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Ontogenetic Diet Shifts Result in Niche Partitioning between Two Consumer Species Irrespective of Competitive Abilities

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ABSTRACT: Tilman's theory predicts the outcome of competition between two consumers sharing two resources on the basis of the shape of zero net-growth isoclines (ZNGIs). In his theory, intraspecific differences in resource use are not accounted for. Here we extend this theory to include situations where organisms undergo ontogenetic diet shifts, as these characterize the life histories of many species. In a situation that without diet shifts would lead to neutral coexistence of consumer species, we investigate whether ontogenetic diet shifts lead to niche partitioning. We analyze a model describing competition for two resources between two competitors with distinctive diets over ontogeny, using copepods (showing ontogenetic diet shifts) and daphnids (not showing ontogenetic diet shifts) as appropriate representatives. We show that an ontogenetic diet shift affects the shape of the ZNGI, changing it from reflecting perfectly substitutable resources to reflecting essential resources. Furthermore, we show that resource supply determines population stage structure and stage-dependent resource consumption in copepods and influences the competitive outcome with daphnids. In particular, we show that in itself, an ontogenetic diet shift can provide a competitive advantage if the supply of the adult resource is lower than the supply of the juvenile resource but that it always causes a disadvantage if the supply of the adult resource exceeds that of the juvenile resource.

Keywords: competition, biomass model, stage structure, coexistence, life history, resource use.

Introduction

Coexistence of consumers that share resources is a fundamental issue in community ecology. According to the competitive exclusion principle (Gause 1934), two consumer species cannot coexist in stable equilibrium if they both specialize on the same shared resource. In the event

that consumers feed on multiple resources, their coexistence crucially depends on the extent to which they partition these resources among themselves (Schoener 1974). Tilman (1982) showed that stable coexistence of two competitors feeding on the same two resources is possible if each species consumes proportionally more of the resource that most limits its own growth. Additionally, he showed that the likelihood of coexistence is determined by differences between competitors in nutrition isoclines and consumption constraint curves.

Tilman implicitly assumed that all individuals of one particular consumer species affect resources equally. This simplifying assumption made it possible to disregard the composition or structure of consumer populations altogether. However, population structure cannot be neglected if consumers in different life stages affect resources differently. For example, these intraspecific differences in resource use can create resource limitation, leading to developmental bottlenecks in particular life stages (Schreiber and Rudolf 2008), and they may therewith cause the total effect of a structured population on its resources to be different from that of an unstructured population (Lehman 1988; Schulze et al. 1995). Taking this into consideration, it is not a priori clear whether Tilman's theory generates correct expectations concerning the outcome of competition between populations in the case of intraspecific differences in resource use. Here we extend Tilman's theory to account for structured populations and analyze competition between two consumer species with contrasting life histories living in the same habitat.

In many species, individuals grow in body size during ontogeny (Werner and Gilliam 1984). Growth not only changes the resource intake rate of an individual (Peters 1983), but it may, in the case of multiple resources, also lead to changes in diet composition over ontogeny. Some species feed on the same set of resources throughout life; others exploit different resources during different life-his-

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tory phases. A change in diet over ontogeny, or ontogenetic niche shift, is widespread in nature (Werner and Gilliam 1984). Ontogenetic niche shifts can be due to metamorphosis and migration between habitats, resulting in what is termed complex life cycles (Loreau and Ebenhoh 1994; Schreiber and Rudolf 2008). However, niche shifts can also result from changes in body size and accompanying changes in the optimal size of the resource particles on which a consumer forages without a change of habitat. Conspecific consumer individuals with different sizes or in different life stages can thus occupy different niches and affect different resources (Werner and Gilliam 1984). Ontogenetic niche shifts link the dynamics of these niches or resources through consumer life history. Changes in consumer reproduction, recruitment, or maturation will hence affect dynamics of all resources exploited by the consumer throughout its life (Polis et al. 1996). As a possible consequence, populations of consumers that undergo an ontogenetic niche shift from feeding on a juvenile-specific resource to exploiting an adult-specific resource have been shown to occur in two alternative stable states, depending on resource supply (Schreiber and Rudolf 2008; Guill 2009). In one stable state, adult consumers acquire sufficient food to reproduce at maximum rate, whereas juveniles suffer from crowding and experience a developmental bottleneck. In the other stable state, there is no juvenile bottleneck and juveniles mature rapidly, resulting in food limitation among abundant adults (De Roos et al. 2007; Schreiber and Rudolf 2008; Guill 2009). Because in each of these two alternative states only a single life stage is limited by its exclusive resource, the two alternative states will respond differently to additional supplies of either the juvenile or the adult resource. More specifically, alternative stable states will be relatively insensitive to an increase in resource that is not limiting, as only resource-limited life stages will be able to increase production with additional resource supply. In contrast, if a consumer feeds on the same resources throughout its entire life, population dynamics will respond to changes in total resource supply, irrespective of which type of resource is changed. These distinct responses to resource supply will likely affect competition with consumers that undergo an ontogenetic niche shift.

The interplay of ontogenetic niche shifts and competition have been the subject of a number of studies (Haefner and Edson 1984; Loreau and Ebenhoh 1994; McCann 1998; Moll and Brown 2008). These studies all a priori assume, however, that some form of niche partitioning between competing populations occurs through either segregation of habitat or segregation of resources. In particular, competition between different life stages is generally excluded by assuming that juveniles of both competitors live in a different habitat (Haefner and Edson 1984; Loreau

and Ebenhoh 1994; Moll and Brown 2008) or forage on a different resource (McCann 1998) than the adults of the two species. Moreover, to allow for coexistence of the two competing populations, these studies invariably assume that the competitor, which dominates competition in the juvenile stage, is subordinate in the competition during the adult stage. These previous studies therefore do not disclose how the change in diet over ontogeny in itself affects competition and can lead to coexistence.

In this article, we account explicitly for competition between consumers for resources and consider ontogenetic diet shifts without changes in habitat. Furthermore, we do not a priori assume that a competitive advantage in the juvenile stage is balanced by a disadvantage in the adult stage, or vice versa. Nor do we assume that juveniles of both consumers compete for a different resource than the adults. Instead, we focus on the effects of ontogenetic diet shifts per se on the outcome of competition between two consumer species competing for two resources, and we put these results in the resource-competition framework of Tilman (1982), thereby extending that framework to structured consumer populations. We formulate a population-dynamic model that describes competition between a consumer that exploits the two resources simultaneously throughout its entire life and a consumer that exhibits a shift in exploitation of the two resources over ontogeny (fig. 1). Growth, maturation, and reproduction are assumed to be resource dependent. To clearly distinguish the effects of ontogenetic diet shifts on the competitive outcome from other differences in consumer traits, we choose our default parameters such that without diet shifts, coexistence would be neutral and no niche partitioning would occur. We show that the distinctive diets over ontogeny affect resource requirements of the two competitors at population-dynamic equilibrium and hence lead to niche partitioning between the two consumers. Further-

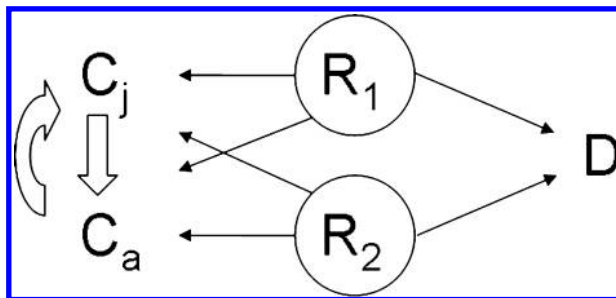


Figure 1: Schematic representation of modeled feeding interactions. Two generalist populations feed on two resources. We distinguish between the resource use of juvenile copepods (C_j) and adult copepods (C_a), whereas we assume that daphnids (D) do not change the use of resources and eat both resources all their life.

more, we show that competitive success of a population with a diet shift depends crucially on its stage structure and stage-dependent resource consumption.

