Coexistence of Predator and Prey in Intraguild Predation Systems with Ontogenetic Niche Shifts

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ABSTRACT: In basic intraguild predation (IGP) systems, predators and prey also compete for a shared resource. Theory predicts that persistence of these systems is possible when intraguild prey is superior in competition and productivity is not too high. IGP often results from ontogenetic niche shifts, in which the diet of intraguild predators changes as a result of growth in body size (life-history omnivory). As a juvenile, a life-history omnivore competes with the species that becomes its prey later in life. Competition can hence limit growth of young predators, while adult predators can suppress consumers and therewith neutralize negative effects of competition. We formulate and analyze a stage-structured model that captures both basic IGP and life-history omnivory. The model predicts increasing coexistence of predators and consumers when resource use of stage-structured predators becomes more stage specific. This coexistence depends on adult predators requiring consumer biomass for reproduction and is less likely when consumers outcompete juvenile predators, in contrast to basic IGP. Therefore, coexistence occurs when predation structures the community and competition is negligible. Consequently, equilibrium patterns over productivity resemble those of three-species food chains. Life-history omnivory thus provides a mechanism that allows intraguild predators and prey to coexist over a wide range of resource productivity.

Keywords: intraguild predation, ontogenetic niche shifts, life-history omnivory, stage-dependent interactions, alternative stable states, tri-trophic food chain.

Introduction

Omnivory is defined as the feeding on different trophic levels (Pimm and Lawton 1978), which allows a species (an intraguild predator) to simultaneously prey on and compete with another species (its intraguild prey), an interaction we refer to as basic intraguild predation (IGP; Polis et al. 1989; Holt and Polis 1997). IGP has received considerable attention, since it is shown to be common in natural communities (Polis 1991; Polis and Strong 1996; Arim and Marquet 2004). Theoretical predictions, however, show limited scope for coexistence of intraguild predators and intraguild prey (Holt and Polis 1997; Diehl and Feiessel 2000; Mylius et al. 2001). Holt and Polis (1997) formulated two necessary conditions for coexistence in basic IGP systems, namely, that the intraguild prey (or intermediate consumer) should be superior in resource competition and that productivity levels should be intermediate. In systems with low productivity, resource competition plays the most dominant role, since consumer density is too low to be beneficial for the intraguild predator, eventually leading to predator exclusion. In contrast, in highly productive systems, intraguild predators become too abundant and, hence, predation too intense for the consumer to persist. Coexistence is therefore maintained only at intermediate productivity levels when competition and predation are by and large balanced. Many subsequent studies have focused on possible mechanisms that promote coexistence of intraguild prey and predators, given that IGP and omnivory are common in natural systems. Among the mechanisms originally proposed by Holt and Polis (1997) are age-restricted predation or prey life stages invulnerable to predation (Mylius et al. 2001; Borer 2002; Rudolf and Armstrong 2008), adaptive foraging behavior by intraguild predators (Krivan 2000; Krivan and Diehl 2005), spatial or temporal refugees for the intraguild prey (Finke and Denno 2006; Janssen et al. 2007; Amarasekare 2008; Okuyama 2008), or additional resources for intraguild prey (Holt and Huxel 2007). In theory, these mechanisms may enhance coexistence of consumers and predators by extending the conditions under which competition and predation are balanced. This effect is, however, often rather marginal, as exemplified by the study by Borer (2006), which showed that an empirically parameterized IGP model is not likely to increase coexistence possibilities. More commonly, these mechanisms increase...
coexistence by reducing the strength of the competitive interactions between intraguild predators and prey to a negligible level, which effectively marginalizes the IGP nature of the interaction (simultaneous predation and competition). In this sense, the frequent occurrence of IGP can still only be understood by assuming that it is a relatively weak interaction (Janssen et al. 2006).

