

Ontogenetic diet shifts promote predator-mediated coexistence

SABINE WOLLRAB,^{1,4} ANDRÉ M. DE ROOS,² AND SEBASTIAN DIEHL^{1,3}

¹*Department Biologie II, Ludwig-Maximilians-Universität München, Grosshaderner Strasse 2,
D-82152 Planegg-Martinsried, Germany*

²*Institute for Biodiversity and Ecosystem Dynamics, University of Amsterdam, P.O. Box 94084, NL-1090 GB Amsterdam,
The Netherlands*

³*Department of Ecology and Environmental Science, Umeå University, SE-90187 Umeå, Sweden*

Abstract. It is widely believed that predation moderates interspecific competition and promotes prey diversity. Still, in models of two prey sharing a resource and a predator, predator-mediated coexistence occurs only over narrow ranges of resource productivity. These models have so far ignored the widespread feature of ontogenetic diet shifts in predators. Here, we theoretically explore the consequences of a diet shift from juvenile to adult predator stages for coexistence of two competing prey. We find that only very minor deviations from perfectly identical diets in juveniles and adults destroy the “traditional” mechanism of predator-mediated coexistence, which requires an intrinsic trade-off between prey defendedness and competitive ability. Instead, predator population structure can create an “emergent” competition–predation trade-off between prey, where a bottleneck in one predator stage enhances predation on the superior competitor and relaxes predation on the inferior competitor, irrespective of the latter’s intrinsic defendedness. Pronounced diet shifts therefore greatly enlarge the range of prey coexistence along a resource gradient. With diet shifts, however, coexistence usually occurs as one of two alternative states and, once lost, may not be easily restored.

Key words: bottleneck; competition; diamond food web; predation; predator-mediated coexistence; stage structure; trade-off.

INTRODUCTION

It is widely believed that the role of interspecific competition in structuring ecological communities decreases with the intensity of physical stress and mortality (Paine 1966, Grime 1973, Lubchenco 1978). This idea is deeply engrained in influential ecological concepts such as intermediate disturbance and predator-mediated coexistence (Levins and Culver 1971, Caswell 1978, Connell 1978). To promote long-term persistence of competitors, all of these concepts require, however, additional niche opportunities such as trade-offs between competitive ability and the abilities to withstand or counter stress and mortality (Chesson and Huntly 1997). On physiological grounds, trade-offs between competitive ability and, e.g., vulnerability to predators or pathogens are indeed expected to be common (e.g., Herms and Mattson 1992).

The empirical evidence for a prevalence of trade-offs between the abilities to compete and to withstand natural enemies is nevertheless rather mixed (Koricheva 2002, Viola et al. 2010). Moreover, such trade-offs alone are insufficient to promote substantial within-guild

diversity (Chase et al. 2002, Chesson and Kuang 2008). For example, theoretical investigations of the smallest food web combining resource competition with shared predation, the “diamond web” (consisting of two prey sharing a limiting resource and a predator) demonstrate that, unless one competitor is completely invulnerable, coexistence occurs only under fairly limited environmental conditions (Holt et al. 1994, Grover 1995, Leibold 1996). Typically, the superior resource competitor prevails at low resource productivity and the less vulnerable competitor at high productivity, while coexistence or priority effects may occur at intermediate productivity (Grover and Holt 1998). Stochastic extinctions during transient or unstable dynamics may further limit coexistence (Noonburg and Abrams 2005).

If intrinsic trade-offs between traits conferring competitive dominance vs. resistance to predation are neither universally found nor sufficient to explain widespread persistence of diverse guilds of competitors, which other mechanisms are then responsible for the frequent observation of positive impacts of predators on prey diversity (Paine 1966, Lubchenco 1978, Olf and Ritchie 1998, Worm et al. 2002)? While switching behavior in predators provides a potentially powerful mechanism promoting coexistence of competing prey (Hutson 1984), we focus here on another, truly fundamental, property of most consumers. Individual growth and development, ontogenetic diet shifts, and

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⁴ Present address: W. K. Kellogg Biological Station, Michigan State University, Hickory Corners, Michigan 49060 USA. E-mail: wollrabs@msu.edu

population size structure are ubiquitous properties of most species; consequently, many consumers exhibit pronounced shifts in resource use during ontogeny (Werner and Gilliam 1984, Werner 1988, Rudolf and Lafferty 2011). In this paper, we therefore explore whether these features provide a mechanism that can prevent competitive exclusion among their prey. We do so by introducing an ontogenetic diet shift between the juvenile and adult stages of the shared predator into a model of the diamond food web (Fig. 1). Such a scenario commonly occurs wherever different consumer stages live in the same habitat. Examples include copepods shifting their optimal phytoplankton prey size during successive stages (Gismervik 2005), spiders feeding on different sized nectar-feeding hymenopteran and dipteran species with increasing body size (Turner 1979), larval and adult diving beetles feeding on different dipteran and ephemeropteran pond species (Klecka and Boukal 2012), gobiid fish shifting from meiobenthic to macrobenthic prey during ontogeny (Jackson et al. 2004), and juvenile and adult lizards feeding on differently sized ant species (Lahti and Beck 2008).

In most organisms, individual growth and development are strongly food dependent. This food dependence generates, in turn, population dynamics that typically differ quite remarkably from the vast majority of models ignoring this perhaps most basic property of life (de Roos et al. 2003, 2008a). For example, feedbacks between stages can lead to counterintuitive population patterns such as biomass accumulating in the most food limited stage (de Roos et al. 2007). So far, theoretical studies of ontogenetic diet shifts in predators have only assumed non-interacting prey (Schreiber and Rudolf 2008, Schellekens et al. 2010). The question how individual development, ontogenetic diet shifts, and population structure in shared predators affect the persistence of competing prey remains, therefore, unexplored.

In the absence of an ontogenetic diet shift in the shared predator, our analyses retrieve the “classical” result that coexistence of all members of the diamond food web is possible over very limited ranges of the parameter space and requires an intrinsic competition–predation trade-off in the prey. For only slight deviations from a perfect diet overlap among predator stages, however, we find that this coexistence mechanism breaks down and that instead a new coexistence mechanism emerges that is characterized by a dominance of the predator stage specializing on the superior competitor and overexploitation of this prey type. The low abundance of the superior competitor in turn promotes the dominance of the predator stage specializing on it and limits recruitment to the other life history stage. Independent of intrinsic defense traits, the resulting recruitment bottleneck to the predator stage specializing on the inferior competitor strongly reduces predation pressure on the inferior competitor and, thus, produces a dynamically “emergent” competition–preda-

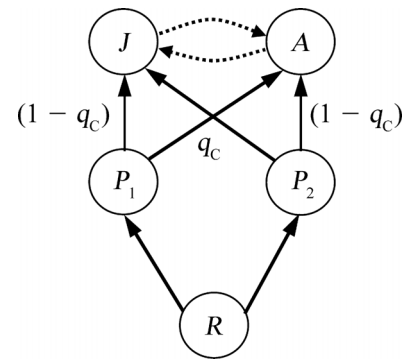


FIG. 1. Diamond food web with a stage-structured consumer. Circles represent the biomasses of R , resource; P_i , primary producer i ($i = 1, 2$); J , juvenile; and A , adult consumers, respectively. Solid arrows are feeding links and point from prey/resource to consumer. Dotted arrows are biomass flows between consumer stages related to maturation and reproduction. Relative foraging efficiency of each consumer stage on each prey species (in terms of q_C , the relative foraging efficiency of adults on P_1 and of juveniles on P_2) is indicated next to the corresponding feeding links, illustrating the symmetrical niche shift.

tion trade-off. The latter enables prey coexistence over an increasingly larger range of resource productivities the more pronounced the predator’s diet shift. Our results, therefore, suggest that predator-mediated coexistence is a relatively uncommon outcome in the absence of predator stage structure, while ontogenetic diet shifts can promote the maintenance of prey diversity. The coexistence state with a diet shifter is, however, only one of two alternative states and, once lost, may not be easily restored.

