon encounter) and depends solely on the absolute abundance of the more profitable prey items (Stephens and Krebs, 1986). Although other factors determining diet breadth can override the importance of a predator’s decision to attack an encountered prey (Persson and Diehl, 1990), optimal diet theory has at least mixed empirical support (Sih and Christensen, 2001) and certainly provides a thorough theoretical foundation for the exploration of the influence of adaptive behaviors on omnivory systems.

In this article, we explore theoretically how species permanence in tri-trophic systems with omnivory is influenced by adaptive foraging. Specifically, we ask the question whether persistence of the intermediate consumer with the omnivore is facilitated if the omnivore forages according to the diet rule. We use a mix of analytical results (based on permanence theory) and of numerical simulations to compare species permanence in three different tri-trophic systems: a strictly linear food chain, a system with fixed omnivory, and a system with adaptive omnivory. Because diet choice is largely determined by prey profitability and because, in models, persistence of the intermediate consumer is strongly dependent on resource productivity, we focus our analysis on the influences of prey quality (measured as conversion efficiencies of consumed resources and intermediate consumers into omnivores) and of system productivity (measured as carrying capacity of the basal resource).

2. Model

We begin by formulating a general model of a tri-trophic food web consisting of a resource (R), consumers (C), and predators (P). Top predators may feed

on consumers or/and the resource. The population dynamics are described by the following system of differential equations

$$\begin{aligned} \frac{dR}{dt} &= R \left(r \left(1 - \frac{R}{K} \right) - \frac{\lambda_{RC}C}{1 + h_{RC}\lambda_{RC}R} \right. \\ &\quad \left. - \frac{u_{RP}\lambda_{RP}P}{1 + u_{RP}\lambda_{RP}h_{RP}R + u_{CP}\lambda_{CP}h_{CP}C} \right), \\ \frac{dC}{dt} &= C \left(\frac{e_{RC}\lambda_{RC}R}{1 + h_{RC}\lambda_{RC}R} \right. \\ &\quad \left. - \frac{u_{CP}\lambda_{CP}P}{1 + u_{RP}\lambda_{RP}h_{RP}R + u_{CP}\lambda_{CP}h_{CP}C} - m_C \right), \\ \frac{dP}{dt} &= P \left(\frac{u_{RP}\lambda_{RP}e_{RP}R + u_{CP}\lambda_{CP}e_{CP}C}{1 + u_{RP}\lambda_{RP}h_{RP}R + u_{CP}\lambda_{CP}h_{CP}C} - m_P \right). \end{aligned} \quad (1)$$

The parameters u_{RP} and u_{CP} ($0 \leq u_{RP}, u_{CP} \leq 1$) describe the attacking probabilities of resource items and consumer items, respectively, by predators. If $u_{RP} = 1$ and $u_{CP} = 0$, then “predators” specialize on the resource and system (1) is a strictly competitive system where consumers and predators compete for the common resource. If $u_{RP} = 0$ and $u_{CP} = 1$ then predators specialize on consumers and (1) describes a food chain. For omnivory to occur both u_{RP} and u_{CP} have to be positive. Parameter λ_{ij} is the search rate of species j for species i , e_{ij} is the efficiency with which food type i is converted to new offspring of species j , h_{ij} is the lost opportunity cost of the j th species handling the i th food type, and m_i is the mortality rate of species i (see Table 1 for a complete list of definitions). The resource population grows at a maximum specific growth rate r and is limited by an environmental carrying capacity K .

We assume that predators choose their diet in order to maximize their fitness measured as the instantaneous per

capita predator growth rate $\frac{dP}{dt}/P$. Maximization of this fitness criterion is equivalent to maximization of the net conversion rate of food into new predator biomass used in optimal foraging theory (Werner and Hall, 1974; Stephens and Krebs, 1986; Křivan, 1996). Conventionally, this is often equated with net energy or carbon intake, but conversion efficiency may be related to a food item’s content of limiting essential elements or toxic compounds rather than energy content (Belovsky, 1978; Denno and Fagan, 2003; Diehl, 2003). The diet of a predator foraging according to these rules depends on the profitability of the two food types. We consider two possibilities: either consumers are more profitable than the resource, which happens if

$$\frac{e_{RP}}{h_{RP}} < \frac{e_{CP}}{h_{CP}}, \quad (2)$$

or the resource is more profitable than consumers if the opposite inequality holds. The predator optimal foraging strategy when it encounters a food item depends on the density of the more profitable food type, which is always attacked upon an encounter. The less profitable, alternative, food type is attacked with probability one if the density of the more profitable food type is below a critical threshold, which is called the switching density. Above the switching density the less profitable food type is excluded from the predator’s diet. If the more profitable food type density is equal to the switching density, then optimal predator diet choice is not uniquely defined, because then predator’s diet is independent of the attacking probability on the less profitable prey type (i.e., partial preferences for the less profitable prey type (= attack probabilities between 0 and 1) all yield the same foraging return as long as the attack probability for the preferred prey type is 1). If the two food types are equally profitable for the predator

Table 1
Definitions of parameters and the basic set of parameter values^a used in the simulation experiments

Parameter	Definition	Value (units)
r	Maximum specific growth rate of the resource	0.3 h^{-1}
K	Environmental carrying capacity of the resource	$0\text{--}20 \text{ mg C/L}$
λ_{RC}	Search rate of consumer for resources	$0.037 \text{ L}/(\text{mg}^a \text{ h})$
λ_{RP}	Search rate of predator for resources	$0.025 \text{ L}/(\text{mg}^a \text{ h})$
λ_{CP}	Search rate of predator for consumers	$0.025 \text{ L}/(\text{mg}^a \text{ h})$
u_{RP}	Attack probability of resources by predator	0 or 1 (dimensionless)
u_{CP}	Attack probability of consumers by predator	0 or 1 (dimensionless)
h_{RC}	Time spent by consumers handling resources	3 h
h_{RP}	Time spent by predators handling resources	4 h
h_{CP}	Time spent by predators handling consumers	4 h
e_{RC}	Conversion efficiency of resources into consumers	0.6 (dimensionless)
e_{RP}	Conversion efficiency of resources into predators	0.36 (dimensionless)
e_{CP}	Conversion efficiency of consumers into predators	0.6 (dimensionless)
m_C	Mortality rate of consumers	0.03 h^{-1b}
m_P	Mortality rate of predators	0.0275 h^{-1b}

^aTaken with minor modifications from Kooi et al. (2002).

^bThe amount of 0.02 has been added to the values of m_i in Kooi et al. (2002) to account for the lack of dilution losses in a closed system.

(i.e., when inequality (2) is replaced by equality) then both food types are included in the predator's diet regardless of other parameters (see Appendix B in Krivan, 1996). Thus, this case converges to the situation where predators are omnivorous generalists, which is studied in the next section.

To analyze effects of adaptive omnivory on species coexistence we will use some results of permanence theory. For 3-species systems, permanence theory gives necessary conditions for indefinite coexistence. One crucial condition requires that all boundary states with one species missing can be invaded by the missing species (Hutson and Law, 1985; Butler and Waltman, 1986). This condition is easy to verify if those boundary states consist of equilibria only. The boundary two-species systems from which either consumers or predators are missing do, however, exhibit limit cycles at high resource carrying capacities due to the paradox of enrichment. To prove the invasibility of these limit cycles is analytically impossible and must be checked numerically. We therefore limit the analytical derivation of conditions for mutual invasibility to the region of parameter space for which limit cycles do not exist. Moreover, to avoid complex expressions, we assume that the consumer has a linear functional response, i.e., we set $h_{RC} = 0$ in model (1). The general case ($h_{RC} > 0$) can be worked out following the same lines, but with more complex formulas. We complement our analyses by numerical exploration of a specific, realistic example, for which the assumption of stable boundary equilibria has been relaxed.