Omnivory often results from changes in body size over ontogeny (Polis et al. 1989). Because many species grow considerably in size during their life, ecological traits that scale with body size—such as metabolic rate, risk to predation, resource availability, and exploitation rate—change over ontogeny (Peters 1983; Werner and Gilliam 1984). Species may therefore shift habitat or feed on different resources in different life stages, a phenomenon referred to as ontogenetic niche shift (Werner and Hall 1979; Werner and Gilliam 1984; Mittelbach 1988; Olson et al. 1995), or life-history omnivory (Pimm and Rice 1987). A species may therefore be an omnivore when considered over its entire life, while all its different life stages are specialist consumers of their own single resource. Commonly, when intraguild predation involves life-history omnivory, adult intraguild predators prey on consumers, while juvenile intraguild predators compete with consumers for a shared resource. Feeding on different prey types during different life stages is generally associated with a trade-off in feeding efficiency, so that predators are inferior in resource competition to their specialist prey species (Werner and Gilliam 1984; Persson 1988). Competing for a shared resource at an early life stage may therefore limit recruitment of juvenile predators to later life stages and thus result in a juvenile competitive bottleneck (Werner and Gilliam 1984; Neill 1988; Persson and Greenberg 1990; Byström et al. 1998). Byström et al. (1998), for example, showed that competition for zooplankton between juveniles of the life-history omnivore perch (Perca fluviatilis) and its prey species roach (Rutilus rutilus) negatively affected growth and condition of perch. In systems where IGP is a consequence of growth in body size, adult intraguild predators can suppress the competitors of their offspring, in this way countering juvenile bottleneck effects (Persson 1988). Walters and Kitchell (2001) dubbed this the cultivation effect, since dominant large species in this way cultivate a favorable environment for their young. When species that are dependent on cultivation for their persistence collapse and reach low abundances, a juvenile competitive bottleneck can prevent recovery, although the species would be able to persist once present, owing to the cultivation by adult predators.

Although life-history omnivory and ontogenetic niche shifts are widespread phenomena (Werner and Gilliam 1984; Polis et al. 1989), their impact on the dynamics of IGP is studied only to a limited extent (Mylius et al. 2001; Van de Wolfshaar et al. 2006; Rudolf 2007). Studies that explicitly focus on stage- or size-dependent interactions in IGP systems model life-history omnivory more as an ontogenetic niche widening than as an ontogenetic niche shift (Van de Wolfshaar et al. 2006; Rudolf 2007). Such a niche widening implies that additional resources become available when intraguild predators grow in size. In that case, juvenile predators feed only on basic resource, while adult predators are involved in IGP and hence prey on both resource and consumers. Such a configuration still allows the intraguild predator to exclude the consumer, since adult predators can exclusively forage on resource biomass when productivity levels are high (Van de Wolfshaar et al. 2006). However, a recent study (V. H. W. Rudolf and K. D. Lafferty, unpublished manuscript) has shown that the resource overlap between different predator stages is limited even among nonmetamorphosing species, for which the ontogenetic niche shifts result from growth in body size. In the most extreme case, each life-history stage of the predator depends on its own exclusive and essential resource type without any resource overlap between stages at all. The study shows that such ontogenetic specialists can alter the otherwise stabilizing effect that complexity has on the stability of food webs (V. H. W. Rudolf and K. D. Lafferty, unpublished manuscript). Since ontogenetic specialists have multiple essential resources, they face a high risk of secondary extinction resulting from the loss of such an essential resource (V. H. W. Rudolf and K. D. Lafferty, unpublished manuscript). To address the question of how such a complete diet shift, in which resource use of juvenile and adult predators is nonoverlapping, affects the dynamics of IGP, we formulate and analyze a stage-structured IGP model. In this model, the interaction of predators with consumers can be varied from basic IGP, as considered in classical IGP models (Holt and Polis 1997; Diehl and Feissel 2000; Mylius et al. 2001), to complete life-history omnivory. First, we address how the parameter region of coexistence of intraguild predators and prey changes as a function of the resource overlap between juvenile and adult intraguild predators. Furthermore, we address to what extent the two conditions that are crucial for coexistence in basic IGP (superior dominance of consumers and intermediate productivity) are required for coexistence in systems where intraguild predation is a result of an ontogenetic niche shift. The model predicts increasing coexistence possibilities when interactions are increasingly stage specific. A balance between competition and predation can indeed lead to equilibrium coexistence over a large range of productivities when the intraguild predator is a life-history omnivore, but this equilibrium is generically unstable. Stable coexistence occurs only when community dynamics are shaped primarily by predation, with competitive interactions playing only a marginal role.
As a result, changes in equilibrium density with increasing productivity in the stable coexistence state largely resemble those of a three-species linear food chain. In contrast, community dynamics may also be governed by strong competition between consumers and juvenile predators, leading to an alternative stable state, in which intraguild prey outcompete predators by imposing a juvenile bottleneck. As a consequence, the assumption that intermediate consumers are superior in the competition for basic resource, which is crucial for coexistence in basic IGP systems, can in fact hinder coexistence in IGP systems with life-history omnivory. Finally, we also show that these results remain valid when consumers are also stage structured and intraguild predators have different feeding preferences for the different life stages of consumers.