METHODS

Model structure

We explore the dynamics of the diamond web (Fig. 1) using a biomass-based model formulation that accounts for food dependence in both reproduction and individual growth/maturation of the top consumer (de Roos et al. 2008b). Model equations and parameter values are given in Tables 1 and 2. The default parameter values are representative of a nutrient-limited plankton system with unicellular producers (phytoplankton) and a stage-structured herbivore (a copepod) and follow allometric scaling of mass-specific rates as derived for invertebrates by de Roos and Persson (2013). Scaling arguments as provided in de Roos et al. (2008b) as well as our own numerical analyses indicate, however, that the results are very robust to changes in parameters, and we are confident that our results extend to other systems and allow general conclusions.

The resource at the base of the web (R) is assumed to be nitrogen. Biomass densities of all species are therefore measured in units of nutrient (mg N/L) and all rates are scaled accordingly. To keep the model directly applicable to systems where state variables are expressed in

TABLE 1. Dynamical equations of the standard (symmetrical niche) model.

Dynamical equations and functions	Description
(T1.1) $\frac{dR}{dt} = l(R_{\max} - R) - a_{P1R}RP_1 - a_{P2R}RP_2$	dynamics of resource
(T1.2) $\frac{dP_1}{dt} = ea_{P1R}RP_1 - (1 - q_C)a_{CP1}P_1J - q_Ca_{CP1}P_1A - m_{P1}P_1$	dynamics of superior resource competitor (P_1)
(T1.3) $\frac{dP_2}{dt} = ea_{P2R}RP_2 - q_Ca_{CP2}P_2J - (1 - q_C)a_{CP2}P_2A - m_{P2}P_2$	dynamics of inferior resource competitor (P_2)
(T1.4) $\frac{dJ}{dt} = v_A^+(P_1, P_2)A + v_J(P_1, P_2)J - y(v_J^+(P_1, P_2))J - m_CJ$	dynamics of juvenile consumers
(T1.5) $\frac{dA}{dt} = y(v_J^+(P_1, P_2))J + v_A(P_1, P_2)A - v_A^+(P_1, P_2)A - m_CA$	dynamics of adult consumers
(T1.6) $v_J(P_1, P_2) = \sigma((1 - q_C)a_{CP1}P_1 + q_Ca_{CP2}P_2) - T$	net biomass production of juveniles
(T1.7) $v_A(P_1, P_2) = \sigma(q_Ca_{CP1}P_1 + (1 - q_C)a_{CP2}P_2) - T$	net biomass production of adults
(T1.8) $y(v_J^+(P_1, P_2)) = \begin{cases} \frac{v_J(P_1, P_2) - m_C}{1 - z^{(1 - m_J/v_J(P_1, P_2))}} & \text{if } v_J > 0 \\ 0 & \text{if } v_J \leq 0 \end{cases}$	maturation rate of juvenile into adult biomass
(T1.9) $v_A^+(P_1, P_2) = \begin{cases} v_A & \text{if } v_A \geq 0 \\ 0 & \text{if } v_A < 0 \end{cases}$	production rate of biomass of newborns by adults

Note: State variables and parameters are defined in Table 2.

carbon biomass, we assume that losses from excretion, respiration, and mortality are not recycled to the inorganic nutrient pool. Results do, however, not depend on this assumption (see *Discussion*). Nutrients enter the system from outside with concentration R_{\max} at rate l , are washed out at the same rate, and are consumed by primary producers P_1 and P_2 , following linear functional responses with clearance rates a_{P_iR} . Producers convert nutrients into biomass with efficiency e_{P_iR} , and lose biomass through density-independent mortality and respiration at rate m_{P_i} and through consumption by herbivores. Parameters were chosen

such that P_1 is the superior resource competitor ($a_{P1R} > a_{P2R}$, $e_{P1R} = e_{P2R}$, and $m_{P1} = m_{P2}$).

Both consumer stages feed on primary producers following linear functional responses and convert this food into biomass with efficiency σ . Net-biomass production by juvenile and adult consumers, indicated as v_J and v_A , respectively, equal the difference between this biomass production and the maintenance rate T . Note that all rates are mass specific. Hence juveniles and adults do not differ in their mass specific rates, but do so on an individual basis dependent on body size (Schellekens et al. 2010; see Appendix A).

TABLE 2. State variables and parameters of the standard (symmetrical niche) model.

Variables and parameters	Values	Unit	Description
J		mg N/L	biomass density of juvenile consumers
A		mg N/L	biomass density of adult consumers
P_1		mg N/L	biomass density of producer 1 (superior resource competitor)
P_2		mg N/L	biomass density of producer 2 (inferior resource competitor)
R		mg N/L	density of shared resource (assumed to be nitrogen)
R_{\max}	0–0.6	mg N/L	maximum resource density
T	0.1	d ⁻¹	maintenance rate of juvenile and adult consumers
L	0.1	d ⁻¹	nutrient renewal rate
z	0.01	mg N/mg N	ratio of newborn to adult body mass
m_C	0.01	d ⁻¹	mortality rate of consumer
q_C	0–1	dimensionless	relative foraging efficiency of adults on P_1 and of juveniles on P_2
σ	0.5	mg N/mg N	conversion efficiency of producer into consumer biomass
a_{CP1}	4	L·mg N ⁻¹ ·d ⁻¹	clearance rate of consumer for P_1
a_{CP2}	2.4	L·mg N ⁻¹ ·d ⁻¹	clearance rate of consumer for P_2
e_{CP1}	1	mg N/mg N	conversion efficiency of P_1 for R
e_{CP2}	1	mg N/mg N	conversion efficiency of P_2 for R
a_{P1R}	20	L·mg N ⁻¹ ·d ⁻¹	clearance rate of P_1 for R
a_{P2R}	15	L·mg N ⁻¹ ·d ⁻¹	clearance rate of P_2 for R
m_{P1}	0.1	d ⁻¹	mortality plus maintenance rate of P_1
m_{P2}	0.1	d ⁻¹	mortality plus maintenance rate of P_2

Juveniles grow in body size at mass-specific rate v_j^+ only if their net biomass production is positive (v_j^+ refers to the value of v_j if the latter is positive and equals 0 under starvation conditions when $v_j < 0$). Juveniles mature to the adult stage at mass-specific rate $y(v_j^+)$ (de Roos et al. 2008b), which equals 0 when net production is negative. Adults do not grow individually. They invest all net production v_A^+ into reproduction, but do not reproduce when starving ($v_A < 0$). Hence, total biomass of juveniles increases through birth (v_A^+A) and somatic growth (v_jJ) and decreases through maturation to the adult stage [$y(v_j^+)J$] and mortality. Total biomass of adults increases through maturation of juveniles and decreases through mortality. The density-independent mortality rate m_C is assumed to be equal for both stages. Juveniles and adults experience an increase in mortality rate of $-v_j$ and $-v_A$, respectively, under starvation conditions when their net production is negative (de Roos et al. 2008b).

The maturation rate $y(v_j^+)$ depends on juvenile net production and mortality and on the ratio of newborn to adult body mass z . This function translates the maturation rate of an individual based, size-structured model at equilibrium into a food-dependent, population-level, maturation rate of a corresponding stage-structured model. The stage-structured model therefore has a rigorous individual basis and its dynamics fully capture the equilibrium behavior of the underlying size-structured model (de Roos et al. 2008b) that is described in Appendix A.