Material and Methods

We describe the competition for two resources, R_1 and R_2 , between two consumers. One consumer D feeds on both resources without distinction throughout its life, whereas the second consumer C shifts its diet when it reaches the size of maturation. For convenience in presentation, we refer to the consumer that shifts its diet as a copepod and the consumer that does not shift its diet as a daphnid, adopting these as appropriate representatives of species exhibiting these lifestyles (e.g., see Kerfoot and Kirk 1991; Bern 1994; Adrian and Schneider-Olt 1999). We emphasize, however, that our model is not a specific model for copepods and daphnids alone but, as argued below, applies to a broader range of invertebrate species. We describe dynamics following the generic bioenergetic approach of Yodzis and Innes (1992), extending it to include population stage structure following De Roos et al. (2008). The model extension is explained in appendix A in the online edition of the *American Naturalist*, while table 1 summarizes the model equations and functions.

Similar to the model of Yodzis and Innes (1992), the stage-structured model is based on the assumption that within species, resource intake and energetic costs to cover maintenance requirements are directly proportional to the body size of individual consumers (Yodzis and Innes 1992, p. 1154). In the bioenergetic stage-structured model, juveniles range in body size from mass at birth to mass at maturation, whereas adults are assumed to not grow in body size. Similar to Yodzis and Innes (1992), we assume that the balance between assimilation through resource feeding and maintenance costs determines the net production of biomass. In contrast to Yodzis and Innes (1992), we distinguish between the net production of juvenile and adult copepods. We assume that juvenile copepods spend a fraction q_c of their foraging effort searching for resource R_1 and a fraction $1 - q_c$ searching for resource R_2 . In contrast to the juveniles, we assume that adults spend a fraction q_c searching for resource R_2 and a fraction $1 - q_c$ searching for resource R_1 (see table 1). When $q_c = 0$, each stage of the population therefore specializes on its own exclusive resource: juveniles specialize on R_1 and adults specialize on R_2 . Net production of juveniles is invested in growth in body mass and maturation, whereas adult net production is invested in reproduction only. When juvenile and adult net production, however, are the same,

Table 1: Ordinary differential equations and state variables

Description	Equation	Equation number
Dynamics of resource 1	$\frac{dR_1}{dt} = \ell(R_{1\max} - R_1) - F_{Cj}C_j - F_{Ca}C_a - F_dD$	(1)
Dynamics of resource 2	$\frac{dR_2}{dt} = \ell(R_{2\max} - R_2) - G_{Cj}C_j - G_{Ca}C_a - G_dD$	(2)
Dynamics of juvenile copepod biomass	$\frac{dC_j}{dt} = \nu_{Ca}C_a + \nu_{Cj}C_j - \gamma(\nu_{Cj})C_j - \mu C_j$	(3)
Dynamics of adult copepod biomass	$\frac{dC_a}{dt} = \gamma(\nu_{Cj})C_j - \mu C_a$	(4)
Net production of juvenile copepods	$\nu_{Cj} = \sigma(F_{Cj} + G_{Cj}) - T$	
Juvenile copepod consumption rate of resource 1	$F_{Cj} = \frac{I_{\max}(1-q_c)R_1}{H+(1-q_c)R_1+q_cR_2}$	
Juvenile copepod consumption rate of resource 2	$G_{Cj} = \frac{I_{\max}q_cR_2}{H+(1-q_c)R_1+q_cR_2}$	
Net production of adult copepods	$\nu_{Ca} = \sigma(F_{Ca} + G_{Ca}) - T$	
Adult copepod consumption rate of resource 1	$F_{Ca} = \frac{I_{\max}q_cR_1}{H+q_cR_1+(1-q_c)R_2}$	
Adult copepod consumption rate of resource 2	$G_{Ca} = \frac{I_{\max}(1-q_c)R_2}{H+q_cR_1+(1-q_c)R_2}$	
Maturation rate	$\gamma(\nu_{Cj}) = \frac{\nu_{Cj} - \mu}{1 - (M_j/M_a)^{1-\mu/\nu_{Cj}}}$	
Dynamics of total daphnid biomass	$\frac{dD}{dt} = (\nu_D - \mu)D$	(5)
Net production of daphnids	$\nu_D = \sigma(F_D + G_D) - T$	
Daphnid consumption rate of resource 1	$F_D = \frac{I_{\max}0.5R_1}{H+0.5R_1+0.5R_2}$	
Daphnid consumption rate of resource 2	$G_D = \frac{I_{\max}0.5R_2}{H+0.5R_1+0.5R_2}$	

which occurs for copepods in our model when $q_c = 0.5$ and which we assume to hold throughout for daphnids, the stage-structured model simplifies to the Yodzis and Innes (1992) model. Refer to appendix A for a more detailed discussion of the stage-structured bioenergetic model and its relation with the Yodzis and Innes (1992) model.

Parameterization

Table 2 lists the model parameters and their default values. A conversion efficiency of $\sigma = 0.5$ is used for conversion of both resources into consumer biomass (Peters 1983). Similar to Yodzis and Innes (1992), we assume that across different species, the mass-specific rates for maximum ingestion (I_{\max}) and maintenance (T) and the per capita background mortality rate (μ) are proportional to the quarter power of adult body size ($cM_a^{-0.25}$). A scaling factor of 0.01 is used for the maintenance rate (Peters 1983; Yodzis and Innes 1992), and 0.001 is used for background mortality (Gillooly et al. 2001). Furthermore, a scaling factor of 0.12 is used for maximum ingestion rate (Hansen et al. 1997). The mass-specific ingestion rate is therefore 12 times higher, whereas the mortality rate is 10 times lower, than the mass-specific maintenance rate. These two ratios, together with the resource turnover rate ℓ , can be shown to completely determine model dynamics. By scaling the time variable in the model with the mass-specific maintenance rate, the dependence on adult consumer body size M_a almost completely disappears, and it influences dynamics only through the value of the resource turnover rate ℓ , expressed as a multiple of the mass-specific maintenance rate. For simplicity, we chose $M_a = 1$ for both consumer species, leading to rates that were equal to their corresponding proportionality constants and identical for both consumers. In addition, the half-saturation constant H represents a resource biomass density (g biomass per unit volume). Changing its value can be considered to reflect changes in the unit volume, in which we express the densities of consumers and resources. Without loss of generality, we can therefore choose a value of H equal to 1. We must bear in mind, however, that this fixes the environmental volume in which the consumer populations are assumed to live, and thus it quantitatively scales all biomass densities.