Model Formulation

The ontogenetic changes in feeding habits of an intraguild predator are modeled using the bioenergetics approach of Yodzis and Innes (1992), with a stage-structured extension as formulated by de Roos et al. (2007). Four ordinary differential equations keep track of biomass changes of resource \( R \), intraguild prey or intermediate consumer \( C \), juvenile intraguild predator \( P_j \), and adult intraguild predator \( P_a \) (Table 1). For reasons provided by Mylius et al. (2001) and to allow comparison with the results of that study, resource follows semi-chemostat dynamics \( \frac{dR}{dt} = \delta (R_{max} - R) \) in the absence of consumers and intraguild predators, with turnover rate \( \delta \) and maximum resource density \( R_{max} \). Resource decreases through feeding by consumers and intraguild predators. Resource feeding by consumers increases their net biomass production, \( \nu(R) \), which equals the balance between biomass production through mass-specific ingestion and biomass loss through mass-specific maintenance rate \( T_c \). Ingestion follows a Type II functional response, with half-saturation constant \( H_c \), maximum ingestion rate \( M_c \), and conversion efficiency \( \sigma \). Hence,

\[
\nu(R) = \sigma M_c \frac{R}{H_c + R} - T_c.
\]  (1)

Consumer biomass decreases through predation by intraguild predators and through background mortality \( \mu_c \) (Table 1).

The intraguild predator is structured into a juvenile and an adult stage and feeds on both consumer and resource biomass. Juvenile net biomass production, \( \nu_j(R, C) \), is used for growth of juveniles and maturation, which is represented by the mass-specific rate \( \gamma(\nu_j(R, C)) \). Net biomass production of adults, \( \nu_a(R, C) \), is used only for production of juveniles, so intraguild predators do not grow any further after entering the adult stage. Both adult and juvenile biomass decrease through background mortality, \( \mu_p \), which is assumed to be equal for both stages.

The mass-specific maturation rate is derived from de Roos et al. (2007) and given by

\[
\gamma(\nu_j(R, C)) = \frac{\nu_a(R, C) - \mu_p}{1 - z^{-\nu_j(R, C)}}.
\]  (2)

This function expresses that the maturation rate increases with net biomass production of juveniles, \( \nu_j(R, C) \), and decreases with predator background mortality \( \mu_p \), as well as with an increasing ratio between the predator body size at birth and at maturation, represented by the parameter \( z \) (de Roos et al. 2007). The maturation function is derived from a structured population model in terms of partial differential equations, which accounts for a class of non-growing, equally sized adult predators and a continuous size distribution of juvenile predators between their size at birth and their size at maturation. The derivation of this function is based on an assumption that at any particular time the size distribution of juveniles between their birth and maturation size has the same shape as the equilibrium size distribution pertaining to the current mass-specific net production rate \( \nu_j(R, C) \) and mortality rate \( \mu_p \) of juveniles. This equilibrium assumption applies only to the relative juvenile biomass distribution and not their total biomass. It is also equivalent to the assumption that the dynamics of the relative within-stage size distribution