A predator’s functional response is the product of three components: (1) prey biomass density, (2) a prey-specific clearance rate a_{CPi} , which may be negatively correlated with a_{PIR} to represent an intrinsic competition–predation trade-off, and (3) a predator-specific component (q_C or $1 - q_C$) that models an ontogenetic trade-off in the foraging efficiencies of juvenile vs. adult consumers. The factor q_C takes on values between 0 and 1. We focus on a “symmetrical niche” model, assuming a linear, symmetrical trade-off such that juveniles forage on P_1 and P_2 with efficiency $(1 - q_C)$ and q_C , respectively, whereas adults forage on P_1 and P_2 with the reversed efficiencies. Therefore q_C determines the degree of niche shift between the two stages. When $q_C = 0$ or 1, the niche shift is complete (juveniles and adults have exclusive resources), whereas there is no niche shift at all when $q_C = 0.5$. In the latter case the dynamics of total consumer biomass (obtained by summing the equations for juveniles and adults) are given by

$$\frac{d(J + A)}{dt} = \left(\sigma(0.5 \times a_{CP1}P_1 + 0.5 \times a_{CP2}P_2) - T \right) \times (J + A) - m_C(J + A) \tag{1}$$

which retrieves the limiting case of an unstructured consumer population (i.e., the classical diamond web). Parameters were chosen such that the inferior resource competitor P_2 is intrinsically less vulnerable to predation

from a non-niche-shifting consumer than P_1 ($a_{CP2} < a_{CP1}$).

Model analyses

We numerically investigated the influence of the degree of ontogenetic diet shift in the top consumer on equilibrium dynamics of the diamond web by systematically varying the parameter q_C for various levels of resource enrichment R_{max} . Our model formulation with linear functional responses, stage-independent biomass-specific rates, and a linear trade-off between the prey-specific foraging efficiencies of the two consumer stages enabled us to clearly separate effects of niche shifts and stage structure from potentially confounding effects of saturating functional responses and stage-specific consumer traits.

Strictly, a stage-structured biomass model captures the dynamics of the underlying size-structured population model only under equilibrium conditions (de Roos et al. 2008b). For a subset of the parameter space we therefore numerically explored how accurately the results for the stage-structured biomass model capture the dynamics of a corresponding, fully size-structured population model (described in Appendix A). For the stage-structured biomass model, we used Matcont 2.4 (Dhooge et al. 2003), a software package usable within Matlab (Mathworks, Natick, Massachusetts, USA), to compute model equilibria and their stability and analyzed non-equilibrium dynamics using numerical simulations. The dynamics of the fully size-structured population model were analyzed using numerical methods specifically developed for this class of population dynamic models (de Roos et al. 1992).

RESULTS

Overview

The system can attain five possible community states: the resource alone, or the resource with the superior competitor (P_1), with P_1 and the consumer (P_1-C), with both prey and the consumer (Coex), and with P_2 and the consumer (P_2-C). Fig. 2 summarizes for the symmetrical niche model how these community states depend on enrichment (R_{max}) and the degree of niche shift in the consumer (q_C). The figure is representative for any parameter choice that assumes an intrinsic competition–predation trade-off in the two prey species (Tables 1 and 2).

Transitions between community states may occur at the threshold lines labeled I_{P1} , I_C , I_{P2} , Co , and E_{P1} , respectively (Fig. 2). I_{P1} is the minimum enrichment level needed for P_1 to invade a system with only the resource. I_C is the threshold at which the consumer can invade a P_1 equilibrium, and I_{P2} is the threshold for invasion of P_2 into a P_1 -consumer system (resulting in either two-prey–consumer coexistence or replacing the P_1 -consumer equilibrium with a P_2 -consumer equilibrium). Co labels the minimal enrichment level for which coexistence of both prey species and the consumer is possible,

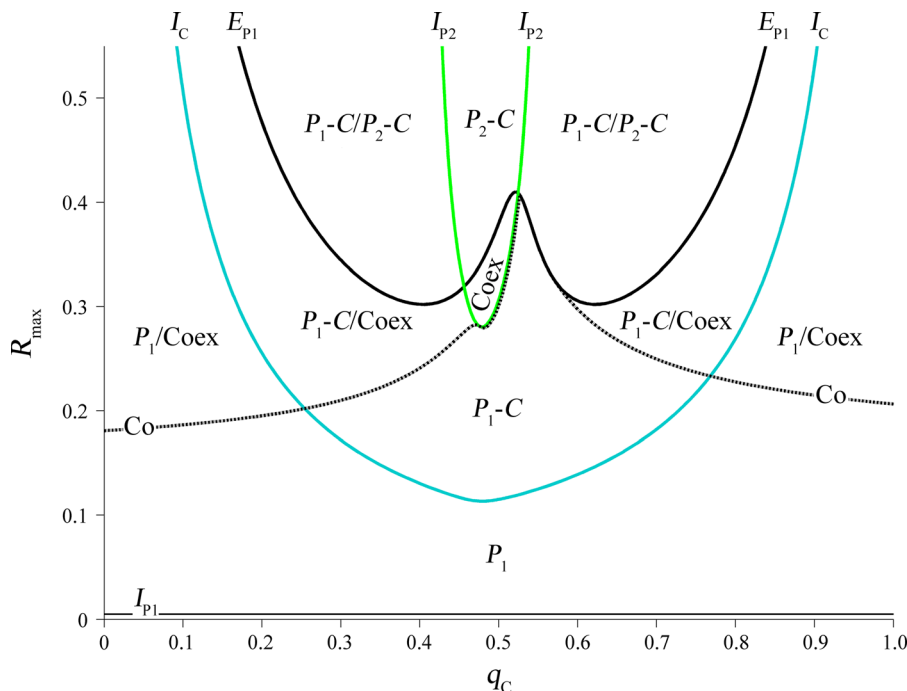


FIG. 2. Symmetrical niche model showing possible stable system states as a function of enrichment (R_{\max}) and the degree of niche shift in the consumer (q_C). Labeling indicates the following states: P_1 alone (P_1), P_1 and consumer (P_1-C), P_2 and consumer (P_2-C), and coexistence (Coex). In areas of bistability, possible states are separated by a slash. Lines separate regions with unique combinations of single or alternative states and indicate invasion thresholds for P_1 into an empty system (I_{P1} , thin black, solid line), for the consumer into a P_1 state (I_C , blue line), for P_2 into a P_1-C state (I_{P2} , green line), an extinction threshold for P_1 from a coexistence equilibrium (E_{P1} , thick black, solid line), and the minimum enrichment level needed for coexistence (Co, black dash-dotted line). Parameters are as in Table 2.

and E_{P1} labels the extinction threshold of P_1 from a two-prey-consumer system.

Compared to the unstructured case ($q_C = 0.5$), niche shifts in the consumer change the competition-predation balance for the prey species through shifts in food dependent recruitment between consumer stages. For a clearer understanding of how different system states and transitions between them depend on enrichment and the degree of niche shift between juvenile and adult consumers, we explore transects through the R_{\max} - q_C plane (Fig. 2) along (1) the R_{\max} axis and (2) the q_C axis. Note the approximate symmetry of the state transition boundaries (Fig. 2). This symmetry arises because the total effects of a niche-shifting consumer (juveniles plus adults) on lower trophic levels depend primarily on the degree of niche shift (the deviation from $q_C = 0.5$ in either direction), whereas the absolute value of q_C primarily determines the population structure of the consumer. Lower trophic levels will therefore respond roughly similarly to consumers with a q_C of, e.g., 0.2 and 0.8, while consumer population structure will show contrasting patterns. Although the symmetry is not perfect, it is therefore sufficient to illustrate enrichment effects in only one half of Fig. 2 ($0 \leq q_C \leq 0.5$; but see Appendix A).