3. A food web with fixed omnivory

Here we consider the case where predators are omnivorous generalists, i.e., $u_{RP} = u_{CP} = 1$ in model (1). Permanence of model (1) requires that the missing species can invade the equilibrational community of the remaining two species. Model (1) has two boundary equilibria (the equilibrium where resources are missing is never positive)

$$E_{RC} = \left(\frac{m_C}{\lambda_{RC}e_{RC}}, \frac{r(K\lambda_{RC}e_{RC} - m_C)}{K\lambda_{RC}^2e_{RC}}, 0 \right), \quad (3)$$

$$E_{RP} = \left(\frac{m_P}{\lambda_{RP}(e_{RP} - m_P h_{RP})}, 0, \frac{r e_{RP} [K\lambda_{RP}(e_{RP} - m_P h_{RP}) - m_P]}{K\lambda_{RP}^2(e_{RP} - h_{RP} m_P)^2} \right), \quad (4)$$

where E_{RC} and E_{RP} are the equilibria of the resource–consumer and the resource–predator system, respectively.

The food web can be permanent only if the growth rate of the consumer exceeds its mortality rate in the absence of the predator which requires

$$\frac{m_C}{\lambda_{RC}e_{RC}} < K. \quad (5)$$

Thus, the existence of a resource–consumer equilibrium E_{RC} is a necessary condition for species permanence.

The existence of a resource–predator equilibrium E_{RP} is not a necessary condition for 3-species permanence (Holt and Polis, 1997; Diehl and Feissel, 2000; Revilla, 2002). An equilibrium E_{RP} does exist if

$$e_{RP} > m_P \left(h_{RP} + \frac{1}{K\lambda_{RP}} \right) \quad (6)$$

and is globally asymptotically stable if

$$e_{RP} < h_{RP} m_P \frac{K\lambda_{RP} h_{RP} + 1}{K\lambda_{RP} h_{RP} - 1}. \quad (7)$$

Thus, for high efficiencies e_{RP} and high resource carrying capacities (above the dashed–dotted curve in Fig. 1) inequality (7) does not hold and a stable limit cycle exists in the R – P phase plane. Here we consider the case where no boundary limit cycle exists, which allows us to obtain analytical results.

Substituting the equilibrational population densities at E_{RC} and E_{RP} into Eq. (1) yields conditions for mutual invasibility (Appendix A). Predators will invade the resource–consumer food web at equilibrium E_{RC} if the efficiency with which they convert resources is sufficiently high, i.e.,

$$e_{RP} > M_{RC} \quad (8)$$

and consumers will invade the resource–predator system at equilibrium E_{RP} (provided it exists) if the efficiency with which predators convert resources is sufficiently low

$$e_{RP} < M_{RP}, \quad (9)$$

where M_{RC} (shown in Fig. 1 as long-dashed line) and M_{RP} (shown in Fig. 1 as dotted line) are given in Table 2.

Importantly, Appendix A shows that 3-species persistence requires condition (9) to be fulfilled also if an equilibrium E_{RP} does not exist.

M_{RC} and M_{RP} intersect at $K = m_C / (\lambda_{RC}e_{RC})$ (shown in Fig. 1 as a vertical line), at which point

$$M_{RC} = M_{RP} = m_P \left(h_{RP} + \frac{\lambda_{RC}e_{RC}}{m_C\lambda_{RP}} \right).$$

Because M_{RP} is a decreasing function of the resource carrying capacity, this gives the following necessary condition for permanence

$$e_{RP} < m_P \left(h_{RP} + \frac{\lambda_{RC}e_{RC}}{m_C\lambda_{RP}} \right). \quad (10)$$

This condition states that the consumer must be the superior competitor for the shared resource, i.e., have the lower R^* , with R^* being the resource density at

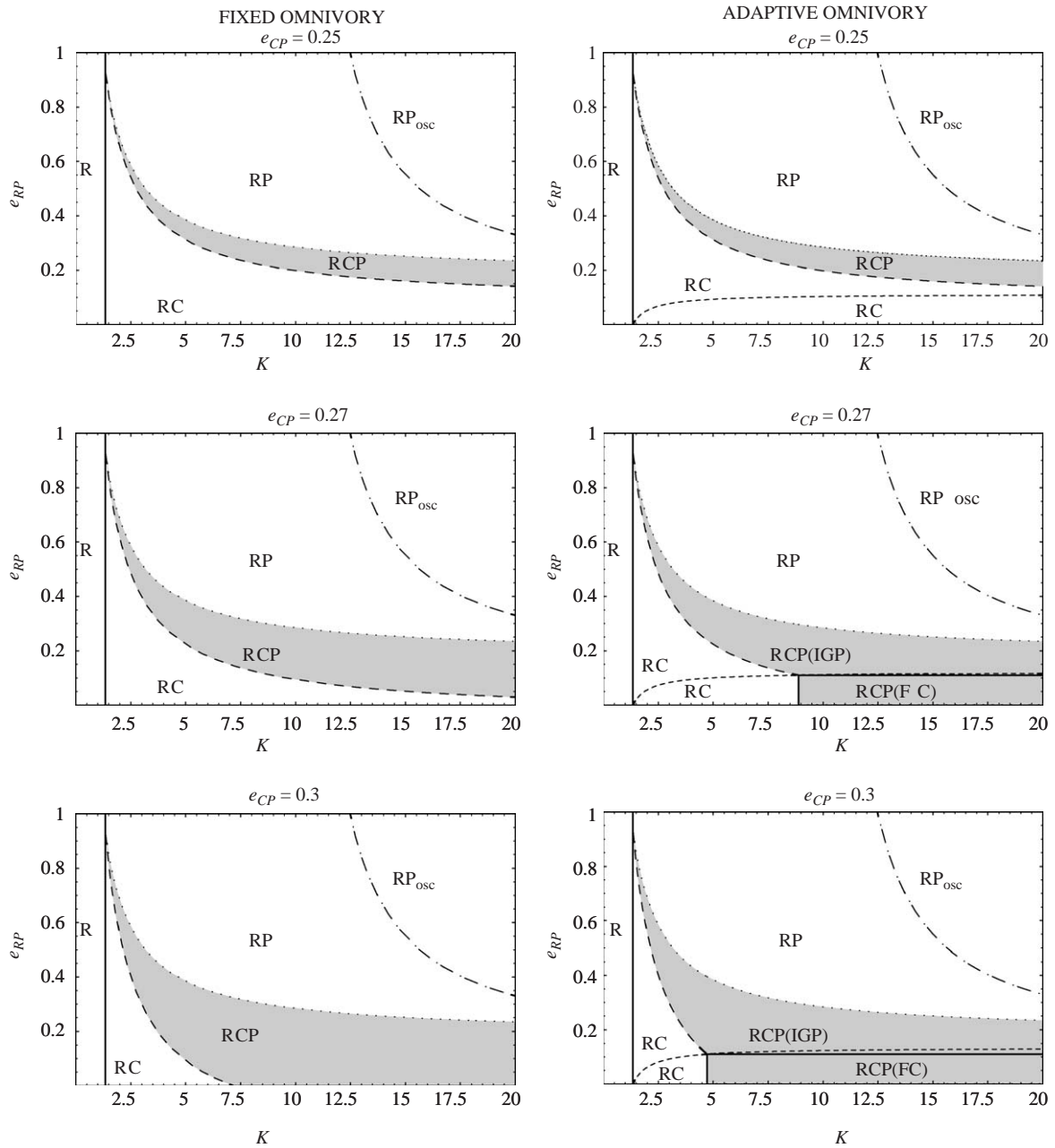


Fig. 1. Influence of the conversion efficiencies of consumers into omnivores (e_{CP}), of resources into omnivores (e_{RP}), and the resource carrying capacity (K) on species persistence in systems where omnivory is either fixed (left panel) or adaptive (right panel). 3-species persistence occurs in the shaded region. The dashed line denotes M_{RC} while the dotted line denotes M_{RP} . These lines bound the set of parameters for which all three species survive in the tri-trophic food web indefinitely. The short dashed increasing line is the line M_* , above which the food web topology of the resource–consumer subsystem when invaded by predators is that of the food web with omnivory, while below it the food web topology is of the food chain (here we assume that consumers are more profitable for predators than are resources). The vertical line is the threshold level below which consumers cannot survive (see inequality (5)). The solid horizontal line indicates $e_{RP} \equiv h_{RPM}$. Different asymptotic community states are labeled by their respective community members (R = resource, C = consumer, P = omnivore) and dynamic behavior. Oscillating attractors are labeled “osc”, the remaining systems settle to stable equilibria. For parameters allowing 3-spp. permanence in the case of adaptive omnivory, it is also indicated whether the community topology is a food chain (FC) or an omnivory system (IGP). Parameters not varied in the figure are as in Table 1 except $h_{RC} = 0$.