Yodzis and Innes (1992) derived and parameterized their generic model to represent three broad classes of species: invertebrate and vertebrate ectotherms, and endotherms. Given that our model can be considered an extension of the Yodzis and Innes model, it also represents a broader class of species, even though for presentational purposes we refer to the consumers as copepods and daphnids. Since scaled model dynamics are independent of consumer body

Table 2: Summary of parameters and variables with default values and/or units

Parameter	Unit	Value	Interpretation
R_1	$g(V)^{-1}$	Variable	Resource 1/juvenile resource
R_2	$g(V)^{-1}$	Variable	Resource 2/adult resource
D	$g(V)^{-1}$	Variable	Daphnid biomass
C_j	$g(V)^{-1}$	Variable	Juvenile copepod biomass
C_a	$g(V)^{-1}$	Variable	Adult copepod biomass
ℓ	day^{-1}	.1	Resource turnover rate
$R_{1\max}$	$g(V)^{-1}$	Varied	Maximum density of R_1
$R_{2\max}$	$g(V)^{-1}$	Varied	Maximum density of R_2
σ	$g(g)^{-1}$.5	Assimilation efficiency
I_{\max}	day^{-1}	.12	Maximum ingestion rate
H	$g(V)^{-1}$	1	Half-saturation constant
q_c		0–.5	Proportional effort of copepods
T	day^{-1}	.01	Maintenance rate
μ	day^{-1}	.001	Mortality rate of all consumers
M_a	g	1	Adult consumer body mass
M_0	g	.01	Newborn consumer body mass

Note: V = unit volume.

size, we argue that our results are more generally applicable to invertebrate consumer species of all body sizes. The assumption that both consumers have equal adult body sizes $M_a = 1$ and, hence, equal energetic parameters furthermore ensures that the analysis of competition focuses on the effects of the ontogenetic diet shift per se, instead of the effect of differences in life-history rates. In “Results,” however, we do explore the interplay between differences in life-history rates with ontogenetic diet shifts.

Results

Following Tilman (1982), we calculate minimum resource requirements that guarantee persistence for each population feeding on two resources without any competition from other populations. The resulting zero net-growth isoclines (ZNGIs) represent all combinations of resource abundances for which a particular population neither increases nor decreases. Intersections of two ZNGIs are potential equilibria that may allow for coexistence of populations. Using local stability analysis of coexistence equilibria, Tilman (1982) showed that there are two necessary conditions for such an equilibrium to be stable: (1) each population must be limited by a different resource, and (2) each population must, relative to the other, consume more of the resource that most limits its population growth rate.

We use these same conditions to determine whether coexistence equilibria of daphnids and copepods in our model system can be stable. To do so, we derive consumption vectors for both daphnids and copepods in co-

existence equilibria to assess whether these conditions apply. However, we must acknowledge that Tilman's (1982) model consisted of four differential equations, whereas our model system consists of five. Because of the higher dimensionality in our system, we cannot claim that the same conditions suffice to describe stable equilibria in our system. For this reason, we verify our conclusions regarding equilibrium stability on the basis of Tilman's (1982) conditions by means of numerical stability analysis (see app. A for computational details).

Single-Population Equilibria

The ZNGI of the daphnid population D , which we denote as ZNGI_D , represents all possible equilibria for a single population of daphnids feeding on two resources. We can derive an expression for ZNGI_D by solving $dD/dt = 0$ (eq. [5] in table 1), leading to the following relationship between R_1 and R_2 :

$$\nu_D - \mu = \sigma I_{\max} \frac{0.5R_1 + 0.5R_2}{H + 0.5R_1 + 0.5R_2} - T - \mu = 0.$$

Here ν_D represents the net biomass production of daphnids (other symbols are explained in table 2). This relationship determines a straight line with a slope equal to -1 in the phase plane spanned by the R_1 - and R_2 -axes (fig. 2, *gray dashed lines*). This type of ZNGI is characteristic for an interaction between perfectly substitutable resources (Tilman 1982). Any point on the ZNGI_D represents a combination of resource densities at which a daphnid population in isolation may potentially equilibrate. The equilibrium actually reached is determined by the equilibrium conditions $dR_1/dt = 0$ and $dR_2/dt = 0$ (eqq. [1] and [2] in table 1) and depends on the value of maximum resource densities $R_{1\max}$ and $R_{2\max}$ and consumption of R_1 and R_2 by daphnids. Following Tilman (1982), we denote the point in the (R_1, R_2) phase plane with coordinates $(R_{1\max}, R_{2\max})$ as the resource supply point. Consumption of resources by daphnids decreases resource densities in the direction of the vector

$$\begin{pmatrix} -F_D \\ -G_D \end{pmatrix},$$

in which F_D and G_D are the foraging rates on resource 1 and resource 2, respectively. Given the expressions for F_D and G_D in terms of R_1 and R_2 (table 1), the direction of this consumption vector can also be expressed as

$$\begin{pmatrix} -R_1 \\ -R_2 \end{pmatrix}. \quad (6)$$

Resource supply increases resource densities in the direction of the vector

$$\begin{pmatrix} R_{1\max} - R_1 \\ R_{2\max} - R_2 \end{pmatrix}.$$

At equilibrium, the consumption by daphnids is balanced by the resource supply, which occurs where the straight line connecting the origin with the resource supply point $(R_{1\max}, R_{2\max})$ intersects the ZNGI_D .

For the ZNGI of the structured copepod population (ZNGI_C), we can derive only an implicit equation relating R_1 and R_2 by combining equilibrium conditions $dC_a/dt = 0$ and $dC_j/dt = 0$ (see app. B in the online edition of the *American Naturalist* for derivation):

$$\frac{\nu_{Ca}}{\mu} \left(\frac{M_0}{M_a} \right)^{(\mu/\nu_{Cj})-1} = 1.$$

Here, ν_{Cj} and ν_{Ca} refer to the net biomass production of juvenile and adult copepods, respectively. Note that the ZNGI_D for daphnids can also be expressed in this form (replacing ν_{Cj} and ν_{Ca} with ν_D), and it is identical to the ZNGI_C if $\nu_{Cj} = \nu_{Ca} = \nu_D$.

If $q_c = 0$, then both resources are essential for persistence of the copepod population. This is reflected in the shape of the ZNGI_C (fig. 2A), which resembles a ZNGI characteristic for two essential resources (Tilman 1982). Although juveniles do not eat R_2 and adults do not eat R_1 , the population as a whole cannot do without either of them. Using the model equations (1)–(4) in table 1, Guill (2009) has shown that depending on the resource supply point $(R_{1\max}, R_{2\max})$, the population exhibiting a diet shift can occur in two alternative stable states (fig. 3) in which either juveniles make up most of population biomass and adult biomass is low or vice versa. In each of these two alternative states, only the most abundant life stage is limited by its exclusive resource: an adult-dominated population by R_2 (reflected in fig. 2A by the horizontal isocline leg) and a juvenile-dominated population by R_1 (reflected in fig. 2A by the vertical isocline leg). Alternative stable states will be relatively insensitive to an increase in resource that is not limiting, as only resource-limited life stages will be able to increase production with additional resource supply. Hence, when juveniles dominate the copepod population at equilibrium (fig. 3, *thick solid lines*) and, consequently, dynamics are mostly limited by juvenile resource density R_1 , equilibrium densities will increase with