Enrichment patterns for different degrees of niche shift q_C

We first review the well-known case of a non-niche-shifting consumer ($q_C = 0.5$, Fig. 3A), which recovers the classical diamond food web (Holt et al. 1994, Leibold 1996). At the lowest enrichment levels no species can persist in the system and (unused) resource concentrations are equal to R_{\max} . At I_{P1} , resource levels become high enough for the superior competitor P_1 to establish. As the consumer is absent, this threshold is independent of q_C (Fig. 2). With further enrichment P_1 increases (and controls the resource at a constant level) until it reaches a sufficient level for the consumer to invade. This occurs at I_C , where the P_1 state is replaced by a P_1 -consumer state. Now P_1 is controlled by the consumer and only the consumer and the resource increase with further enrichment. When the resource has increased sufficiently, the inferior but less vulnerable competitor P_2 can invade and the P_1 -consumer state is replaced by the coexistence state. The corresponding threshold is labeled I_{P2}/Co , as the threshold for invasion of P_2 (I_{P2}) coincides with the threshold for coexistence (Co) at $q_C = 0.5$ (but not for most other values of q_C). Within the coexistence state resource and consumer biomasses remain constant with further enrichment, while the superior competitor P_1 decreases and the less vulnerable competitor P_2

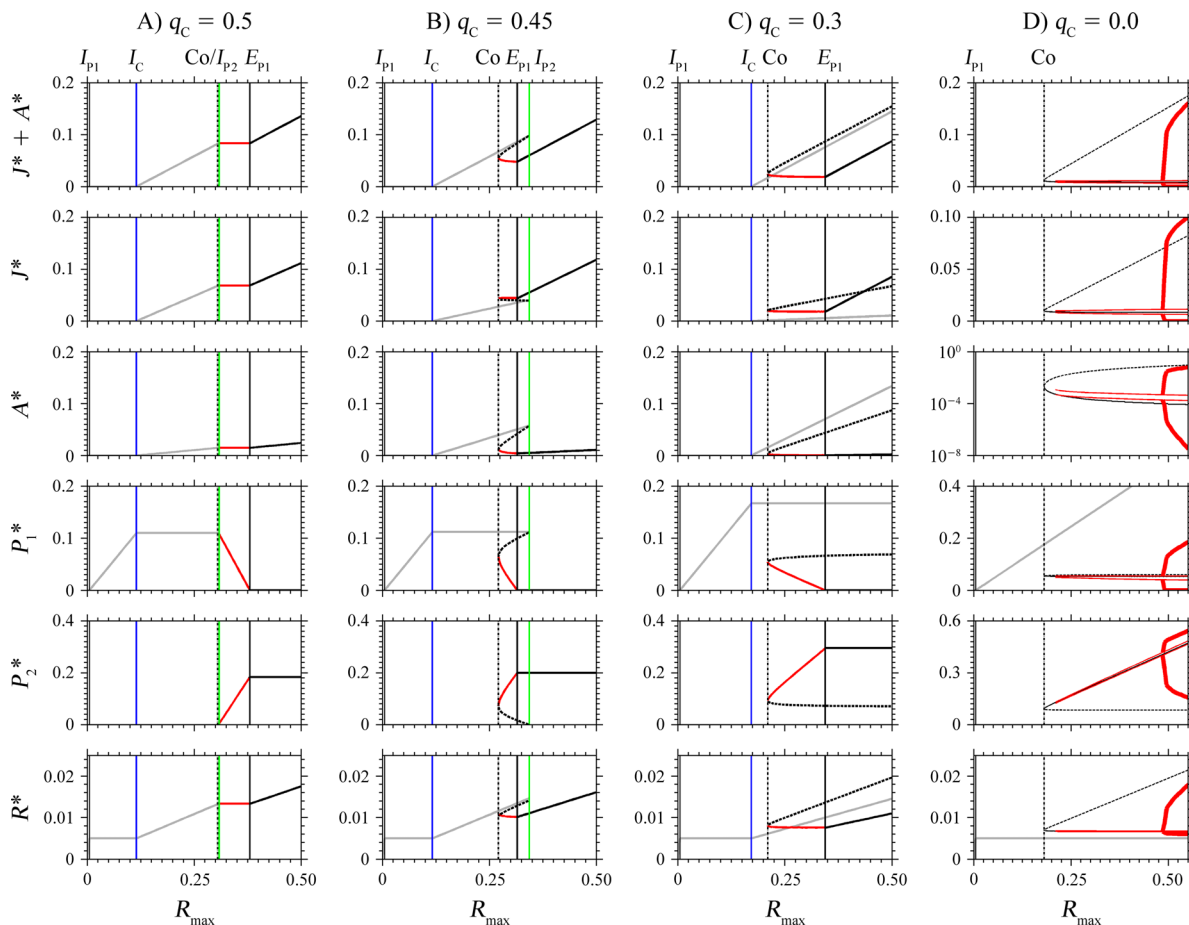


FIG. 3. Symmetrical niche model. Plots show equilibrium biomasses (mg N/L) as a function of enrichment (R_{max}) for values of the niche shift parameter q_C of (A) 0.5, (B) 0.45, (C) 0.3, and (D) 0.0. Rows display equilibrium biomasses of total consumers ($C^* = J^* + A^*$), juveniles (J^*), adults (A^*), primary producers P_1^* and P_2^* , and resource (R^*). Vertical lines indicate invasion and extinction thresholds, labeled as in Fig. 2. Different community states are color coded as follows: gray, P_2 absent; red, coexistence; black, P_1 absent. Dashed lines indicate unstable (saddle) equilibria separating two alternative states. The coexistence state for $q_C = 0$ exhibits a small amplitude cycle over the whole range (thin red lines) and a second, large-amplitude cycle at higher enrichment (heavy red lines; shown are cycle minima and maxima). Note that the scales of most y-axes in panel D differ from panels A–C (A^* being shown on a logarithmic scale). Parameters are as in Table 2.

increases. With sufficient enrichment (threshold E_{P1}) P_1 goes extinct and coexistence is replaced by a P_2 -consumer state. Hence, for $q_C = 0.5$ there is a continuous sequence of unique stable states along an enrichment gradient ($P_1 \rightarrow P_1-C \rightarrow$ coexistence $\rightarrow P_2-C$). This continuous sequence remains qualitatively the same only within a very narrow range around $q_C = 0.5$ where the Co and I_{P2} lines coincide (Fig. 2).

With only a minor degree of niche shift in the consumer this pattern breaks down and alternative states become possible in increasingly larger regions of parameter space. For $q_C = 0.45$ the same five community states occur as in the unstructured case, but not in a continuous sequence. Instead, at intermediate enrichment levels we find bistability between the P_1 -consumer state and either the coexistence state (between Co and E_{P1}) or the P_2 -consumer state (between E_{P1} and I_{P2} ; Fig. 3B). The coexistence threshold (Co) and the minimum

threshold for successful invasion of P_2 (I_{P2}) no longer coincide, and both the coexistence threshold (Co) and the threshold for extinction of P_1 from a coexistence state (E_{P1}) now occur at lower enrichment levels than I_{P2} . Bistability is accompanied by the appearance of an unstable (saddle) equilibrium (dashed line in Fig. 3B) between alternative stable states. Similar to the unstructured case, P_1 will outcompete P_2 at low enrichment levels (below Co), whereas P_2 will outcompete P_1 at high enrichment levels (above I_{P2}). Over intermediate ranges of enrichment, smooth transitions are, however, only possible between stable states with P_2 present, but not between stable states with P_2 present in one and absent in the other state. Alternative states are, in turn, stabilized by contrasting consumer population structure, with P_1 -dominated states being associated with high biomass of the stage preferentially feeding on P_2 (adults in Fig. 3B), and P_2 -dominated states with high biomass

of the stage preferentially feeding on P_1 (juveniles in Fig. 3B). As a consequence, a competition–predation trade-off and hence coexistence only occurs when P_2 is dominant over P_1 , which also explains why a smooth transition between a state without P_2 to a coexistence state with (low biomass of) P_2 is impossible.