equilibrium in a two-species system with either the consumer or the predator missing (setting $R^*(E_{RC}) < R^*(E_{RP})$ and solving for e_{RP} yields inequality (10), see formulas (3) and (4); (Holt and Polis, 1997)).

The two invasibility conditions (8) and (9) can simultaneously hold only if $M_{RC} < M_{RP}$. Solving $M_{RC} < M_{RP}$ for e_{CP}/h_{CP} (under the condition $K \geq m_C/(\lambda_{RC}e_{RC})$, inequality (5)) gives yet another

Table 2

Summary of conditions for 3-species permanence in food webs with stable boundary equilibria E_{RC} and E_{RP} ^a

Type of food web	Conditions involving $\frac{e_{CP}}{h_{CP}}$	Conditions involving K	Conditions involving e_{RP}
Food chain	$\frac{e_{CP}}{h_{CP}} > m_P \left(1 + \frac{\lambda_{RC}}{r\lambda_{CP}h_{CP}}\right)$	$K > \frac{m_C}{e_{RC}\lambda_{RC}} \left(1 + \frac{m_P\lambda_{RC}}{r\lambda_{CP}h_{CP} \left(\frac{e_{CP}}{h_{CP}} - m_P \left(1 + \frac{\lambda_{RC}}{r\lambda_{CP}h_{CP}}\right)\right)}\right)$	NA
Fixed omnivory or Adaptive omnivory, Resource more profitable $\left(\frac{e_{RP}}{h_{RP}} > \frac{e_{CP}}{h_{CP}}\right)$	$\frac{e_{CP}}{h_{CP}} > m_P \left(1 + \frac{\lambda_{RC}}{h_{CP}(r\lambda_{CP} + m_C\lambda_{RP})}\right)$	$K > \frac{m_C}{\lambda_{RC}e_{RC}}$	$M_{RC} < e_{RP} < M_{RP}$
Adaptive omnivory, Consumer more profitable $\left(\frac{e_{RP}}{h_{RP}} < \frac{e_{CP}}{h_{CP}}\right)$	$\frac{e_{CP}}{h_{CP}} > m_P \left(1 + \frac{\lambda_{RC}}{r\lambda_{CP}h_{CP}}\right)$ or $\frac{e_{CP}}{h_{CP}} > m_P \left(1 + \frac{\lambda_{RC}}{h_{CP}(r\lambda_{CP} + m_C\lambda_{RP})}\right)$	$K > \frac{m_C}{e_{RC}\lambda_{RC}} \left(1 + \frac{m_P\lambda_{RC}}{r\lambda_{CP}h_{CP} \left(\frac{e_{CP}}{h_{CP}} - m_P \left(1 + \frac{\lambda_{RC}}{r\lambda_{CP}h_{CP}}\right)\right)}\right)$ or $K > \frac{m_C}{\lambda_{RC}e_{RC}}$	$e_{RP} < M_{\star}$ $M_{RC} < e_{RP} < M_{RP}$
	$M_{RC} = \frac{(e_{RC}K\lambda_{RC} - m_C)(h_{CP}m_P - e_{CP})\lambda_{CP}r}{Km_C\lambda_{RC}\lambda_{RP}} + m_P \left(h_{RP} + \frac{e_{RC}\lambda_{RC}}{m_C\lambda_{RP}}\right)$ $M_{RP} = m_P \left(h_{RP} + \frac{r\lambda_{CP} + e_{RC}K\lambda_{RC}\lambda_{RP}}{K\lambda_{RP}(r\lambda_{CP} + m_C\lambda_{RP})}\right)$ $M_{\star} = \frac{e_{CP}h_{RP}r\lambda_{CP}(e_{RC}K\lambda_{RC} - m_C)}{e_{RC}K\lambda_{RC}^2 + h_{CP}r\lambda_{CP}(e_{RC}K\lambda_{RC} - m_C)}$		

^aBased on Eq. (1). For simplicity $h_{RC} = 0$ is assumed.

necessary inequality

$$m_P \left(1 + \frac{\lambda_{RC}}{h_{CP}(r\lambda_{CP} + m_C\lambda_{RP})}\right) < \frac{e_{CP}}{h_{CP}}. \quad (11)$$

Condition (11) states that, for permanence of the food web with fixed omnivory, the profitability of consumers for predators (i.e., the energy return per handling time e_{CP}/h_{CP}) must exceed predator mortality (m_P) by a sufficient amount to compensate for the negative growth rate that would be attained by invading predators if they fed only on resources. Fig. 1 shows that the parameter space allowing 3-species permanence becomes larger as the nutritional benefit from the consumer for the predator e_{CP} increases (cf. Fig. 1 left panel). This is because omnivores invading a resource–consumer system need to be less efficient at converting the resource if their conversion efficiency for consumers is increased (i.e., M_{RC} decreases with increased e_{CP} , see also (Diehl (2003)).

3.1. Comparison with a food chain

Here we compare the conditions for permanence of a food web with omnivory with a tri-trophic food chain described by model (1) where we substitute $u_{RP} = 0$ and $u_{CP} = 1$. Model (1) has then only one boundary

equilibrium E_{RC} which, if positive, is always globally asymptotically stable in the resource–consumer phase space (Svirezhev and Logofet, 1983, p. 83).

The food chain can be permanent only if the growth rate of the consumer exceeds its mortality rate in the absence of the predator (i.e., equilibrium E_{RC} is positive), which requires inequality (5) to hold. Predators can invade the resource–consumer equilibrium E_{RC} if the following two inequalities are satisfied (Appendix B, Table 2):

$$\frac{e_{CP}}{h_{CP}} > m_P \left(1 + \frac{\lambda_{RC}}{r\lambda_{CP}h_{CP}}\right) \quad (12)$$

and

$$K > \frac{m_C}{e_{RC}\lambda_{RC}} \times \left(1 + \frac{m_P\lambda_{RC}}{r\lambda_{CP}h_{CP} \left(\frac{e_{CP}}{h_{CP}} - m_P \left(1 + \frac{\lambda_{RC}}{r\lambda_{CP}h_{CP}}\right)\right)}\right). \quad (13)$$

Thus, 3-species permanence requires that consumer profitability be sufficiently high, i.e., inequality (12) holds. If inequality (12) holds, the denominator in the parenthesis of inequality (13) is positive and condition (13) sets the lower threshold for the resource carrying

capacity at which the food chain is persistent. This threshold is a decreasing function of e_{CP} (Fig. 2(A)). Because predators do not feed on resources, conversion of resources to predators is irrelevant in a food chain and the permanence region is independent of e_{RP} (Fig. 2(B)).