<table>
<thead>
<tr>
<th>Table 1: Model equations</th>
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<tr>
<td>Dynamic equation</td>
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</tbody>
</table>
| \[
\frac{dR}{dt} = \delta (R_{max} - R) - M_c \frac{R}{H_c + R} - \sigma P_j \frac{M_c}{H_c + R} - \sigma P_a \frac{M_c}{H_c + R} - T_c.
\] |
| Resource biomass |
| \[
\frac{dC}{dt} = \nu_j(R, C) - \mu_c C - \sigma C \frac{M_c}{H_c + R} - \sigma C \frac{M_c}{H_c + R} + \gamma(\nu_j(R, C)) - \mu_p P_j/
\] |
| Consumer biomass |
| \[
\frac{dP_j}{dt} = \nu_j(R, C) P_j + \nu_a(R, C) P_j - \gamma(\nu_j(R, C) P_j - \mu_p P_j |
\] |
| Juvenile predator biomass |
| \[
\frac{dP_a}{dt} = \gamma(\nu_j(R, C) P_j - \mu_p P_a |
\] |
| Adult predator biomass |
of juveniles takes place on a faster timescale than the changes in resource and absolute juvenile and adult biomass density. In addition, this is the only choice for the maturation function, which ensures that all equilibria occurring in the stage-structured biomass model are one-to-one identical to the equilibria occurring in the underlying size-structured model (de Roos et al. 2008). Despite its formulation in only two ordinary differential equations, the model thus consistently translates the assumption about individual life history that forms the basis of the underlying size-structured model to the population level. Under nonequilibrium conditions, dynamics of the stage-structured biomass model have also been shown to be qualitatively similar to the dynamics of a underlying size-structured model, except when the latter exhibits single-cohort or single-generation oscillations, in which not all size classes of individuals are continuously present in the population, but the population is dominated by individuals with body sizes within a restricted range (de Roos et al. 2008; Guill 2009).

Mass-specific net biomass production of juveniles and adults, denoted by \( \nu_j(R, C) \) and \( \nu_j(R, C) \), respectively, equals the difference between mass-specific ingestion and mass-specific maintenance \( T_p \). Ingestion follows a Type II functional response with maximum ingestion \( M_p \), half-saturation constant \( H_p \), and conversion efficiency \( \sigma \). Because all model variables represent biomass densities, the maximum ingestion rate and half-saturation constant are assumed independent of whether predator individuals feed on resource or on consumers. Hence, \( \nu_j(R, C) \) and \( \nu_j(R, C) \) become:

\[
\nu_j(R, C) = \sigma M_p \frac{(1 - \Phi) R + \Phi C}{H_p + (1 - \Phi) R + \Phi C} - T_p, \tag{3}
\]

\[
\nu_j(R, C) = \sigma M_p \frac{\Phi R + (1 - \Phi) C}{H_p + \Phi R + (1 - \Phi) C} - T_p. \tag{4}
\]

The total rates with which predators forage on resource and consumers can be derived from the sum of the foraging rates of juveniles and adults, given by

\[
M_p \frac{(1 - \Phi) R}{H_p + (1 - \Phi) R + \Phi C} + M_p \frac{\Phi R}{H_p + \Phi R + (1 - \Phi) C}, \tag{5}
\]

\[
M_p \frac{\Phi C}{H_p + (1 - \Phi) R + \Phi C} + M_p \frac{(1 - \Phi) C}{H_p + \Phi R + (1 - \Phi) C}. \tag{6}
\]