With stronger niche shifts in the consumer (e.g., $q_C = 0.3$), all of the patterns described for $q_C = 0.45$ become more accentuated. In particular, the enrichment threshold I_{P_2} for invasion of P_2 into a P_1 –consumer system shifts to infinity (Fig. 2). Thus P_2 cannot invade a P_1 –consumer equilibrium from low density at any enrichment level (Fig. 3C). Instead, a P_1 –consumer equilibrium exists as an alternative stable state to either a P_2 –consumer equilibrium (at high enrichment) or a coexistence state (at intermediate enrichment; Fig. 3C). This coexistence region is considerably larger than the coexistence region in the unstructured case and becomes even larger with further diet specialization of the consumer stages (Fig. 2). Note that for most enrichment levels total consumer biomass is higher in the P_1 –consumer state than in both the coexistence and the P_2 –consumer states (Fig. 3C), suggesting that communities dominated by the inferior competitor P_2 channel energy less efficiently to the consumer than do communities with abundant P_1 .

For $q_C = 0$ juvenile and adult diets do not overlap at all. The consumer then cannot persist in a system with only one prey (E_{P_1} and I_C shift to infinity; Fig. 2). Hence the only possible states are a P_1 -only and a coexistence state, the latter again being dominated by P_2 (Fig. 3D). In coexistence all populations cycle with very small amplitude. At higher enrichment levels a second large amplitude cycle emerges around the first one. Importantly, compared to the unstructured case, the range of enrichment permitting coexistence is substantially enlarged, extending to infinite enrichment (Fig. 2). Losing an arbitrary community member from a coexistence state makes subsequent extinctions of other species inevitable, leaving a system with only one primary producer from which it is difficult to return to the coexistence state.

Shifting mechanisms of predator-mediated coexistence with shifting diet specialization

For very weak niche shifts (q_C near 0.5 in the symmetrical niche model), predator mediated coexistence is governed by the same mechanism as in the unstructured case; i.e., the inferior resource competitor balances its competitive disadvantage by being intrinsically better defended against both stages of the consumer. For most parameterizations this balance is only met over a narrow range of enrichment. Because the superior resource competitor P_1 always has a higher per capita growth rate than P_2 , a competition–predation trade-off must also be responsible for coexistence at intermediate to complete niche shifts. This trade-off is, however, not defined a priori but emerges from changes

in the consumer population structure. With the baseline parameterization, for example, the inferior competitor P_2 suffers from higher predation by adults than does P_1 for all $q_C < 0.375$, whereas P_1 remains more vulnerable to juvenile consumers. Conversely, at $q_C > 0.625$ P_2 suffers from higher predation by juveniles than does P_1 . Thus, an “emergent” competition–predation trade-off arises for $q_C < 0.375$ if adult biomass is not too high relative to juvenile biomass, and for $q_C > 0.625$ if juvenile biomass is not too high. Accordingly, the coexistence state is always characterized by high juvenile and low adult consumer biomass at low q_C and by the opposite consumer population structure at high q_C (Fig. 4).

In the same vein, emergence of a consumer population structure that weakens the intrinsic competition–predation trade-off explains why an alternative P_1 –C state cannot be invaded by P_2 from low density. P_1 –C states are always dominated by the consumer stage (adults at $q_C < 0.5$, juveniles at $q_C > 0.5$) that has a relatively higher feeding rate on the inferior competitor P_2 and a relatively lower feeding rate on the superior competitor P_1 . Consequently, the intrinsic competition–predation trade-off is weakened (and disappears completely at values of $q_C < 0.375$ and $q_C > 0.625$, respectively), making the P_1 –C state non-invasible for P_2 . Contrasting patterns of consumer population structure also characterize situations where P_1 –C and P_2 –C are the respective alternative states (at higher R_{\max} , see Fig. 4C, D).

Typically, in systems with non-interacting prey species, a niche-shifting consumer population tends to settle to one of two alternative coexistence states, which are dominated by either juvenile or adult biomass (de Roos et al. 2007, Schreiber and Rudolf 2008, Guill 2009, Schellekens et al. 2010). Because prey species compete, only one of these two coexistence states is possible in the diamond food web. This coexistence state is always characterized by strong predation pressure on the superior competitor P_1 and dominance of the inferior competitor P_2 over P_1 . Therefore, the consumer stage relying more on P_1 is strongly food limited, and biomass transfer (through maturation or reproduction) from this stage to the next is low, whereas biomass transfer from the stage relying more on P_2 to the limited stage is high. Hence, consumer biomass accumulates in the food limited bottleneck stage feeding on P_1 . This feedback between the two stages relaxes predation pressure on P_2 , but enhances predation pressure on the superior competitor P_1 , thus enabling coexistence.

The degree of niche shift not only influences consumer population structure but, as indicated above, feeds also back on the absolute biomasses of consumers, prey, and the resource. Generally, within a given equilibrium state total consumer biomass and the resource increase with decreasing niche shift (moving from extreme values of q_C toward $q_C = 0.5$), while total prey biomass ($P_1 + P_2$) decreases (Fig. 4). For most values of q_C , total consumer biomass is higher in the P_1 –C state than in the