Comparing invasibility conditions for the food chain with those for the food web with fixed omnivory we observe that (Table 2): (i) The minimum threshold for consumer profitability (e_{CP}/h_{CP}) can be slightly lower in the food web with omnivory than in the food chain (cf. inequality (11) vs. inequality (12)). (ii) The minimum threshold for the carrying capacity of the resource is slightly lower for the food web with omnivory (cf. compare inequality (5) with inequality (13)). (iii) While permanence conditions for the food chain are independent of e_{RP} (which is zero in a food chain), the food web with omnivory must fulfill the additional conditions $M_{RC} < e_{RP} < M_{RP}$ that reduce the perma-

nence region in e_{RP} - K parameter space (cf. Fig. 2(B) with Fig. 1, left panel).

In productive environments (high resource carrying capacities), the above analytical results do not hold, because the equilibrium of the resource–predator system becomes unstable (inequality (7) is reversed). The conditions under which a consumer can invade a resource–predator system that oscillates along a limit cycle cannot be analytically computed and must be checked numerically. Graphically, this situation arises at sufficiently high resource carrying capacities where the dash-dotted line in Fig. 1 intersects with M_{RP} , which is out of the range of realistic carrying capacities for our numerical example (see section Numerical example).

4. Food web with adaptive omnivory

In this section we assume that predators choose their diet adaptively following the diet rule. We will consider two cases: (i) the resource is more profitable for predators than consumers, and (ii) consumers are more profitable for predators than the resource.

4.1. Resource is more profitable

The resource is more profitable than the consumer when inequality (2) is reversed. The optimal predator foraging strategy is then to attack the resource upon each encounter ($u_{RP} = 1$) while consumers will be included in the predator diet only if the resource density is below the switching density

$$R_{\star} = \frac{e_{CP}}{\lambda_{RP}(e_{RP}h_{CP} - e_{CP}h_{RP})}.$$

The food web topology is not fixed but it switches between a purely competitive food web ($u_{RP} = 1, u_{CP} = 0$ in model (1)) and a food web with omnivorous generalists as resource density passes through the switching density R_{\star} (Fig. 3(A)).

The resource–consumer equilibrium E_{RC} must be positive (i.e., inequality (5) must hold) if the system is to be persistent, because otherwise consumers would die out (whether predators feed on them or not), whereas a resource–predator equilibrium E_{RP} may or may not exist.

If E_{RP} exists (which happens when inequality (6) holds) the consumer can only invade E_{RP} , if it is the superior resource competitor, which requires that inequality (10) holds. With the consumer being the superior resource competitor, predators invading a resource–consumer system at equilibrium would, however, have negative population growth if they only fed on the resource. Consequently, predators invading E_{RC}

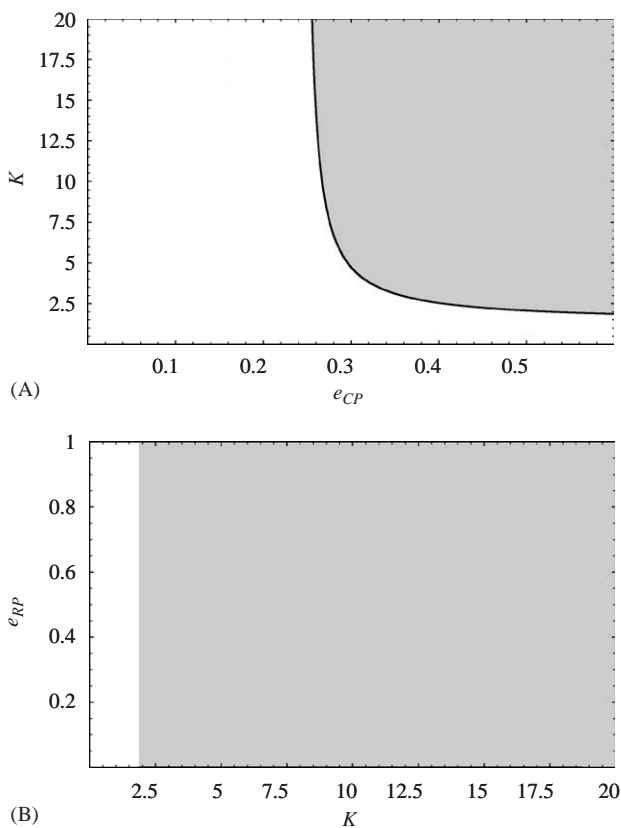


Fig. 2. Permanence region of the tri-trophic food chain in (A) e_{CP} - K parameter space and in (B) K - e_{RP} parameter space. Panel A shows that permanence of the food chain requires a minimum conversion efficiency e_{CP} of consumers into predators (see formula (12); in the example, $e_{CP} > 0.245667$). Beyond that threshold, the minimum resource carrying capacity K allowing permanence is a decreasing function of e_{CP} described by inequality (13). Panel B illustrates (for $e_{CP} = 0.6$) that permanence of the food chain does not depend on the conversion e_{RP} of resources into predators (which should be zero in a food chain). Parameters are those given in Table 1 except $h_{RC} = 0$.

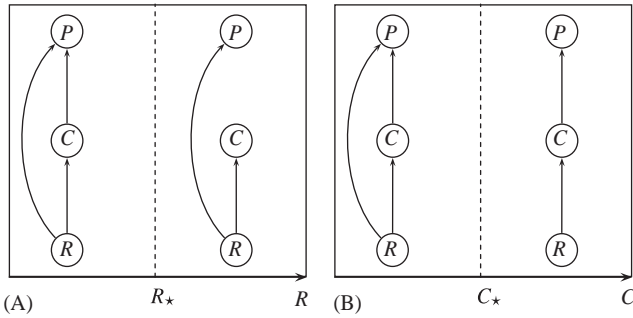


Fig. 3. Food web topologies associated with adaptive omnivory. In (A) is shown food web topology as a function of resource density (R) when resources are more profitable than consumers while in (B) is shown food web topology as a function of consumer density (C) when consumers are more profitable than resources. R_* and C_* denote switching thresholds.

can only achieve positive population growth if they also feed on the consumer and if feeding on the consumer provides a sufficient benefit, i.e., if inequality (11) holds. This inequality implies that

$$\frac{e_{CP}}{h_{CP}} > m_P. \tag{14}$$

Finally, if (14) is fulfilled, predators will always feed on consumers invading a resource–predator system at equilibrium, because, by definition, predators have zero net population growth at E_{RP} if they only feed on the resource and feeding on the consumer will allow them to achieve positive population growth. In other words, condition (14) implies that the resource–predator equilibrium is in the part of the species density phase space where predators behave as generalists. Thus, if a resource–predator equilibrium exists, mutual invasibility requires the predator to be an omnivore at both boundary equilibria E_{RP} and E_{RC} (Appendix A, Table 2).

If a resource–predator equilibrium does not exist (i.e., when inequality (6) is reversed), the resource carrying capacity is not high enough to support a predator feeding on the resource alone. Consequently, the predator cannot invade a resource–consumer system at equilibrium if it only feeds on the resource. Thus, invasion of E_{RC} by predators is again only possible, if the predator is an omnivore (invasion then requires $e_{RP} > M_{RC}$) and if the benefit from feeding on the consumer is sufficiently high (see inequality (14)). We finally recall that the reversal of inequality (6) automatically implies that $e_{RP} < M_{RP}$ at all resource carrying capacities fulfilling (5) (see inequality (10)).

In summary, whether a resource–predator equilibrium exists or not, successful mutual invasion requires the predator to be an omnivore at both boundary equilibria and invasibility conditions are identical to the case of fixed omnivory (Table 2). Thus, compared to the case of fixed omnivory and counter to intuition,

coexistence of the consumer with an optimally foraging omnivore is not facilitated if the consumer is less profitable than the resource.