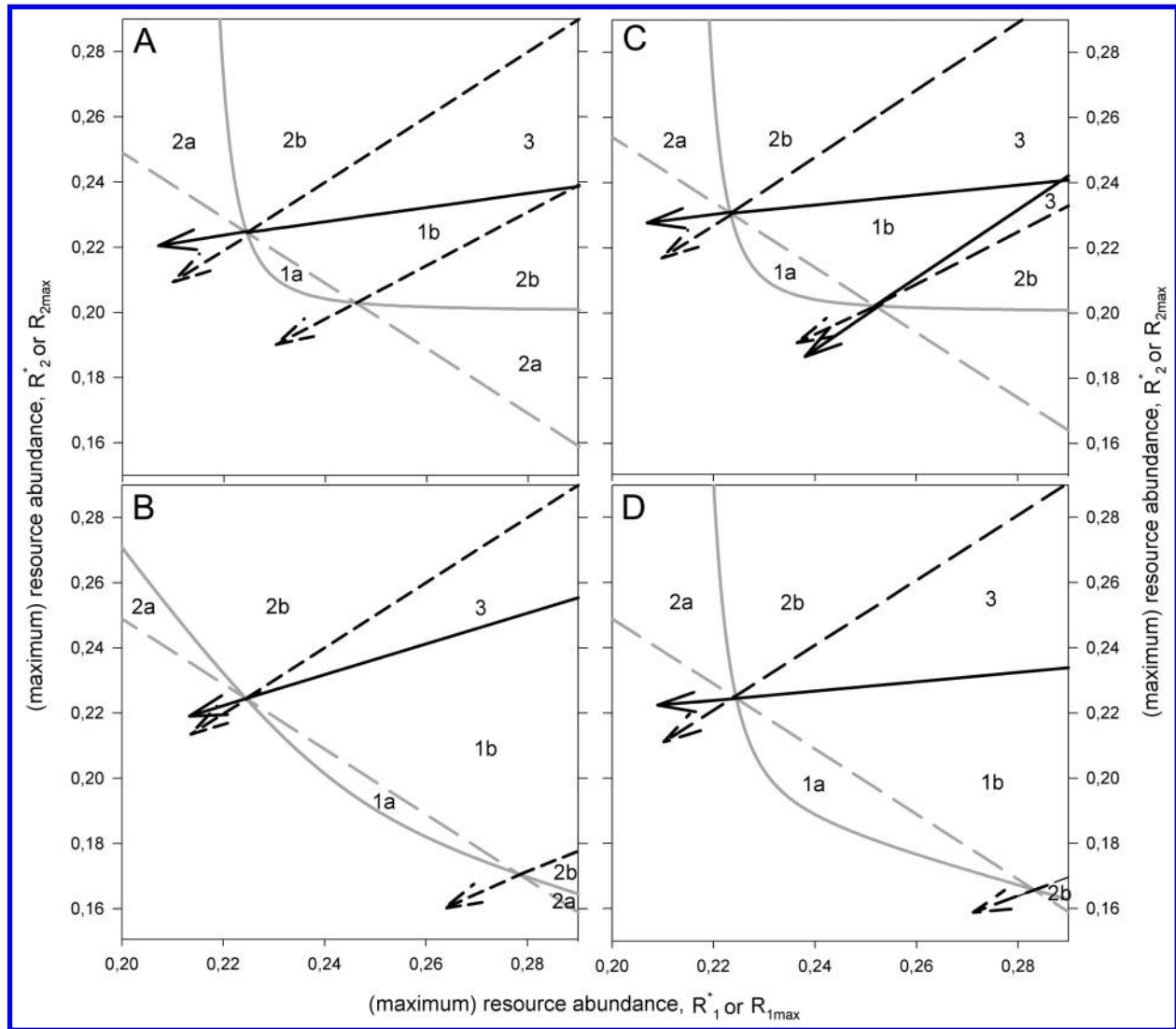


Figure 2: Zero net-growth isoclines (ZNGIs; gray) and consumption vectors (black arrows) in coexistence equilibria. Solid isoclines and vectors indicate copepods; dashed lines indicate daphnids. Note the different scaling of X- and Y-axes. *A*, Copepods exhibit a complete diet shift ($q_c = 0$). Resource supply regions with different competitive outcomes are determined based on the consumption vectors of both populations: *1a* and *1b* indicate (competitive) exclusion of daphnids; *2a* and *2b* indicate (competitive) exclusion of copepods; and *3* indicates coexistence. *B*, Partial diet shift during copepod ontogeny ($q_c = 0.3$). The change in copepod consumption vectors enlarges the region of resource supply where copepods competitively exclude daphnids (*1*) and diminishes the region where both populations can coexist (*3*). *C*, Complete diet shift during copepod ontogeny ($q_c = 0$), while the two species are no longer energetically equivalent (daphnids experience a 10% higher mortality). Now equilibrium *2* is also stable (compare with in the other panels), such that coexistence between daphnids and copepods is possible in two different stable states, depending on resource supply. *D*, Ontogenetic diet shifts through niche widening: juvenile copepods feed only on R_1 ($q_c = q_i = 0$), while adults feed on R_1 and R_2 ($q_c = q_a = 0.3$). The change in the ZNGI_C enlarges region *1a*, while the change in consumption vectors enlarges region *3* but diminishes region *1b*.

increases in $R_{1\max}$ but will be insensitive to or even decrease with increases in $R_{2\max}$. Similarly, in an adult-dominated equilibrium, only increases in $R_{2\max}$ will translate into increases in consumer equilibrium densities (fig. 3, *thin solid lines*). For a further analysis of the single-consumer equi-

libria of equations (1)–(4) and the alternative stable states found therein, we refer to Guill (2009).

Any point on the ZNGI_C (fig. 2) represents a combination of resource densities at which the copepod population may equilibrate. The equilibrium conditions