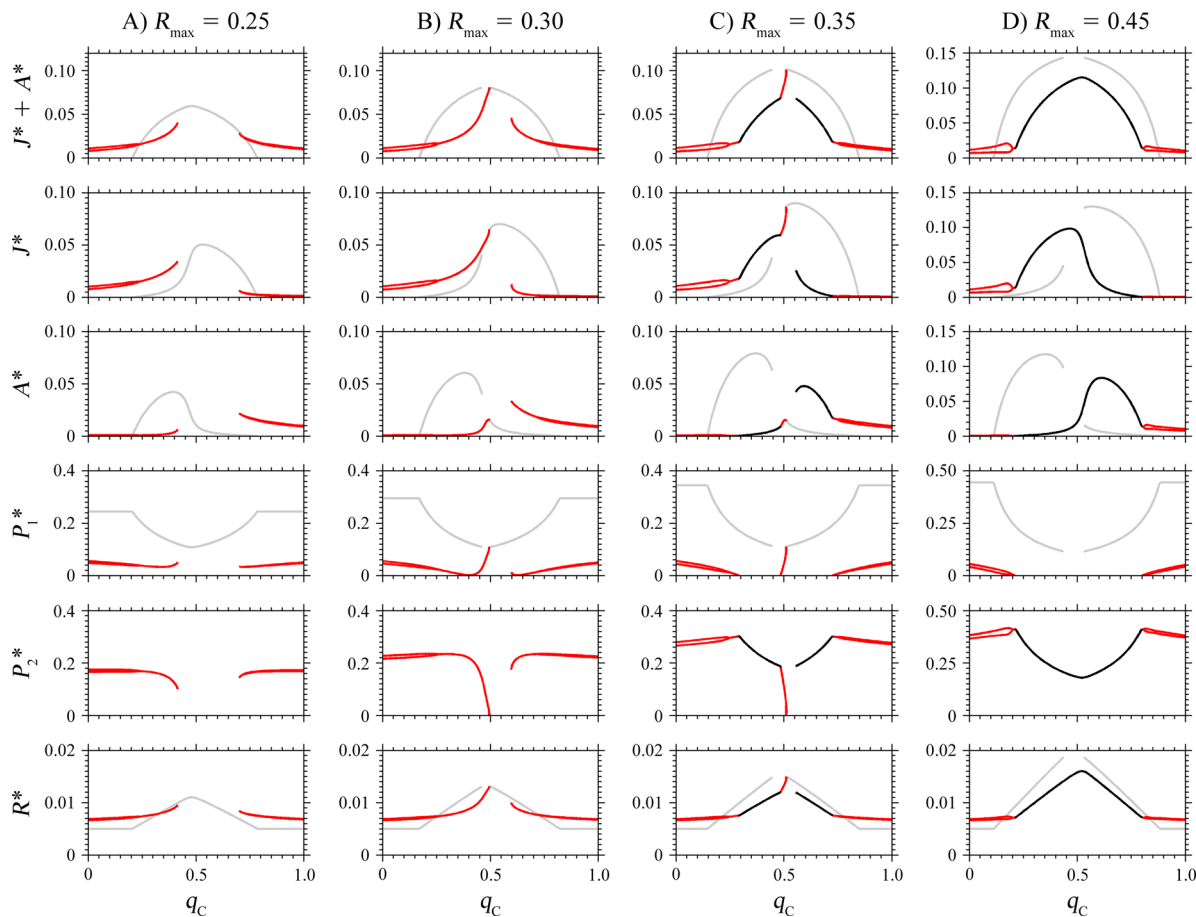


FIG. 4. Symmetrical niche model. Equilibrium biomasses (mg N/L) as a function of the niche-shift parameter q_C for values of R_{max} of (A) 0.25, (B) 0.30, (C) 0.35, and (D) 0.45. Rows display equilibrium biomasses of total consumers ($C^* = J^* + A^*$), juveniles (J^*), adults (A^*), primary producers P_1^* and P_2^* , and resource (R^*). Different community states are color coded as in Fig. 3. For better visibility, invasion and extinction thresholds from Fig. 2 are not displayed. Note that the scales of the y-axes in panel D differ from panels A–C. Parameters are as in Table 2.

alternative coexistence or P_2 -C states. Prey biomass is always dominated by P_2 in coexistence states, and P_1 is always greatly reduced in a coexistence state compared to an alternative P_1 -C state (Fig. 4). The potential of a niche shift to enhance coexistence becomes most obvious at the lowest and highest levels of enrichment (Fig. 4A and D), where coexistence is possible for extreme to intermediate degrees of niche shift, but impossible near $q_C = 0.5$ (unstructured case). Thus, the predator facilitates itself by enabling prey coexistence in regions of the R_{max} - q_C space (near $q_C = 0$ and 1) where it cannot establish in a one-prey system (Figs. 2, 4).

Coexistence in absence of an intrinsic competition-predation trade-off

The role of consumer niche shifts and the operation of the emergent competition-predation trade-off in mediating coexistence of resource competitors is nicely illustrated with a different model parameterization. When clearance rates for the two prey species are identical ($a_{CP1} = a_{CP2}$), the formerly assumed intrinsic

competition-predation trade-off disappears. Coexistence is then impossible in the absence of a consumer niche shift (i.e., in the unstructured diamond web with $q_C = 0.5$) but is still fully feasible (as one of two alternative states) over increasingly larger ranges of enrichment toward more pronounced niche shifts (Fig. 5). Bistability between a P_1 -consumer and a P_2 -consumer state is also possible with moderately niche-shifting consumers, but the absence of an emergent competition-predation trade-off makes it impossible for P_2 to persist at weaker niche shifts, regardless of the level of enrichment (Fig. 5).

Comparisons with the fully size-structured population model

Analyses of the fully size-structured population model reveals similarities and differences to the stage-structured biomass model. We illustrate these with a representative numerical example along a transect of varying q_C (Appendix A), but several other parameterizations yielded qualitatively similar results. Similar to

the stage-structured biomass model, the underlying size-structured population model predicts stable coexistence of all species when diet shifts are absent or weak, and cyclic behavior of the coexistence state for more pronounced diet shifts (Appendix A: Fig. A1). Predictions for the coexistence state match qualitatively and quantitatively very well between both model variants when juveniles forage more efficiently on the superior resource competitor P_1 ($q_C < 0.5$; Appendix A: Fig. A1). In contrast, congruence between model variants is more limited when adults forage more efficiently on P_1 ($q_C > 0.5$); most notably, coexistence does not occur in the size-structured population model when adults specialize almost completely on the superior resource competitor P_1 ($q_C > 0.8$; Appendix A: Fig. A1), which is likely a consequence of the appearance of pronounced cohort cycles during which adults temporarily disappear from the population, allowing P_1 to outcompete P_2 .

The analyses of the fully size-structured model thus confirm that, compared to the unstructured case ($q_C = 0.5$), ontogenetic diet shifts enhance the parameter space allowing for coexistence, with the qualification that coexistence seems to be particularly favored when it is the juvenile consumer stage that is more specialized on the superior resource competitor.

DISCUSSION

We have shown that an ontogenetic diet shift in a shared consumer can strongly promote coexistence of competing prey, the effect being the stronger the more pronounced the consumer's diet shift. The underlying mechanism involves the development of a bottleneck stage in the consumer population, which increases predation pressure on the superior resource competitor while simultaneously relaxing predation pressure on the inferior resource competitor. Thus, while coexistence in the classical diamond food web requires an intrinsic competition–predation trade-off in the prey (Holt et al. 1994, Leibold 1996), this condition is not required when the consumer undergoes an ontogenetic diet shift. Instead, such a trade-off can emerge dynamically as a consequence of consumer population structure regardless of the traits of the prey species. Note, however, that the (realistic!) assumption of food dependence of both reproduction and individual growth and maturation (de Roos et al. 2007) is crucial for this feedback mechanism to become expressed.

Highlighting the generality of this mechanism, the results are robust against different parameter settings (Fig. 5 and data not included) and against different model assumptions. In addition to the symmetrical niche model, we also investigated an inclusive niche model, in which the two consumer stages are always fully specialized on opposite prey types and attack the alternative prey with efficiency q_C . Hence, this case is identical to the symmetrical niche model at $q_C = 0$ (complete niche shift), whereas equality with the unstructured case (no niche shift) is reached at $q_C = 1$.

Overall, this alternative model yields qualitatively similar results (see Appendix B). The same results are also obtained under the assumption of a closed system in which losses from excretion, respiration and mortality are immediately recycled to the inorganic nutrient pool (see Appendix C). However, results from the fully size-structured model variant of the diamond web suggest that stage identity may be important as diet specialization seems particularly likely to favor coexistence when it is the juvenile consumer stage that forages more on the superior resource competitor. Given the prevalence of ontogenetic shifts in resource use among many consumer species (Werner and Gilliam 1984, Werner 1988, Rudolf and Lafferty 2011) the reported phenomena should therefore be of high relevance to real food webs.

Our results suggest, furthermore, that the predictions derived for the case of an unstructured consumer may be applicable to only a limited set of natural systems. Just a slight ontogenetic niche shift in the consumer is required to introduce bistability and produce qualitatively different predictions. The resulting alternative stable states are a very general property of webs with stage-structured consumer populations, provided that both stages can potentially control their respective food source (Guill 2009, Nakazawa 2011), and are typically characterized by contrasting dominance patterns within the structured population (de Roos et al. 2007, Schreiber and Rudolf 2008, Guill 2009, Hin et al. 2011).