4.2. Consumers are more profitable

Now, we consider the case where consumers are more profitable for predators than the resource, i. e., inequality (2) holds. When consumer density is below the switching density

$$C_* = \frac{e_{RP}}{\lambda_{CP}(e_{CP}h_{RP} - e_{RP}h_{CP})}$$

predators behave as omnivorous generalists ($u_{RP} = u_{CP} = 1$), whereas above the switching density they specialize on consumers ($u_{RP} = 0, u_{CP} = 1$). Thus, food web topology is not fixed but switches between a food chain and a food web with omnivory, depending on consumer density (Fig. 3(B)). As in the case of fixed omnivory, we assume that the resource–predator equilibrium is non-existent or stable which allows us to derive explicit conditions for permanence.

Whether food web topology is a food chain or a food web with omnivory, a necessary condition for species persistence is that the resource carrying capacity satisfies inequality (5), because otherwise consumers die out. If a resource–predator equilibrium E_{RP} exists, the density of consumers invading E_{RP} will, by definition, be very low (i.e., below C_*) so that the predator feeds as a generalist. Thus, permanence requires $e_{RP} < M_{RP}$. This condition holds also, if a resource–predator equilibrium E_{RP} does not exist, because the condition for non-existence of E_{RP} (i.e., the opposite of inequality (6)) automatically implies that $e_{RP} < M_{RP}$ (Appendix A). Finally, there are two possibilities concerning the food web topology of a resource–consumer system at equilibrium E_{RC} that is invaded by a predator. If $e_{RP} > M_*$, where M_* is given in Table 2 (short-dashed increasing line in Figure 1, adaptive omnivory), then the consumer density at E_{RC} is below the switching density C_* and predators feed as generalists. The invasibility conditions are then the same as for the food web with fixed omnivory, i.e., $M_{RC} < e_{RP} < M_{RP}$ and conditions (5) and (11) (Table 2).

If $e_{RP} < M_*$, then consumer density at E_{RC} is above C_* and predators invading a resource–consumer system feed exclusively on consumers. This happens when consumers are sufficiently abundant and of sufficient quality, i.e., if inequalities (12) and (13) are fulfilled. Thus, conditions for 3-species permanence are in this case identical to the conditions for permanence of the food chain, with the additional requirement that the consumer must be able to invade a resource–predator equilibrium (if one exists), i.e., $e_{RP} < M_{RP}$ (Table 2).

It is easy to show that when

$$e_{RP} < h_{RP}m_P$$

the consumer equilibrium density of the linear tri-trophic food chain is above the switching consumer density C_* . Thus, the food web topology at the 3-spp. equilibrium will be of the linear food chain. If the inequality is reversed then the consumer equilibrium of the food web with omnivory is below C_* and the food web topology at the 3-spp. equilibrium is of the food web with omnivory (Fig. 1, adaptive omnivory).

Compared with non-optimal omnivorous predators (Fig. 1, left panel vs. right panel, second and third row) we observe that the range of parameters for which the model with adaptive omnivory is permanent is larger provided inequality (12) holds. If the opposite of inequality (12) holds then the range of parameters that satisfy the invasibility conditions is the same both for adaptive and inflexible predators (Fig. 1, first row). Thus, optimal foraging may indeed facilitate permanence at high resource carrying capacities but, counter to intuition, only when the consumer is the preferred prey type. Also, this facilitative effect is significant only for intermediate profitabilities of the consumer. At both high and low values of e_{CP} the facilitative effect is negligible to non-existent (Fig. 1, first and third rows).

Again, the above analytical results do not hold in productive environments (high resource carrying capacities), because the equilibrium of the resource–predator system becomes unstable (inequality (7) is reversed). The invasibility of the missing species along a limit cycle must be checked numerically.

5. Numerical example

To explore the robustness of the analytical predictions derived in the preceding sections in a situation where the simplifying assumption of stable boundary equilibria is relaxed, we parameterized the full model (1) for a specific example. As our example we chose a microbial food web consisting of a bacterium fed upon by two species of ciliates, one of which may also feed on the other ciliate. Simple microbial food webs have been intensely studied in the lab (Lawler, 1998). Estimates of realistic parameter values are therefore readily available. Studies of optimal foraging in protozoa are, however, still very rare (e.g., Stibor and Sommer, 2003), and to our knowledge the applicability of the diet rule to the foraging behavior of ciliates has not been tested. Also, a ciliate example may on first sight not appear ideal for the study of diet choice, because ciliates are filter feeders. Diet choice can therefore only take place after a prey item has already been captured. Protists have, however, been shown to selectively ingest and egest encountered prey items (Boenigk et al., 2002; Matz et al., 2002). Adaptive prey choice therefore seems a likely feature of microbial food webs. In any case, our example is not meant to exactly mimic the behavior of a specific system.

Rather, we wanted to base the parameter choices for our numerical simulations on estimates from well-studied systems.

5.1. Simulation approach and parameter values

To explore the influence of optimal diet choice by an omnivorous ciliate on the potential for 3-species coexistence, we conducted a series of simulations in which we mimicked a typical experimental situation where a batch of medium is inoculated with a small population of organisms from each species (0.1 mg carbon/L of bacteria and 0.01 mg carbon/L of each of the ciliates). Omnivory by the predatory ciliate was assumed to be either fixed or to follow the diet rule. We ran each simulation until the system settled to an attractor and recorded the final community composition and the nature of the attractor (i.e., equilibrium, limit cycle, or something more complex). As in the analytical section, we used the conversion efficiencies e_{RP} and e_{CP} and the bacterial carrying capacity K as our bifurcation parameters. For each value of e_{CP} , we first ran numerical simulations along a fixed grid of e_{RP} and K values. The exact locations of bifurcation boundaries were then determined down to the third digit in e_{RP} – K space through iteration of additional simulations in the vicinity of numerous bifurcation points. All simulations were run in MATLAB and/or Mathematica using a variable (fixed omnivory) or fixed (adaptive omnivory) time step routine. We confirmed the simulation results with the bifurcation software LOCBIF. Also, several bifurcation boundaries (the lines M_{RC} , M_{RP} , and the boundaries separating stable from unstable RC - and RP -systems, respectively, Fig. 4) could be confirmed analytically.

The parameter values used in our simulations were taken from Kooi et al. (2002) who modeled a microbial omnivory system in a chemostat environment. Kooi et al. used a set of generic parameter values derived by Nisbet et al. (1983) through averaging over a number of lab experiments with different bacteria and ciliate species. The parameter values and their units are listed in Table 1. With two exceptions these parameters are identical to the ones in Kooi et al. (2002) converted from the Monod notation used by these authors to the Holling type 2 notation used by us. Kooi et al. (2002) explicitly modeled the dynamics of a limiting bacterial substrate, the availability of which is implicitly modeled in (1) through the logistic growth term of the bacterial resource. We selected a value of r that, in the absence of ciliates, gives similar bacterial dynamics as does Kooi et al.'s chemostat system. Our simulations cover the full range of theoretically possible conversion efficiencies e_{RP} (i.e., 0 to 1; note that the model is scaled to units of biomass) and include some of the highest bacterial carrying capacities encountered in batch experiments (Diehl and Feissel, 2000).