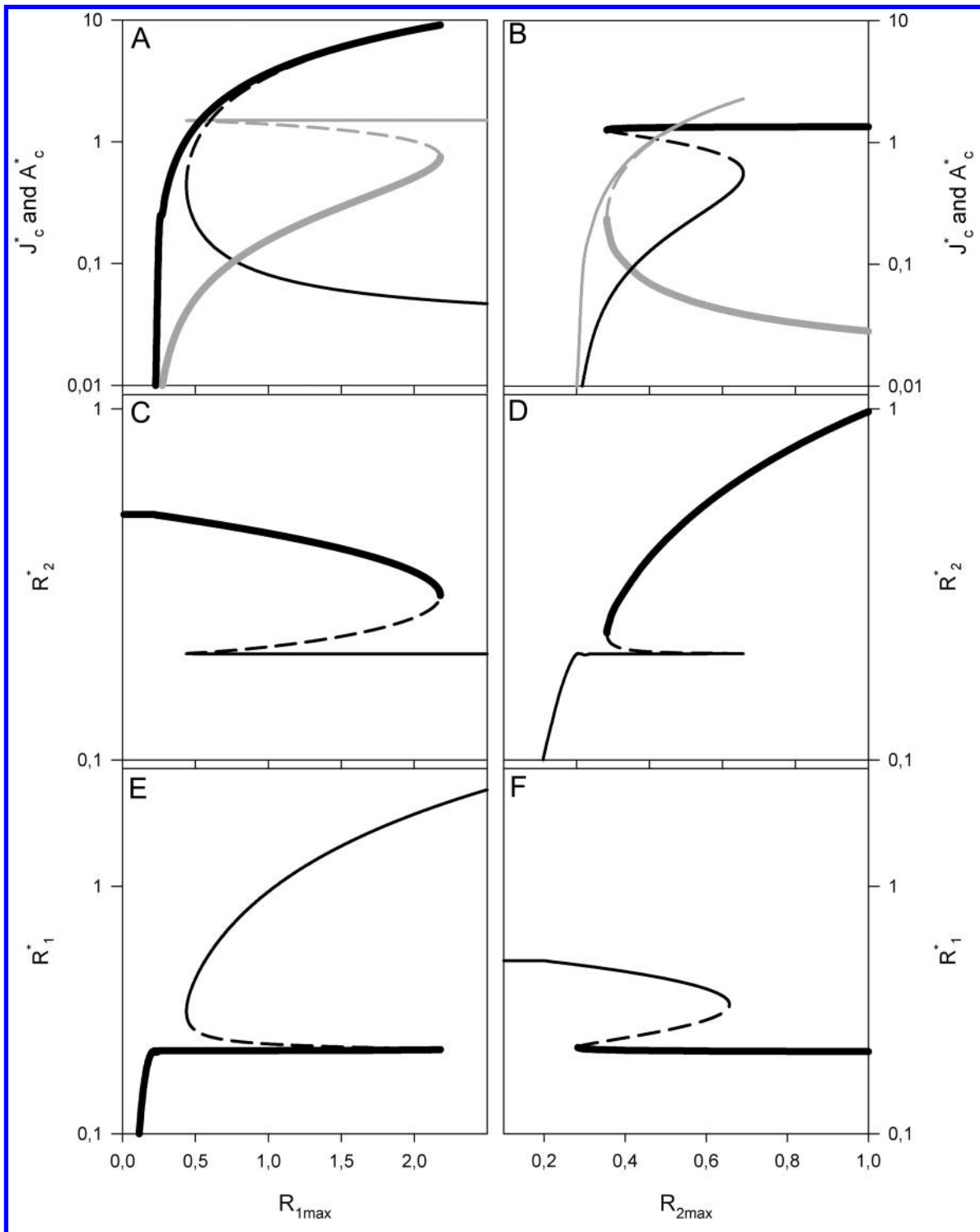


Figure 3: Changes in equilibrium copepod and resource densities in the absence of daphnids and for $q_c = 0$ as a function of maximum resource densities $R_{1\max}$ (with $R_{2\max} = 0.5$; A, C, E) and $R_{2\max}$ (with $R_{1\max} = 0.5$; B, D, F). A, B, Adult (gray lines) and juvenile (black lines) copepod biomasses. C–F, Corresponding changes in R_2^* and R_1^* , respectively. Note the logarithmic Y-axes. In all panels, solid lines indicate stable equilibrium states and dashed lines represent unstable equilibrium states (saddle points). Thin solid lines refer to stable equilibrium states with low juvenile and high adult copepod biomass and therefore high R_1^* and low R_2^* values. Thick solid lines refer to stable equilibrium states with high juvenile and low adult copepod biomasses and thus low R_1^* and high R_2^* values.

$dR_1/dt = 0$ and $dR_2/dt = 0$ (table 1, eqq. [1] and [2]), and hence the value of supply and consumption by copepods of R_1 and R_2 , once again determine the equilibrium reached. Copepod consumption of resources decreases resource densities in the direction of the vector

$$\begin{pmatrix} -C_j F_{C_j} & -C_a F_{C_a} \\ -C_j G_{C_j} & -C_a G_{C_a} \end{pmatrix},$$

in which F_{C_j} and F_{C_a} are the intake of resource 1 by juveniles and adults, respectively, and G_{C_j} and G_{C_a} are their intake of resource 2. This expression makes it clear that consumption of resources depends as much on the copepod population's stage structure as on the functional responses to resources. However, using the expression for the adult-juvenile biomass ratio in equilibrium $C_a/C_j = \gamma(\nu_{C_j})/\mu$ derived from $dC_a/dt = 0$, the copepod consumption vector can be shown to have the same direction as the vector

$$\begin{pmatrix} -\mu F_{C_j} & -\gamma(\nu_{C_j})F_{C_a} \\ -\mu G_{C_j} & -\gamma(\nu_{C_j})G_{C_a} \end{pmatrix}, \tag{7}$$

which is a function of resource equilibrium densities only ($\gamma(\nu_{C_j})$ represents the mass-specific maturation rate of juvenile copepods). Consequently, given a particular equilibrium point on the $ZNGI_C$ with known resource densities, one can use expression (7) to construct a straight line through this equilibrium in the direction of this consumption vector. This line, in turn, encompasses all resource supply points ($R_{1,max}, R_{2,max}$) that will eventually lead to this particular equilibrium point on $ZNGI_C$.

Coexistence Equilibria

Intersections of the two single-population ZNGIs (fig. 2) are equilibria potentially allowing for coexistence of daphnids and copepods. The first intersection, henceforth called equilibrium 1, has coordinates $R_1^* = R_2^*$. At those coordinates, all consumption rates of daphnids and copepods are equal ($F_{C_j}^* = G_{C_a}^* = F_D^* = G_D^*$, whereas $G_{C_j}^* = F_{C_a}^* = 0$, since $q_c = 0$), making production rates equal as well ($\nu_{C_j} = \nu_{C_a} = \nu_D$). Because the juvenile and adult copepod production terms are equal in this particular equilibrium, maturation $\gamma(\nu_{C_j})$ becomes equal to $-\mu/\ln(M_0/M_a)$ (following De Roos et al. 2008). The direction of the copepod consumption vector, expression (7), in equilibrium 1 thus equals

$$\begin{pmatrix} \ln(M_0/M_a) \\ -1 \end{pmatrix}.$$

This vector will rotate clockwise if the ratio of mass at birth and maturation decreases. The direction of the consumption vector of daphnids, expression (6), in equilibrium 1 equals

$$\begin{pmatrix} -1 \\ -1 \end{pmatrix}.$$

We can state that in equilibrium 1, copepods are, proportional to daphnids, most limited by R_1 , and their consumption vector, relative to that of daphnids, reduces R_1 the most as long as $\ln(M_0/M_a) < -1$. Tilman's (1982) conditions thus suggest that stable coexistence of daphnids and copepods in equilibrium 1 is possible. For all parameter combinations we investigated, this conclusion is indeed confirmed by numerical stability analysis.

The second intersection of the $ZNGI_D$ and the $ZNGI_C$, in which $R_1^* > R_2^*$, we henceforth refer to as equilibrium 2. In this equilibrium, the consumption vector of copepods (expression [7]) is graphically indistinguishable from the vector

$$\begin{pmatrix} -R_1 \\ -R_2 \end{pmatrix}$$

(fig. 2A), representing the daphnid consumption vector. Even though all of our numerical analysis suggests that the two consumption vectors are indeed the same, we have not been able to prove this equivalence analytically.

The two coexistence equilibrium points divide both ZNGIs into three sections (fig. 2) and give rise to distinct regions of resource supply that result in either coexistence or competitive exclusion of either population. For low and high values of R_1^* , the $ZNGI_D$ is located at lower values of R_2^* than is the $ZNGI_C$. Hence, for resource supply points between the corresponding sections of the $ZNGI_D$ and the $ZNGI_C$ (fig. 2, region 2a), only daphnids persist, as copepods cannot persist alone. Furthermore, for resource supply points ($R_{1,max}, R_{2,max}$) that would allow for copepod persistence when alone (region 2b), daphnids can invade the corresponding copepod-only equilibrium and subsequently outcompete their competitor.

In coexistence equilibrium 1, the combined consumption rate of daphnids and copepods has to balance resource supply, which is possible only for resource supply points ($R_{1,max}, R_{2,max}$) below the line where $R_{1,max} = R_{2,max}$ (region 3). Lines through the equilibrium point 1 that are spanned by the consumption vectors of daphnids and copepods

bound this resource supply region from above and below, respectively. Given a resource supply point in this region, daphnids and copepods stably coexist.

The section of the $ZNGI_C$ between the two coexistence equilibrium points is located at lower values of (R_1^*, R_2^*) than the corresponding section of the $ZNGI_D$. This results in a small region of resource supply for which only copepods can persist (region 1a) and a larger region for which copepods can invade the daphnid-only equilibrium that occurs for these resource supply points (region 1b) and outcompete their competitor.

We based the conclusions above only on considerations of consumption vectors following the lines of analysis used by Tilman (1982). However, extensive numerical bifurcation studies of changes in equilibrium density and stability confirm that these conclusions provide an almost complete summary of the outcome of competition between daphnids and copepods. For only a small region of resource supply points (overlapping regions 1b, 2b, and 3 in fig. 2) have we found a more complex pattern of competitive outcomes. For these parameter values, the copepod population can reach two alternative stable states (fig. 3), of which one can be invaded by daphnids and the other cannot. A more detailed discussion of these complications is, however, beyond the scope of this article.