Independently of whether prey species compete or not, coexistence states are always governed by the same mechanism, i.e., high biomass of prey for one consumer stage leads to fast recruitment to and hence dominance by the other consumer stage (Schreiber and Rudolf 2008). The major difference between systems with and without an additional competitive link between prey species is that at most one of the alternative states allows for prey coexistence if the prey compete. A competition–predation trade-off emerges dynamically only if the consumer stage that preys most efficiently on the superior resource competitor is dominant. If the consumer stage preying most efficiently on the inferior resource competitor dominates, the latter is excluded. At extreme values of niche shift, however, exclusion of one prey also leads to the exclusion of the consumer itself. Hence the alternative state to coexistence is a depauperate community with only the superior resource competitor.

Our results share some commonalities with another simple food web that integrates competition and predation, i.e., the intraguild predation (IGP) web. Here, the intraguild predator simultaneously feeds on the intraguild prey and competes with it for the shared resource. Coexistence in an unstructured IGP web requires that the intraguild prey is the superior resource competitor, but coexistence is typically predicted over only a narrow range of intermediate enrichment levels (Holt and Polis 1997, Diehl and Feißel 2000, Diehl 2003). The assumption that the intraguild predator

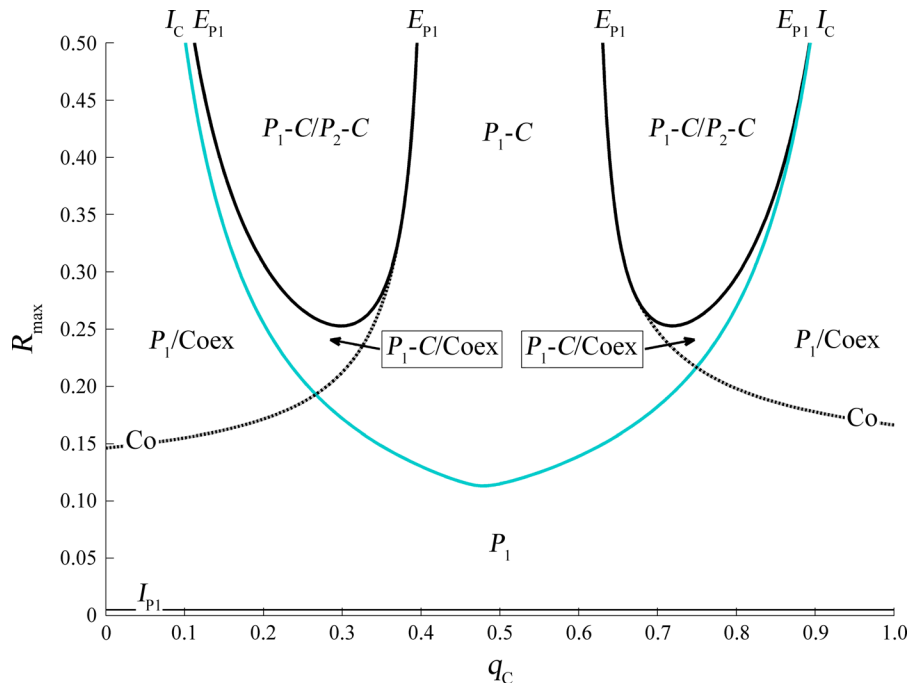


FIG. 5. Symmetrical niche model showing possible stable system states as a function of enrichment (R_{\max}) and the degree of niche shift in the consumer (q_C). Parameters as in Table 2, except that clearance rates of the consumer for both prey species are identical ($a_{CP1} = a_{CP2} = 4$). Labeling of system states and definitions of lines as in Fig. 2.

performs an ontogenetic diet shift between its two alternative prey yields similar results as in the diamond web. Specifically, the region of coexistence becomes enlarged with more pronounced diet shifts and extends toward infinite enrichment at extreme diet shifts (Hin et al. 2011).

Despite the potentially positive effect of pronounced ontogenetic diet shifts on prey coexistence our results also suggest that, once such a coexistence state is lost, it may not be easily restored. The sensitivity of highly specialized life stages to resource loss and its consequences for food web stability and resilience have recently been highlighted by Rudolf and Lafferty (2011), who cautioned that stage structure can reverse a positive complexity–stability relationship into a negative one. Ecologists have become increasingly aware of the potential for alternative stable states in many real ecosystems (Scheffer and Carpenter 2003, Folke et al. 2004), including freshwater (Carpenter et al. 1999), marine (Hare and Mantua 2000), and terrestrial systems (Staver et al. 2011). The potential role of stage structure in the occurrence of regime shifts and the stabilization of alternative states has, however, so far received relatively little attention (de Roos and Persson 2002, Persson and de Roos 2003, Persson et al. 2007, Rudolf 2007, Schreiber and Rudolf 2008, Van Leeuwen et al. 2008, Schröder et al. 2012). Particularly in the context of overexploited fish stocks, there is strong evidence that feedbacks between different life stages may be respon-

sible for the lack of recovery in spite of fishing moratoria (de Roos and Persson 2002, Huss et al. 2012).

Our results strengthen the importance of recognizing population structure with food-dependent transitions between size classes or stages as a critical dynamical component of natural communities. While feedbacks between predator stages and their prey species potentially enhance diversity, they also introduce the possibility of alternative states, and disturbances can lead to sudden shifts to depauperate communities. Future research should therefore investigate how diverse alternative community states can be maintained and restored. Two candidate mechanisms have recently been explored in the unstructured diamond food web. Seasonality of the environment can create temporal invasion windows (Klausmeier and Litchman 2012), while source–sink dynamics can locally maintain threatened populations in larger meta-communities (Amarasekare 2008). This calls for future investigations of the potential influence of these processes on local and regional persistence of stage-structured consumers and the communities they depend on.

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LITERATURE CITED

Amarasekare, P. 2008. Spatial dynamics of keystone predation. *Journal of Animal Ecology* 77:1306–1315.