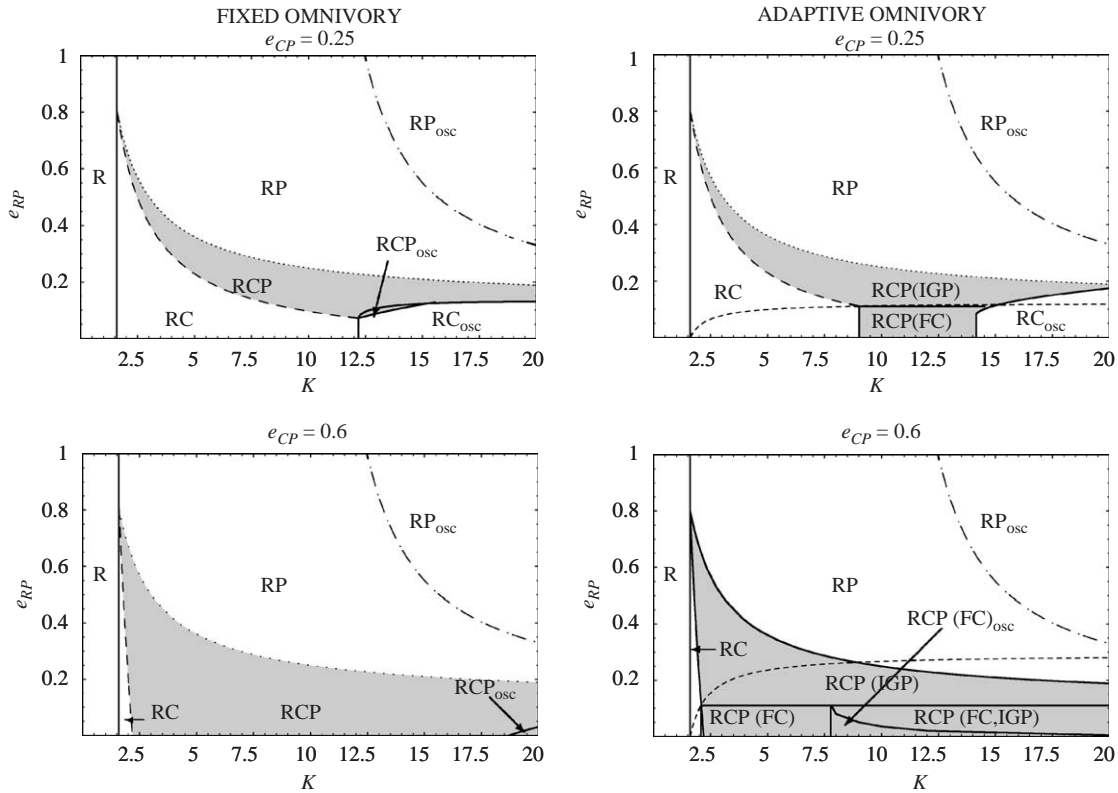


Fig. 4. Influence of the conversion efficiencies of consumers into omnivores (e_{CP}), bacteria into omnivores (e_{RP}), and the bacterial carrying capacity (K) on final community states of the parameterized bacteria–ciliate system, where omnivory is either fixed (left panel) or adaptive (right panel). 3-species persistence occurs in the shaded region. With the exception of the short-dashed line, all lines denote bifurcation boundaries separating qualitatively different asymptotic community states (as reached from the initial conditions $R = 0.1$ mg C/L, $C = P = 0.01$ mg C/L). Different asymptotic community states are labeled by their respective community members ($R =$ resource, $C =$ consumer, $P =$ omnivore) and dynamic behavior. Oscillating attractors are labeled “osc”, the remaining systems settle to stable equilibria. For parameters allowing 3-spp. permanence in the case of adaptive omnivory, it is also indicated whether the community topology is a FC, an IGP, or a mix of both. The meaning of various types of lines is the same as in Fig. 1. Parameters not varied in the figure are as in Table 1.

5.2. Results of numerical simulations

Fig. 4 shows regions of qualitatively different community states in e_{RP} – K parameter space for two values of e_{CP} (0.25 and 0.6) that bracket a range of relatively low to relatively high conversion efficiencies of consumers into omnivore biomass. We note that this figure looks largely similar to the corresponding plots of the analytical results from the simpler model assuming no handling time h_{RC} (Fig. 1), with the exception of the lower right corners (i.e., at high bacterial carrying capacities and low conversion efficiencies of bacteria into omnivore biomass). Specifically, if omnivory is fixed and the conversion efficiency of consumers into omnivores e_{CP} is low, there is a sickle-shaped region of stable 3-spp. coexistence that is bracketed by stable resource–consumer and resource–predator systems (Fig. 4, upper left panel). As in the simpler, analytical case (Fig. 1, $e_{CP} = 0.25$), the boundaries of this coexistence region correspond to the thresholds M_{RC} (above which predators can invade a stable R – C system) and M_{RP} (below which consumers can invade a stable R – P

system). In model (1) with $h_{RC} > 0$, the expressions for M_{RC} and M_{RP} are more complex than those expressions given in Table 2, but can be obtained analytically using some symbolic algebra package such as Mathematica. Above a bacterial carrying capacity of 12.19, the resource–consumer boundary equilibrium becomes unstable and the R – C system oscillates on a limit cycle. At low conversion efficiency of consumers into omnivores e_{CP} (Fig. 4, upper left panel), this limit cycle is more difficult to invade by the omnivore than the corresponding (unstable) R – C equilibrium, because the amplitude and period of the R – C limit cycle both increase with increasing bacterial carrying capacity. Consequently, periods of low consumer biomass become more extended (data not shown) and the average population growth rate of the omnivore over a cycle period becomes negative if the omnivore cannot make efficient use of the resource. A higher conversion efficiency of resources into omnivores e_{RP} is therefore required to allow invasion by the omnivore at higher K . In contrast, at high conversion efficiency of consumers into omnivores (Fig. 4, lower left panel), the omnivore

can efficiently exploit even low consumer densities. Consequently, the $R-C$ limit cycle can be invaded by the omnivore, and the system settles to a stable 3-spp. equilibrium.

As in the simpler, analytical case, adaptive omnivory enlarges the region of 3-spp. permanence. Compared to the case of fixed omnivory, at low conversion efficiency of consumers into omnivores an additional region of stable 3-spp. persistence appears at values of K above 9.02 (Fig. 4, upper right panel). At this bacterial carrying capacity, adaptive omnivores feed exclusively on consumers for all conversion efficiencies of resources into omnivore biomass e_{RP} below 0.111 and the community topology is a food chain. As in the simpler, analytical case, this K is defined as the one where M_{RC} and M_* intersect (cf. Figs. 1 and 4; again, the expression for M_* in the full model is more complex than that which is given in Table 2 but still analytically solvable). As with fixed omnivory, 3-spp. permanence becomes

again more difficult to achieve when the $R-C$ boundary equilibrium is unstable. Periods of low consumer density become too extended at bacterial carrying capacities exceeding 14.1 to allow invasion of adaptive omnivores (Fig. 4, lower right panel. Both the proportion of total time spent at consumer densities below the switching density C_* and the period of $R-C$ cycles increase with K (results not shown). Note, however, that, in contrast to the case of fixed omnivory, the system with adaptive omnivores can resist the destabilizing influence of an unstable $R-C$ boundary equilibrium to some extent; i.e., while the permanence region starts to shrink at $K > 12.19$ in the case of fixed omnivory it does not do so until $K > 14.1$ in the case of adaptive omnivory (cf. Fig. 4, lower right vs. lower left panel). At high conversion efficiency of consumers into omnivores the permanence region is only minimally enlarged (in the lower left corner) compared to the case of fixed omnivory (Fig. 4, $e_{CP} = 0.6$, left panel vs. right panel).