Relaxing the Diet Shift

From analysis of equations (1)–(5) in table 1 when $q_c = 0$, we conclude that distinctive diets over ontogeny, whereby juvenile and adult copepods interact with only one resource each and daphnids exploit both resources throughout their lives, allow for coexistence of the two populations for certain ranges of resource supply. In particular, a necessary condition for coexistence to occur is that resource supply for juvenile copepods is higher than it is for adult copepods ($R_{1max} > R_{2max}$). What if the diet shift is less extreme, however, and juvenile and adult copepods also exploit both resources to some extent?

Increasing q_c from 0 to 0.5 makes the diets of the two species more similar. If $q_c > 0$, then the consumption rates F_{Ca} and G_{Cj} are larger than 0 and all functional responses are a function of both resource densities. With increasing q_c , both C_a and C_j divide their feeding efforts more and more over both resources. As a consequence, the $ZNGI_C$ changes shape from reflecting an interaction of essential to complementary and eventually substitutable resources as q_c is increased (fig. 4). Ultimately, for $q_c = 0.5$, the $ZNGI$ s and consumption vectors of both populations coincide, as we have assumed the two consumer species to be energetically equivalent and thus completely equal when $q_c = 0.5$.

Changes of the $ZNGI_C$ with increasing q_c potentially

change the competitive outcome between daphnids and copepods for a particular resource supply point. Coexistence equilibrium point 1, in which $R_1^* = R_2^*$, is independent of q_c and hence does not change coordinates (fig. 4). As figure 4 shows, this leads to the conclusion that any consumer species with $q < 0.5$ can potentially coexist with daphnids in equilibrium point 1. Moreover, because both resources still equilibrate to the same density, the daphnid consumption vector does not change, nor do biomass production rates of juvenile and adult copepods ($\nu_{Cj} = \nu_{Ca}$) or the ratio of adult and juvenile copepod biomass in equilibrium, $C_a/C_j = \gamma(\nu_{Cj})/\mu$. Given that $R_1^* = R_2^*$, the copepod consumption vector can be rewritten for nonzero values of q_c as

$$\begin{pmatrix} (1 - q_c) \ln(M_o/M_a) - q_c \\ -(1 - q_c) + q_c \ln(M_o/M_a) \end{pmatrix}.$$

This expression makes it clear that for increasing values of q_c , the copepod consumption vector rotates counterclockwise from

$$\begin{pmatrix} \ln(M_o/M_a) \\ -1 \end{pmatrix}$$

at $q_c = 0$ to

$$\begin{pmatrix} -1 \\ -1 \end{pmatrix}$$

at $q_c = 0.5$. As a consequence, the region of resource supply that allows for coexistence of daphnids and copepods, which is bounded by the two lines spanned by the daphnid and copepod consumption vectors, respectively, becomes smaller (cf. region 3 in fig. 2A and fig. 2B).

The location of coexistence equilibrium point 2, in which $R_1^* > R_2^*$, changes with increasing q_c such that R_1^* increases while R_2^* decreases (fig. 4). As is the case for $q_c = 0$, the consumption vectors of both populations in this equilibrium are also numerically indistinguishable from each other for nonzero values of q_c and can hence be written as

$$\begin{pmatrix} -R_1^* \\ -R_2^* \end{pmatrix}.$$

The line through equilibrium point 2 spanned by these vectors therefore rotates clockwise when q_c is increased due to changes in equilibrium resource densities.

Relaxing the discrete diet shift of the copepods therefore increases the region of resource supply points where C_a

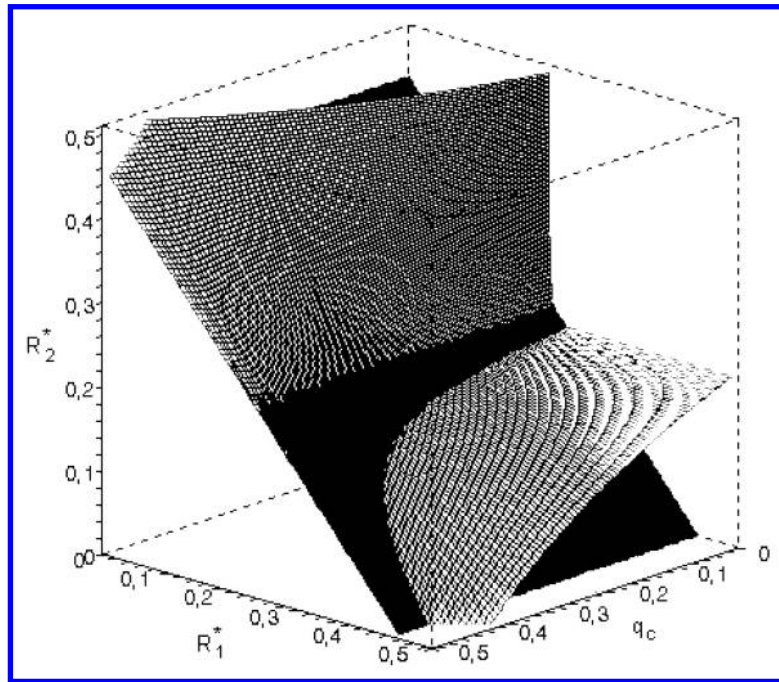


Figure 4: Changes in the zero net-growth isocline (ZNGI) for the copepod population (ZNGI_C; *gray manifold*) and for the daphnid population (ZNGI_D; *black plane*) for increasing values of q_c . From back to front, the ZNGI_C flattens out from the strongly curved shape shown in figure 2A (for $q_c = 0$) to coincide with the plane that represents the ZNGI_D for $q_c = 0.5$. This change does not alter the coordinates (R_1^* , R_2^*) of equilibrium 1 (visible as a straight line on the ZNGI_D plane parallel to the q_c -axis), but it leads to a shift of equilibrium 2 to higher values of R_1^* and lower values of R_2^* with increasing q_c values.

and C_j competitively exclude D (fig. 2B, region 1b) at the expense of the region of resource supply for which both populations coexist (region 3) and the region for which daphnids competitively exclude copepods (region 2b). Invariably, however, daphnids will outcompete copepods if the supply of resource that is mostly fed on by adults is larger ($R_{1\max} < R_{2\max}$). Note from figure 4 that if q_c is only a little smaller than 0.5, the ZNGI_C crosses the ZNGI_D only once at equilibrium 1, while consumption vectors (6) and (7) in that point differ only marginally. For this choice of q_c , the resource supply plane is equally divided in supply regions where either copepods or daphnids are competitively dominant (results not shown). When R_1 is supplied in a greater amount than R_2 , copepods have a competitive advantage. When $R_{2\max} > R_{1\max}$, daphnids are dominant.

Energetically Not Equivalent Competitors

If we relax the assumption that both competitors are energetically equivalent, for instance, by changing the intake or loss rate of daphnids, then the general pattern of competitive outcomes remains qualitatively the same except for the occurrence of an additional region of resource supply leading to coexistence in equilibrium point 2 (fig.

2C). When daphnids and copepods are not energetically equivalent, their consumption vectors in equilibrium 2 differ. When loss rates of daphnids are increased (or, equivalently, intake rates are decreased), equilibrium point 2 moves along the ZNGI_C isocline to higher values of R_1^* (fig. 2C). With higher values of R_1^* , adult copepods are more abundant in equilibrium and their impact on resource R_2 is more pronounced (fig. 3A, 3C, 3E), causing a counterclockwise rotation of consumption vector (7) relative to the daphnid consumption vector

$$\begin{pmatrix} -R_1 \\ -R_2 \end{pmatrix}.$$

This results in a second region of resource supply that leads to stable coexistence of the two consumers (region 3). In contrast, when daphnid loss rates are decreased or intake rates are increased, equilibrium point 2 shifts toward lower values of R_1^* , increasing the relative abundance of juvenile copepods in equilibrium (fig. 3A, 3C, 3E), causing a clockwise rotation of consumption vector (7) relative to vector (6). In that case, the resulting region of resource supply leads to competitive exclusion of either daphnids or copepods, depending on initial conditions.