- Carpenter, S. R., D. Ludwig, and W. A. Brock. 1999. Management of eutrophication for lakes subject to potentially irreversible change. *Ecological Applications* 9:751–771.
- Caswell, H. 1978. Predator-mediated coexistence: a nonequilibrium model. *American Naturalist* 112:127–154.
- Chase, J. M., P. A. Abrams, J. P. Grover, S. Diehl, P. Chesson, R. D. Holt, S. A. Richards, R. M. Nisbet, and T. J. Case. 2002. The interaction between predation and competition: a review and synthesis. *Ecology Letters* 5:302–315.
- Chesson, P., and N. Huntly. 1997. The roles of harsh and fluctuating conditions in the dynamics of ecological communities. *American Naturalist* 150:519–553.
- Chesson, P., and J. J. Kuang. 2008. The interaction between predation and competition. *Nature* 456:235–238.
- Connell, J. H. 1978. Diversity in tropical rain forests and coral reefs. *Science* 199:1302–1310.
- de Roos, A. M., O. Diekmann, and J. A. J. Metz. 1992. Studying the dynamics of structured population models: a versatile technique and its application to *Daphnia* population dynamics. *American Naturalist* 139:123–147.
- de Roos, A. M., and L. Persson. 2002. Size-dependent life-history traits promote catastrophic collapses of top predators. *Proceedings of the National Academy of Sciences USA* 99:12907–12912.
- de Roos, A. M., and L. Persson. 2013. Population and community ecology of ontogenetic development. Princeton University Press, Princeton, New Jersey, USA.
- de Roos, A. M., L. Persson, and E. McCauley. 2003. The influence of size-dependent life-history traits on the structure and dynamics of populations and communities. *Ecology Letters* 6:473–487.
- de Roos, A. M., T. Schellekens, T. Van Kooten, and L. Persson. 2008a. Stage-specific predator species help each other to persist while competing for a single prey. *Proceedings of the National Academy of Sciences USA* 105:13930–13935.
- 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.
- de Roos, A. M., T. Schellekens, T. Van Kooten, K. Van De Wolfshaar, D. Claessen, and L. Persson. 2008b. Simplifying a physiologically structured population model to a stage-structured biomass model. *Theoretical Population Biology* 73:47–62.
- Dhooge, A., W. Govaerts, and Y. A. Kuznetsov. 2003. MATCONT: a MATLAB package for numerical bifurcation analysis of ODEs. *ACM Transactions on Mathematical Software* 29:141–164.
- Diehl, S. 2003. The evolution and maintenance of omnivory: dynamic constraints and the role of food quality. *Ecology* 84:2557–2567.
- Diehl, S., and M. Feiel. 2000. Effects of enrichment on three-level food chains with omnivory. *American Naturalist* 155:200–218.
- Folke, C., S. Carpenter, B. Walker, M. Scheffer, T. Elmqvist, L. Gunderson, and C. S. Holling. 2004. Regime shifts, resilience, and biodiversity in ecosystem management. *Annual Review of Ecology, Evolution, and Systematics* 35:557–581.
- Gismervik, I. 2005. Numerical and functional responses of choreo- and oligotrich planktonic ciliates. *Aquatic Microbial Ecology* 40:163–173.
- Grime, J. P. 1973. Competitive exclusion in herbaceous vegetation. *Nature* 242:344–347.
- Grover, J. P. 1995. Competition, herbivory, and enrichment: nutrient-based models for edible and inedible plants. *American Naturalist* 145:746–774.
- 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.
- Hare, S. R., and N. J. Mantua. 2000. Empirical evidence for North Pacific regime shifts in 1977 and 1989. *Progress in Oceanography* 47:103–145.
- Harms, D. A., and W. J. Mattson. 1992. The dilemma of plants: to grow or defend. *Quarterly Review of Biology* 67:283–335.
- Hin, V., T. Schellekens, L. Persson, and A. M. de Roos. 2011. Coexistence of predator and prey in intraguild predation systems with ontogenetic niche shifts. *American Naturalist* 178:701–714.
- 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.
- Holt, R. D., and G. A. Polis. 1997. A theoretical framework for intraguild predation. *American Naturalist* 149:745–764.
- Huss, M., A. Grdmark, A. Van Leeuwen, and A. M. de Roos. 2012. Size- and food-dependent growth drives patterns of competitive dominance along productivity gradients. *Ecology* 93:847–857.
- Hutson, V. 1984. Predator mediated coexistence with a switching predator. *Mathematical Biosciences* 68:233–246.
- Jackson, A. C., S. D. Rundle, M. J. Attrill, and P. A. Cotton. 2004. Ontogenetic changes in metabolism may determine diet shifts for a sit-and-wait predator. *Journal of Animal Ecology* 73:536–545.
- Klausmeier, C. A., and E. Litchman. 2012. Successional dynamics in the seasonally forced diamond food web. *American Naturalist* 180:1–16.
- Klecka, J., and D. S. Boukal. 2012. Who eats whom in a pool? A comparative study of prey selectivity by predatory aquatic insects. *PLoS ONE* 7:e37741.
- Koricheva, J. 2002. Meta-analysis of sources of variation in fitness costs of plant antiherbivore defenses. *Ecology* 83:176–190.
- Lahti, M. E., and D. D. Beck. 2008. Ecology and ontogenetic variation of diet in the pigmy short-horned lizard (*Phrynosoma douglasii*). *American Midland Naturalist* 159:327–339.
- 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.
- Levins, R., and D. Culver. 1971. Regional coexistence of species and competition between rare species. *Proceedings of the National Academy of Sciences USA* 68:1246–1248.
- Lubchenco, J. 1978. Plant species diversity in a marine intertidal community: importance of herbivore food preference and algal competitive abilities. *American Naturalist* 112:23–39.
- Nakazawa, T. 2011. Ontogenetic niche shift, food-web coupling, and alternative stable states. *Theoretical Ecology* 4:479–494.
- Noonburg, E. G., and P. A. Abrams. 2005. Transient dynamics limit the effectiveness of keystone predation in bringing about coexistence. *American Naturalist* 165:322–335.
- Ollif, H., and M. E. Ritchie. 1998. Effects of herbivores on grassland plant diversity. *Trends in Ecology and Evolution* 13:261–265.
- Paine, R. T. 1966. Food web complexity and species diversity. *American Naturalist* 100:65–75.
- Persson, L., P.-A. Amundsen, A. M. de Roos, A. Klemetsen, R. Knudsen, and R. Primmer. 2007. Culling prey promotes predator recovery—alternative states in a whole-lake experiment. *Science* 316:1743–1746.
- Persson, L., and A. M. de Roos. 2003. Adaptive habitat use in size-structured populations: linking individual behavior to population processes. *Ecology* 84:1129–1139.
- Rudolf, V. H. W. 2007. The interaction of cannibalism and omnivory: consequences for community dynamics. *Ecology* 88:2697–2705.

- Rudolf, V. H. W., and K. D. Lafferty. 2011. Stage structure alters how complexity affects stability of ecological networks. *Ecology Letters* 14:75–79.
- Scheffer, M., and S. R. Carpenter. 2003. Catastrophic regime shifts in ecosystems: linking theory to observation. *Trends in Ecology and Evolution* 18:648–656.
- Schellekens, T., A. M. de Roos, and L. Persson. 2010. Ontogenetic diet shifts result in niche partitioning between two consumer species irrespective of competitive abilities. *American Naturalist* 176:625–637.
- Schreiber, S., and V. H. W. Rudolf. 2008. Crossing habitat boundaries: coupling dynamics of ecosystems through complex life cycles. *Ecology Letters* 11:576–587.
- Schröder, A., L. Persson, and A. M. de Roos. 2012. Complex shifts between food web states in response to whole-ecosystem manipulations. *Oikos* 121:417–427.
- Staver, A. C., S. Archibald, and S. A. Levin. 2011. The global extent and determinants of savanna and forest as alternative biome states. *Science* 334:230–232.
- Turner, M. 1979. Diet and feeding phenology of the green lynx spider, *Peucetia viridans* (Araneae: Oxyopidae). *Journal of Arachnology* 7:149–154.
- Van Leeuwen, A., A. M. de Roos, and L. Persson. 2008. How cod shapes its world. *Journal of Sea Research* 60:89–104.
- Viola, D. V., E. A. Mordecai, A. G. Jaramillo, S. A. Sistla, L. K. Albertson, J. S. Gosnell, B. J. Cardinale, and J. M. Levine. 2010. Competition–defense tradeoffs and the maintenance of plant diversity. *Proceedings of the National Academy of Sciences USA* 107:17217–17222.
- Werner, E. E. 1988. Size, scaling and the evolution of complex life cycles. Pages 60–81 in B. Ebenman and L. Persson, editors. *Size-structured populations*. Springer, Berlin, Germany.
- 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.
- Worm, B., H. K. Lotze, H. Hillebrand, and U. Sommer. 2002. Consumer versus resource control of species diversity and ecosystem functioning. *Nature* 417:848–851.

SUPPLEMENTAL MATERIAL

Appendix A

A description of the fully size-structured population model ([Ecological Archives E094-266-A1](#)).

Appendix B

A description of the inclusive niche model ([Ecological Archives E094-266-A2](#)).

Appendix C

A description of the symmetrical niche model under the assumption of nutrient recycling ([Ecological Archives E094-266-A3](#)).