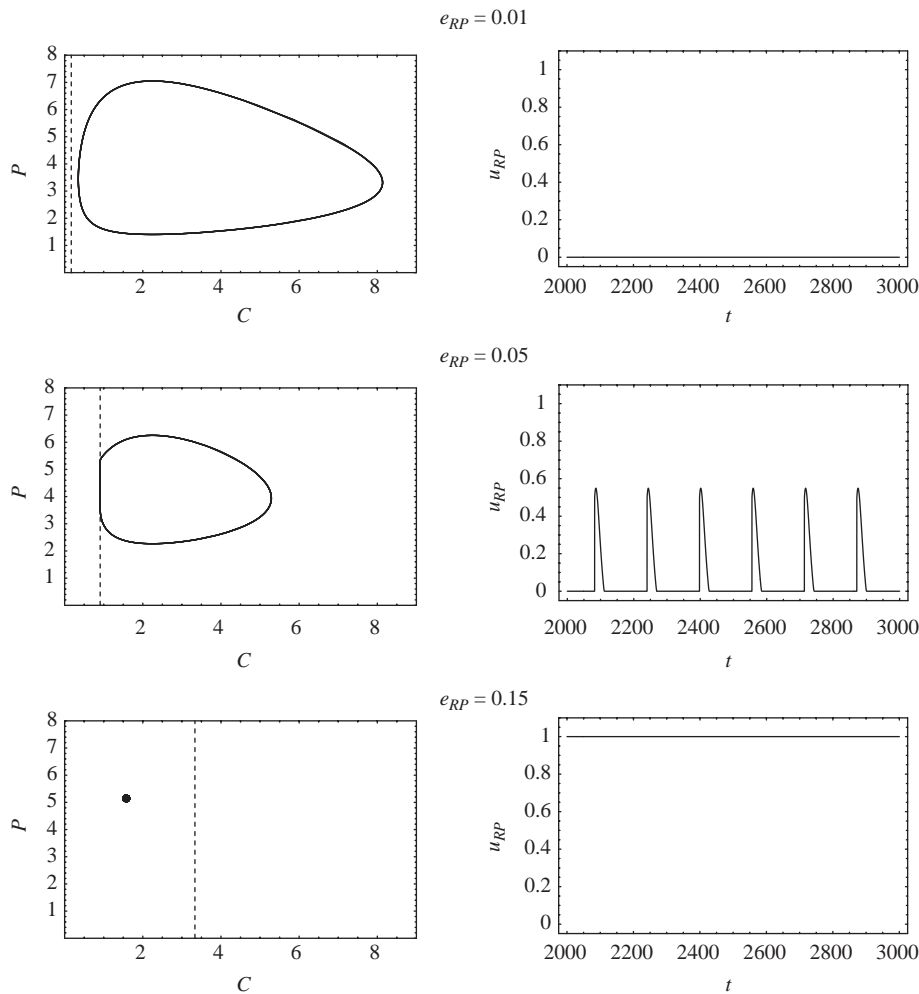


Fig. 5. Influence of the conversion efficiencies of resources into omnivores e_{RP} on population dynamics where omnivory is adaptive. Left column: asymptotic population dynamics in the consumer–predator phase space. Also shown is the switching density C_* at and below which the predator includes the resource in its diet. Right column: preference of predators for resources (u_{RP}) against time. In these simulations $K = 12$, $e_{CP} = 0.6$ and other parameters are the same as those given in Table 1.

Starting at the bacterial carrying capacity where M_{RC} and M_* intersect and for values of e_{RP} below 0.111 there is again a region of permanence where the community topology is (for most of the time) a food chain. The dynamics in this region can be complex, including the case where food web topology switches at regular intervals to an omnivory system. When the efficiency with which resources are converted to omnivores is low ($e_{RP} = 0.01$, Fig. 5), the system oscillates on a limit cycle and the food web topology is that of the linear food chain ($u_{RP} = 0$). While for increasing efficiencies e_{RP} the amplitude of the limit cycle decreases, the switching threshold C_* increases and sets a boundary for the population minima of the consumer ($e_{RP} = 0.05$, Fig. 5). In this range of e_{RP} values the consumer trajectories follow the switching plane $C = C_*$ during population minima, but do not cross it. Consequently, partial preferences for resources ($0 < u_{RP} < 1$) arise during such periods (Fig. 5). They can be explicitly calculated following Křivan (1996), Křivan and Sikder (1999), van Baalen (2001), and Křivan and Eisner (2003). With further increasing e_{RP} the amplitude of the limit cycle decreases further until at $e_{RP} = 0.11$ the system settles to an equilibrium and the food web topology is that of the food web with omnivory (Fig. 4).

In summary, compared to the simpler, analytical case, the region of 3-spp. permanence is decreased in the numerical example at values of K for which the R – C boundary system becomes unstable, but only if e_{CP} is low and not if e_{CP} is high (cf. Fig. 1 with Fig. 4). The qualitative result that, compared to the case of fixed omnivory, adaptive omnivory enlarges the region of permanence (in a fairly limited region of parameter space) if the consumer is more profitable than the resource does, however, carry over from the simpler, analytical case to the numerical example.

6. Discussion

The four most important results from our analyses are: (1) Compared to systems where omnivory is fixed, optimal foraging by an omnivore according to the diet rule enlarges the set of parameter values that lead to 3-species permanence. Counter to intuition, however, the added region of permanence occurs only in the region of parameter space where the intermediate consumer would otherwise displace the omnivore (i.e., below the M_{RC} line in Figs. 1 and 4). In contrast, the persistence region of the intermediate consumer is not affected by optimal foraging. (2) The latter is explained by the fact that, also counter to intuition, optimal foraging can only facilitate 3-species persistence if the intermediate consumer is the more profitable prey and, consequently, is never dropped from the omnivore's diet. (3) Overall, the added region of permanence is rather small and

restricted to a combination of parameters involving a low conversion efficiency of resources into omnivores e_{RP} , an intermediate conversion efficiency of consumers into omnivores e_{CP} , and intermediate to high resource carrying capacities K (Figs. 1 and 4). (4) Whether omnivory is fixed or adaptive, 3-species permanence is most likely under conditions where conversion of resources into omnivores is inefficient (low e_{RP}) in combination with a relatively high conversion efficiency of intermediate consumers into omnivores (high e_{CP} ; Figs. 1 and 4).

The latter result corroborates similar findings by Diehl (2003) and Kuijper et al. (2003). Diehl (2003) suggested that this combination of conversion efficiencies might apply to the situation of omnivores feeding on both plant and animal material, because the quality of most plant tissues is rather low compared to animal prey. This combination of parameter values allows for stable 3-species persistence over potentially very large ranges of resource carrying capacities (Diehl, 2003). It might therefore be worthwhile investigating whether this combination of high e_{CP} and low e_{RP} is widespread in omnivory systems in general. Based on the nitrogen content of different prey types, Denno and Fagan (2003) have recently argued that $e_{RP} > e_{CP}$ should be common in carnivorous arthropod omnivores. <

Why is the added region of persistence restricted to a rather narrow parameter space? This can best be explained by the fact that optimal foraging only promotes permanence in regions of parameter space where the trophic topology at mutual invasion is a food chain (below the short-dashed line in Figs. 1 and 4). The latter requires that e_{RP} be not too high, because otherwise the profitability of the resource becomes high enough to include it in the predator's diet. Conversely, if e_{CP} is too high, consumers are sufficiently profitable to allow 3-species persistence over a larger region in e_{RP} – K space even at fixed omnivory. Consequently, optimal foraging can only minimally enlarge this persistence region (Fig. 1 lower panels). Finally, if e_{CP} is too low, a strict food chain would not be persistent (Fig. 2A). In this case, the predator can only invade a resource–consumer system at equilibrium if it feeds as an omnivore (Fig. 1 upper left panel).

Why does optimal foraging promote 3-species persistence only when the food web topology at invasion is a food chain, i.e., if the intermediate consumer is the more profitable prey? Our results under the assumption of stable boundary equilibria show that, whenever the resource is more profitable, permanence conditions are identical to the case of fixed omnivory; i.e., permanence can only be achieved if the omnivore feeds on both prey species under all invasion scenarios. This can be intuitively understood by the fact that the intermediate consumer must be the superior competitor for the shared resource in order to persist. Consequently, an

omnivore invading a resource–consumer equilibrium must feed on both prey items to achieve positive growth. Similarly, an intermediate consumer invading a resource–omnivore system at equilibrium must always be included in the omnivore’s diet, because the omnivore would otherwise have negative population growth (note that an invading consumer will depress resources below their original density at the resource–omnivore equilibrium).