Parameter \( \Phi \) models the extent of ontogenetic diet shift between juveniles and adults. Although \( \Phi \) represents differences in feeding habits rather phenomenologically, it can be interpreted as the relative time spent feeding on a particular prey species. For simplicity, we do not vary the diet composition of juvenile and adult predators independently, but restrict the model formulation and analysis to the situation where feeding preferences of both predatory life stages are symmetric and therefore use a single parameter to model feeding habits of juvenile and adult predators. At \( \Phi = 0.5 \), no diet shift occurs and both predatory stages equally divide feeding time between resource and consumers. In this case, net biomass production is equal for both stages, since \( \nu_j(R, C) \) and \( \nu_j(R, C) \) simplify to

\[
\nu_j(R, C) = \sigma M_p \frac{0.5 R + 0.5 C}{H_p + 0.5 R + 0.5 C} - T_p. \tag{7}
\]

The structured model in table 1 in this case reduces to an unstructured population model in which the intraguild predator is not divided into different life stages \( (P + P_p = P) \) and can be described with a single ordinary differential equation:

\[
\frac{dP}{dt} = \nu_j(R, C)P - \mu_p P. \tag{8}
\]

In this case, the model simplifies to the IGP model analyzed by Mylius et al. (2001). If \( \Phi \neq 0.5 \), the stage-structured model in table 1 rather than equation (8) describes predator dynamics. Decreasing \( \Phi \) increases adult preference for consumers and simultaneously increases juvenile preference for resource. At \( \Phi = 0 \), adults prey solely on consumers, and juveniles forage only on the resource, representing a complete diet shift during development of the intraguild predator. Analyzing the dynamical consequences of changing \( \Phi \) thus provides a method to study the effect of various intensities of life-history omnivory on an intraguild predation system.

**Model Parameterization**

Default model parameters are summarized in Table 2. Maximum ingestion (\( M \)) and maintenance (\( T \)) are both mass-specific rates (expressed in unit biomass per unit biomass per unit time), whereas the mortality parameter (\( \mu \)) represents a per capita rate. Default values for these rates are taken inversely proportional to the quarter power of adult body size, with proportionality constants of 0.01 for maintenance (Peters 1983; Yodzis and Innes 1992) and 0.001 for background mortality (Gillooly et al. 2001). Maximum ingestion rate is assumed equal to 10 times the maintenance rate (Peters 1983; Yodzis and Innes 1992). The dependence on adult body size can be simplified by adopting the mass-specific maintenance rate of consumers, \( T_c \), to scale the time variable and hence set \( T_c = 1 \). Given this scaling of time, maximum ingestion rate and mortality rate become 10 and 0.1, respectively.

Adult predators are assumed to be 100 times larger than consumers (Yodzis and Innes 1992). The quarter power scaling relations then dictate \( M_p = 3, T_p = 0.3 \), and
\[ R_{\text{max}} = \text{Varied} \]
\[ \delta = 1 \]
\[ \sigma = 0.5 \]
\[ M = 10 \]
\[ T = 1 \]
\[ \mu = 0.1 \]
\[ H = 1 \]
\[ \Phi = 0.5 \]
\[ z = 0.01 \]

Table 2: Default model parameters

<table>
<thead>
<tr>
<th>Parameter</th>
<th>Resource</th>
<th>Consumer</th>
<th>Predator</th>
<th>Description</th>
</tr>
</thead>
<tbody>
<tr>
<td>( R_{\text{max}} )</td>
<td>Varied</td>
<td></td>
<td></td>
<td>Resource maximum biomass density</td>
</tr>
<tr>
<td>( \delta )</td>
<td></td>
<td></td>
<td></td>
<td>Resource turnover rate</td>
</tr>
<tr>
<td>( \sigma )</td>
<td>0.5</td>
<td></td>
<td></td>
<td>Assimilation efficiency</td>
</tr>
<tr>
<td>( M )</td>
<td>10</td>
<td>2.5</td>
<td></td>
<td>Maximum ingestion rate (mass specific)</td>
</tr>
<tr>
<td>( T )</td>
<td>1</td>
<td></td>
<td></td>
<td>Maintenance rate (mass specific)</td>
</tr>
<tr>
<td>( \mu )</td>
<td>0.1</td>
<td>0.03</td>
<td></td>
<td>Background mortality rate</td>
</tr>
<tr>
<td>( H )</td>
<td>1</td>
<td>1</td>
<td></td>
<td>Half-saturation constant</td>
</tr>
<tr>
<td>( \Phi )</td>
<td>0.5</td>
<td>0.0</td>
<td></td>
<td>Ontogenetic diet shift</td>
</tr>
<tr>
<td>( z )</td>
<td></td>
<td></td>
<td>0.01</td>
<td>Newborn-adult predator size ratio</td>
</tr>
</tbody>
</table>