Until now, we have assumed that a single parameter q_c determines the diet of juvenile and adult copepods, such that consumers switch from one resource to the other at maturation and resource selection by juvenile copepods is the mirror image of that of adults. On the one hand, this assumption simplifies analysis, as it involves a single parameter, but on the other hand, it represents only a special case of all possible forms of ontogenetic diet shifts that do occur in natural systems. Another, perhaps more common configuration would involve adult copepods consuming a wider range of resources than juveniles (Werner and Gilliam 1984). To investigate the consequences of such an ontogenetic “niche widening,” we assume in the following values for the parameter q_c that differ between juvenile and adult copepods. In particular, for juveniles we assume that $q_c = q_j = 0$, such that they feed on only R_1 , while for adults we assume that $q_c = q_a = 0.3$, such that they preferentially feed on R_2 but also include R_1 to some extent into their diet. Figure 2D illustrates the consequences of this ontogenetic niche widening for the ZNGI_C and the consumption vector of copepods. The ZNGI_C now has a shape that is intermediate between the shapes of the ZNGI_C in the cases of completely exclusive ($q_c = 0$; fig. 2A) and partially exclusive ($q_c = 0.3$; fig. 2B) resources. On the one hand, R_1 is an essential resource for juvenile copepods, resulting in a minimum requirement of R_1^* for copepods to persist, while on the other hand, adults can compensate for a lack of R_2 with the use of R_1 , enabling the persistence of copepods without R_2 . Although the coexistence equilibrium 1 remains located at $R_1^* = R_2^*$, a consequence of the wider diet of adults compared with that of juveniles is that in equilibrium 1, juvenile copepod biomass is even more abundant. Hence, in coexistence, equilibrium 1 copepods consume more of R_1 , rotating the copepod consumption vector clockwise. This change in consumption vector enlarges the region of resource supply, leading to coexistence of daphnids and copepods (region 3), and it diminishes the region, leading to the competitive exclusion of daphnids (region 1b). The location of coexistence equilibrium point 2, in which $R_1^* > R_2^*$, changes with ontogenetic niche widening such that R_1^* increases whereas R_2^* decreases (fig. 2D). As is the case for the configuration with a single parameter q_c for both juveniles and adults and energetic equivalence assumed as before, the consumption vectors of daphnids and copepods in this equilibrium are numerically indistinguishable from each other and can again be written as

$$\begin{pmatrix} -R_1^* \\ -R_2^* \end{pmatrix}.$$

We conclude from the analysis of this ontogenetic niche-

widening scenario that, despite the changes in shape of the ZNGI_C, the condition for coexistence to occur is still that resource supply for juvenile copepods is higher than that for adult copepods ($R_{1\max} > R_{2\max}$).

Discussion

Classical theory predicts that coexistence of two competitors feeding on two resources can occur if resources are partitioned differently among the competitors (Schoener 1974). Partitioning between competitors can occur because of differences in nutrition isoclines and consumption constraint curves as well as a spatial distribution of resources. Tilman (1982) provided a resource-competition framework to portray and analyze these consumer-resource interactions. This resource-competition framework has been useful for studies on competition, both theoretically and experimentally, in part because it generates easily interpretable graphical predictions of competitive outcomes, given measurable resource requirements of two competitors. The framework has subsequently been expanded to include heterogeneous environments as a source of niche partitioning between populations (Pacala and Tilman 1994) and predators as a limiting factor (Holt et al. 1994; Leibold 1996; Grover and Holt 1998). The theory has been further extended to include nonequilibrium dynamics that enable a limited number of resources to support a larger number of species (Huisman and Weissing 1999). Intraspecific differences in resource use, however, have not been considered in the framework. Rather, within the framework, the assumption has always been that all individuals of one particular consumer species affect resources equally. This assumption neglects the fact that individuals of many species grow in body size during a considerable part of their ontogeny (Werner and Gilliam 1984) and growth may lead to differences in resource use between different life stages. As such, contemporary competition theory in this framework could not explain the competitive outcomes in structured populations with intraspecific differences in resource use (Lehman 1988; Schulze et al. 1995), among which are ontogenetic shifts in diet.

We studied a system with two competing consumer populations, of which one exhibited an ontogenetic diet shift and the other did not, and we always accounted for explicit resource-dependent growth, maturation, and reproduction. Changing the extent of the diet shift by changing parameter q_c resulted in differently shaped ZNGIs. Specifically, decreasing q_c changed the ZNGI shape from one resembling interactions of substitutable resources to one resembling interactions of complementary and eventually essential resources. This result shows that the ZNGI shape is affected by ontogenetic changes in resource use similar to how it is affected by nutritional quality, spatial distri-

bution of resources, and searching performance of consumers as shown by Tilman (1982).

Differences in ZNGI shape resulting from an ontogenetic diet shift in one population affected the competitive outcome between populations, depending on resource supply. Whenever $R_{1\max} < R_{2\max}$, juveniles were highly abundant in the population, exhibiting an ontogenetic diet shift even if the shift in diet over ontogeny was very slight. Consequently, R_1 was reduced at a higher rate than R_2 . The population not exhibiting a diet shift had a competitive advantage at these resource supply ratios. It did not experience any intraspecific differences in resource consumption, and it reduced R_2 more than the population with a diet shift. The consumer population exhibiting an ontogenetic diet shift could coexist with or exclude the consumer population that did not exhibit an ontogenetic diet shift only if the resource supply enabled a stage structure that could reduce resources to the same or a larger extent than their competitors could. This was possible only if $R_{1\max} > R_{2\max}$. This pattern remained the same even when the extent of ontogenetic diet shift was relaxed. We conclude, therefore, that in itself, an ontogenetic diet shift can provide a competitive advantage whenever the supply of resource used by adults is lower than the supply of resource used by juveniles, but it creates a competitive disadvantage whenever the adult resource supply exceeds the juvenile resource supply.

The presence of ontogenetic niche shifts is well recognized empirically (Werner and Gilliam 1984), and their population-dynamical and structural effects have also been studied theoretically (Schreiber and Rudolf 2008; Guill 2009). Schreiber and Rudolf (2008) and Guill (2009) showed that ontogenetic niche shifts affect population stage structure such that these populations can occur in two alternative stable states, depending on resource supply. In one state, few adult consumers reproduced at a maximum rate, whereas the more abundant juveniles suffered from shortage of food and experienced a developmental bottleneck. In the other state, juveniles matured rapidly, resulting in food limitation among the more abundant adults.

In regard to interspecific competition, however, theory has focused on the interactions with populations exhibiting ontogenetic habitat shifts (Haefner and Edson 1984; Loreau and Ebenhoh 1994; Mougi and Nishimura 2005; Moll and Brown 2008). Some studies even represented competitive interactions as negative density dependence affecting reproduction and maturation instead of explicitly representing competition for resources (e.g., Haefner and Edson 1984; Mougi and Nishimura 2005; Moll and Brown 2008). This emphasizes the focus of these studies on the effect of habitat segregation on competition instead of the effect of differences in resource use. Haefner and Edson (1984) and Loreau and Ebenhoh (1994) have studied the

competitive interactions between a population exhibiting an ontogenetic habitat shift and a population not changing habitats during their lifetime, with competition occurring only in the habitat shared by both populations. Consequently, the success of the population exhibiting a habitat shift and the possibility of coexistence depended crucially on the success of the life stage escaping competition. For coexistence to occur, for instance, the population exhibiting a habitat shift had to be most resource limited in the (adult) habitat where the other population was absent (Loreau and Ebenhoh 1994). In analogy with our results, coexistence was impossible if resource limitation was highest among juvenile habitat shifters. In contrast to our results that show that the diet shifter was excluded whenever $R_{1\max} < R_{2\max}$, Loreau and Ebenhoh (1994) showed that the population exhibiting a habitat shift was superior in this situation. They concluded that unless the population did not show that a habitat shift was more efficient in resource use, a habitat shift provided a competitive advantage because it prevented intraspecific competition across habitats and interspecific competition in one habitat. In contrast, the competitor that did not shift habitats experienced intra- and interspecific competition over its complete ontogeny, leading to a lower equilibrium density. Still, Loreau and Ebenhoh (1994) hinted that in the absence of habitat shifts, the conditions that competitively favor ontogenetic niche shifts may be more stringent, as we found in our analysis.