The four major qualitative results listed above are also upheld in our numerical example, in which the assumption of stable boundary equilibria is relaxed. Allowing for an unstable resource–consumer equilibrium tends, however, to decrease the region of 3-species persistence for both fixed and adaptive omnivory. In both cases, the omnivore cannot easily invade a resource–consumer system on a limit cycle, because periods of low consumer density during cycle troughs get more extended and more severe with increasing resource carrying capacity. The concomitant reduction in food intake cannot be entirely compensated for during periods of high consumer density (because the functional response of the predator gets satiated) and the average growth rate of an invading predator becomes negative beyond a certain level of resource carrying capacity. In the case of flexible omnivory (where trophic topology is a food chain at low values of e_{RP} and K , Fig. 4 upper right panel), this mechanism is identical to the one causing the (specialist) top predator in a strict 3-level food chain to go extinct at high levels of enrichment (Abrams and Roth, 1994).

Armstrong and McGehee (1980) and Abrams and Holt (2002) have pointed out that 3-species persistence is possible in a purely competitive system (where P does not feed on C), if at least one of the two boundary systems exhibits a limit cycle and if the functional responses of the two consumers differ strongly in shape. Such a system may remain persistent on an oscillatory trajectory also after the addition of a fair amount of omnivory, with the intriguing possibility that the intermediate consumer may persist in the system in spite of being the inferior resource competitor (as indicated by the minimum resource density R^* required to obtain zero net population growth; results not shown). Still, in the limited parameter space where we have explored 3-species persistence through the “Armstrong–McGehee mechanism”, populations fluctuate wildly and go through long periods of extremely low densities. It seems therefore likely that one or more species would go extinct in the presence of only a small amount of stochasticity.

The latter contrasts sharply with the oscillatory behavior of the system with flexible omnivores in regions of parameter space for which the trophic topology is (most of the time) a food chain (e.g., $K > 7.76$ in Fig. 4 lower right panel). Here, fluctuations

of all three populations stay bounded from below and population troughs of the consumer always stay above a critical density of 0.05 mg C/L (corresponding to 100 small-sized ciliates/mL). In spite of this rather limited risk of stochastic extinction, optimal diet choice nevertheless destabilizes the system in this region of parameter space; i.e., persistent oscillations occur at $K > 7.76$ and $e_{RP} < 0.111$, for which the system with fixed omnivory would settle to a stable equilibrium (compare lower left and right panels in Fig. 4). This contrasts with results from studies investigating the influence of optimal foraging on one predator–two prey systems without omnivory. In these studies optimal foraging according to the diet rule has frequently been found to decrease the amplitude of population fluctuations (Gleeson and Wilson, 1986; Křivan, 1996; Křivan and Schmitz, 2003).

Overall, optimal foraging according to the diet rule promotes 3-species permanence only in a rather limited region of parameter space. Our results therefore suggest that optimal foraging according to the diet rule is not a mechanism that alone can solve the puzzle why omnivory is so common in natural communities. Is there at all then a significant role for optimal foraging in promoting persistence of omnivory system? Classical switching (sensu Murdoch and Oaten, 1975), where consumption of a prey type by a consumer approaches zero when that prey type goes to low densities, has been shown to be a much more powerful mechanism promoting 3-species permanence in omnivory systems (Gismervik and Andersen, 1997). In a fine-grained environment (where both the resource and the intermediate consumer are encountered in the same habitat) it is, however, not entirely easy to envision a mechanism that produces classical switching. On the contrary, many widely used phenomenological switching functions are actually maladaptive (Holt, 1983).

A mechanism that would produce classical switching in a fine-grained environment requires that foraging on the resource and on the intermediate consumer poses a trade-off to the omnivore. Our example of a bacteria–ciliate system may actually be a good candidate for the operation of such a mechanism (possibly more so than for the application of the diet rule). Many species of bacterivorous ciliates increase their body size when formerly abundant bacteria become rare, which enables them to feed on smaller ciliates (Giese, 1973; Wicklow, 1988; Holyoak and Sachdev, 1998; Tuffrau et al., 2000). This morphological shift comes at the cost of reduced feeding efficiency on bacteria, because the filter apparatus of larger ciliates is less efficient at retaining small particles (Fenchel, 1980). The shift in morphology is reversed when bacteria or other small prey become more abundant (Giese, 1973; Kopp and Tollrian, 2003). Such an adaptive shift in morphology may produce a system behavior similar to the one observed by Křivan

(2000), who explored the consequences of optimal diet switching by an omnivore that uses mutually exclusive foraging modes when searching for resources and intermediate consumers, respectively. Under these assumptions, optimal foraging greatly enlarges the region of 3-species persistence, in particular in productive environments with high resource carrying capacities (Křivan, 2000). In the specific case of the bacteria–ciliate system it would then be most interesting to explore how this result is modified by the fact that a shift in morphology is not instantaneous but has a lag time.

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Appendix A. Permanence for non-adaptive omnivorous predators

A necessary condition for permanence of the food web with omnivory is that the consumer can exist with the resource in the absence of the predator, which requires that E_{RC} exists, i.e.,

$$m_C < e_{RC} \lambda_{RC} K. \tag{15}$$

The existence of a resource–predator equilibrium E_{RP} is not a necessary condition for permanence of the omnivory system. We therefore distinguish two cases.

(i) Equilibrium E_{RP} exists. This requires that inequality (6) is fulfilled. Mutual invasibility of E_{RC} and E_{RP} by the respective missing species can be easily checked by substituting the equilibrium densities of R , C , and P at E_{RP} and E_{RC} into the per capita population growth rates of consumers and predators, respectively (i.e., into the parentheses of 1). To invade, per capita population growth rates of both invading species must be positive and solving for e_{RP} yields the following condition for mutual invasibility

$$M_{RC} < e_{RP} < M_{RP}. \tag{16}$$

Here M_{RC} (see Table 2) is the minimum conversion efficiency e_{RP} required for invasibility of a resource–consumer system by the predator and M_{RP} (see Table 2) is the maximum conversion efficiency e_{RP} allowing the consumer to invade a resource–predator system.

(ii) Equilibrium E_{RP} does not exist, which requires that inequality (6) is reversed, i.e.,

$$e_{RP} < m_P \left(h_{RP} + \frac{1}{K \lambda_{RP}} \right). \tag{17}$$

As in case (i), invasibility of the resource–consumer equilibrium requires $M_{RC} < e_{RP}$. Furthermore, the right-hand side of inequality (17) is always smaller than M_{RP} at all resource carrying capacities fulfilling (15).

In summary, whether a resource–predator equilibrium E_{RP} exists or not, permanence of the 3-species system with fixed omnivory requires the simultaneous fulfillment of conditions (15) and (16). Substitution of (15) into (16) then yields inequality (11) as yet another necessary condition for permanence.

Appendix B. Permanence for the food chain

The food chain can be permanent only provided E_{RC} exists (i.e., $K > m_C / (\lambda_{RC} e_{RC})$, because otherwise consumers are excluded from the system). Predators can invade this equilibrium if

$$\frac{1}{P} \frac{dP}{dt} \Big|_{E_{RC}} > 0.$$

If inequality (12) is satisfied then the invasibility condition holds provided inequality (13) holds.

If opposite inequality to that of (12) holds then the invasibility condition requires that

$$K < \frac{m_C}{e_{RC} \lambda_{RC}} \left(1 + \frac{m_P \lambda_{RC}}{r \lambda_{CP} h_{CP} \left(\frac{e_{CP}}{h_{CP}} - m_P \left(1 + \frac{\lambda_{RC}}{r \lambda_{CP} h_{CP}} \right) \right)} \right) < \frac{m_C}{\lambda_{RC} e_{RC}}.$$

However, in this case the condition for existence of E_{RC} and its invasibility cannot hold simultaneously.

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