Note: All figures are made with default parameters, unless indicated otherwise.

\( \mu_s = 0.03 \), given the scaling of the time variable with \( T_z \). However, theory on IGP stipulates that coexistence is possible only when consumers are superior in resource competition (Holt and Polis 1997). At \( \Phi = 0 \), juvenile predators and consumers are engaged in full resource competition. Minimum resource requirements that allow for biomass growth of consumers and juvenile predators can then be obtained by solving \( \frac{dC}{dt} = 0 \) and \( \frac{dp_j}{dt} = 0 \), respectively, while setting \( P_j = 0 \) and \( C = 0 \):

\[ R_c^* = \frac{H_i(T_p + \mu_c)}{dM_c - T_c - \mu_c}, \]  
\[ R_p^* = \frac{H_i(T_p + \mu_c)}{dM_p - T_p - \mu_p}. \]

The parameter setting as described above results in \( R_c^* = R_p^* \), which is not in line with the assumption of competitive dominance of consumers (i.e., \( R_c^* < R_p^* \)). We therefore assume the default maximum ingestion rate of intraguild predators to equal 2.5 instead of 3.0, representing a reduction in feeding efficiency resulting from the different prey types that an omnivore has to cope with during ontogeny (Werner and Gilliam 1984). We, however, also study the case where juvenile predators have lower minimum resource requirements than consumers (i.e., \( R_c^* > R_p^* \)), by setting \( M_p = 3.5 \).

In this study, the Type II functional responses are modeled using a maximum ingestion rate \( (M) \) and a half-saturation density \( (H) \). They can, however, easily be turned into the alternative formulation using attack (or clearance) rate in combination with handling time, which would reveal that the maximum ingestion is identical to the inverse of the handling time and that the half-saturation density \( H \) equals the ratio of maximum ingestion and attack rate. This latter identity suggests that the half-saturation density is in fact independent of body size, since it equals the ratio between two per capita rates that both tend to scale with adult body size to the three-quarters power (Brown et al. 2004). Data on diverse groups of zooplankton confirm this expectation (Hansen et al. 1997). The maximum resource density \( R_{\text{max}} \) and both half-saturation densities \( H_i \) and \( H_c \) are expressed as gram biomass per unit volume and are therefore the only parameters containing the unit of volume. Given that \( H_i \) and \( H_c \) are equal, they can hence both be set to 1 without loss of generality, since this merely implies a scaling of the unit of the total system volume. Maximum resource density \( R_{\text{max}} \) is then expressed as multiples of the half-saturation density. Similarly, because of the scaling of time, the resource turnover rate \( \delta \) is expressed as multiples of the half-saturation density. Similarly, because of the scaling of time, the resource turnover rate \( \delta \) is expressed as multiples of maintenance rate \( T_z \). We adopt the default value \( \delta = 1 \) such that resource turnover takes place at the same rate as consumer biomass turnover through metabolism. The ratio between newborn and adult predator body size \( (z) \) is set to 0.01, so that newborn body size equals consumer body size. A conversion efficiency of 0.5 is used for conversion of both resource and consumer biomass (Peters 1983).

Model predictions are analyzed for different values of \( R_{\text{max}} \) and \( \Phi \). Maximum resource densities \( R_{\text{max}} \) correspond to different productivity levels, which equal \( \delta R_{\text{max}} \). We will hence use maximum resource density and resource productivity as synonyms. We used Content, a numerical bifurcation software package (Kuznetsov et al. 1996), to calculate equilibrium densities as a function of \( R_{\text{max}} \) and \( \Phi \) and to assess equilibrium stability.