McCann (1998) analyzed a model describing competition between two consumers, both of which had ontogenetic niche shifts, without assuming an explicit change in habitat. He argued that without "recourse to temporal or spatial partitioning" (p. 2957) between competitors, his model analysis showed that coexistence was possible. In contrast to his claim, however, it was assumed that the resource for juvenile competitors was completely distinct from that of adults, excluding competition between the life stages. This resource segregation between life-history stages is conceptually identical to the habitat segregation between stages assumed in other studies (Haefner and Edson 1984; Loreau and Ebenhoh 1994; Mougi and Nishimura 2005; Moll and Brown 2008). Consequently, the type of coexistence that McCann (1998) referred to as "density-dependent coexistence" occurs under the same conditions as coexistence in studies with explicit habitat segregation, namely, that a competitive advantage at one life stage has to be balanced by a disadvantage at another life stage. In contrast, competition in our model between copepod stages was separated only when $q_c = 0$, whereas at all times, daphnid individuals competed intraspecifically and interspecifically with copepods. Furthermore, we did not a priori assume that daphnids or copepods ever changed their competitive ability during their lifetimes. Instead, the changes in competitive

abilities of copepods and the resulting niche partitioning between consumers was a property emerging from the ontogenetic diet shift itself.

The competition configuration in our model thus allowed us to focus specifically on the effects on competition of ontogenetic diet shifts themselves, as opposed to innate differences in competitive ability. In combination with the explicit consideration of exploitative competition for resources and the assumption that growth, reproduction, and maturation of consumers are resource dependent, this competition configuration allowed us to analyze resource competition of structured populations, using the framework developed by Tilman (1982) for unstructured populations. As we assumed that mortality, ingestion, and maintenance rates, as well as half-saturation constants and conversion efficiencies, of both competitors were identical, the consumption constraint and nutrition isoclines were identical between the two competing populations, resulting in neutral coexistence when $q_c = 0.5$. On this basis, we can conclude that inclusion of ontogenetic diet shifts per se result in niche partitioning between the two consumer species, a result that has not been covered by Tilman (1982) or by competition theory in general.

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Literature Cited

- Adrian, R., and B. Schneider-Olt. 1999. Top-down effects of crustacean zooplankton on pelagic microorganisms in a mesotrophic lake. *Journal of Plankton Research* 21:2175–2190.
- Bern, L. 1994. Particle selection over a broad size range by crustacean zooplankton. *Freshwater Biology* 32:105–112.
- De Roos, A. M., T. Schellekens, T. van Kooten, K. van de Wolfshaar, D. Claessen, and L. Persson. 2007. Food-dependent growth leads to overcompensation in stage-specific biomass when mortality increases: the influence of maturation versus reproduction regulation. *American Naturalist* 170:E59–E76.
- . 2008. Simplifying a physiologically structured population model to a stage-structured biomass model. *Theoretical Population Biology* 73:47–62.
- Gause, G. F. 1934. *The struggle for existence*. Williams & Wilkins, Baltimore.
- Gillooly, J. F., J. H. Brown, G. B. West, V. M. Savage, and E. L. Charnov. 2001. Effects of size and temperature on metabolic rate. *Science* 293:2248–2251.
- Grover, J. P., and R. D. Holt. 1998. Disentangling resource and apparent competition: realistic models for plant-herbivore communities. *Journal of Theoretical Biology* 191:353–376.
- Guill, C. 2009. Alternative dynamical states in stage-structured consumer populations. *Theoretical Population Biology* 76:168–178.
- Haefner, J. W., and J. L. Edson. 1984. Community invasion by complex life cycles. *Journal of Theoretical Biology* 108:377–404.
- Hansen, P. J., P. K. Bjornsen, and B. W. Hansen. 1997. Zooplankton grazing and growth: scaling within the 2–2,000- μm body size range. *Limnology and Oceanography* 42:687–704.
- Holt, R. D., J. Grover, and D. Tilman. 1994. Simple rules for interspecific dominance in systems with exploitative and apparent competition. *American Naturalist* 144:741–771.
- Huisman, J., and F. J. Weissing. 1999. Biodiversity of plankton by species oscillations and chaos. *Nature* 402:407–410.
- Kerfoot, W. C., and K. L. Kirk. 1991. Degree of taste discrimination among suspension-feeding cladocerans and copepods: implications for detritivory and herbivory. *Limnology and Oceanography* 36:1107–1123.
- Lehman, J. T. 1988. Ecological principles affecting community structure and secondary production by zooplankton in marine and fresh-water environments. *Limnology and Oceanography* 33:931–945.
- Leibold, M. A. 1996. A graphical model of keystone predators in food webs: trophic regulation of abundance, incidence, and diversity patterns in communities. *American Naturalist* 147:784–812.
- Loreau, M., and W. Ebenhoh. 1994. Competitive-exclusion and coexistence of species with complex life-cycles. *Theoretical Population Biology* 46:58–77.
- McCann, K. 1998. Density-dependent coexistence in fish communities. *Ecology* 79:2957–2967.
- Moll, J. D., and J. S. Brown. 2008. Competition and coexistence with multiple life-history stages. *American Naturalist* 171:839–843.
- Mougi, A., and K. Nishimura. 2005. Coexistence of competitive species with a stage-structured life cycle. *Ecological Research* 20:581–589.
- Pacala, S. W., and D. Tilman. 1994. Limiting similarity in mechanistic and spatial models of plant competition in heterogeneous environments. *American Naturalist* 143:222–257.
- Peters, R. H. 1983. *The ecological implications of body size*. Cambridge University Press, Cambridge.
- Polis, G. A., R. D. Holt, B. A. Menge, and K. O. Winemiller. 1996. Time, space and life history: influences on food webs. Pages 435–460 in G. A. Polis and K. O. Winemiller, eds. *Food webs: integration of patterns and dynamics*. Chapman & Hall, New York.
- Schoener, T. W. 1974. Resource partitioning in ecological communities. *Science* 185:27–39.
- Schreiber, S., and V. H. W. Rudolf. 2008. Crossing habitat boundaries: coupling dynamics of ecosystems through complex life cycles. *Ecology Letters* 11:576–587.
- Schulze, P. C., H. E. Zagarrese, and C. E. Williamson. 1995. Competition between crustacean zooplankton in continuous cultures. *Limnology and Oceanography* 40:33–45.
- Tilman, D. 1982. *Resource competition and community structure*. Monographs in Population Biology. Princeton University Press, Princeton, NJ.
- Werner, E. E., and J. F. Gilliam. 1984. The ontogenetic niche and species interactions in size-structured populations. *Annual Review of Ecology and Systematics* 15:393–425.
- Yodzis, P., and S. Innes. 1992. Body size and consumer-resource dynamics. *American Naturalist* 139:1151–1175.