Results

For \( \Phi = 0.5 \), predator dynamics are described by equation (8), and the model simplifies to a basic IGP system, in which juvenile and adult intraguild predator to the same extent compete with and prey on intermediate consumers. While qualitative similar dynamics have been described by Mylius et al. (2001), we will shortly summarize them here for completeness and the introduction of symbols. In the basic IGP system, four equilibrium types occur: (1) a resource-only equilibrium; (2) a consumer-resource equi-
librium; (3) a coexistence equilibrium with resource, consumers, and intraguild predators; and (4) a predator-resource equilibrium (fig. 1, left). The resource-only equilibrium is stable as long as the population growth rates of consumers and predators are negative at the particular equilibrium resource density. Since consumers have lower resource requirements than predators (i.e., \( R^* < R^p \)), consumers can invade the resource-only equilibrium when predator growth rate is still negative. At the consumer-resource equilibrium, resource density stays constant at \( R^c \) while consumer density increases with increasing \( R_{\text{max}} \). Invasion of predators in the consumer-resource equilibrium can occur when net biomass production of predators becomes high enough to overcome their background mortality \( (\nu_p(R^*, C^*) = \mu_p) \). This productivity threshold is denoted as the predator invasion point \( (I_p; \text{fig. 1, left}) \). Increasing productivity in the coexistence equilibrium increases predator and resource biomass and decreases consumer biomass. At a particular resource productivity, a stable predator-resource equilibrium becomes possible. This productivity level is denoted as the consumer invasion point \( (I_c) \), since it is the highest \( R_{\text{max}} \) value for which consumers can invade the predator-resource equilibrium (fig. 1, left). In the absence of consumers, a predator-resource equilibrium is feasible as soon as \( R_{\text{max}} \) is above the minimum resource density that predators need for persistence. This occurs already for \( R_{\text{max}} \) values below \( I_c \) (at \( \Phi = 0.5 \), predators can in fact persist on resource alone at \( R_{\text{max}} \approx 0.717 \)). However, as long as \( R_{\text{max}} < I_c \), consumers can invade the predator-resource equilibrium, which makes the latter equilibrium unstable. Above the productivity threshold \( I_c \), this invasion is no longer possible because of too

**Figure 1:** Resource, consumer, and intraguild predator equilibrium biomass densities as a function of \( R_{\text{max}} \) for \( \Phi = 0.5 \) (left) and \( \Phi = 0.3 \) (right), with default values for all other parameters (table 2). Solid lines represent stable equilibria and dotted lines unstable equilibria. In the top row, juvenile predator biomass is indicated with gray lines and adult predator biomass with black lines. Dashed lines mark different productivity thresholds, at which a qualitative change in possible equilibria occurs. The threshold at which predators invade the consumer-resource equilibrium leading to coexistence is the predator invasion point \( (I_p) \), the threshold where a stable predator-resource equilibrium becomes possible is the consumer invasion point \( (I_c) \), and the threshold where consumers are excluded from the coexistence state is the consumer exclusion point \( (E_c) \).
high predation pressure, causing the predator-resource equilibrium to become stable (Mylius et al. 2001). Increasing productivity in the coexistence state eventually leads to exclusion of consumers, as predation pressure becomes too high for their persistence. This threshold is referred to as the consumer exclusion point ($E_c$; fig. 1, left). The two threshold levels of productivity $I_p$ and $E_c$ may not coincide, resulting in bistability with the coexistence equilibrium and the predator-resource equilibrium as alternative stable states. Here, consumers can persist when present but are unable to invade when absent because of high predation pressure. Beyond $E_c$, the predator-resource equilibrium is the only stable state. For a more detailed description of dynamics and equilibrium conditions of a closely related basic IGP model, we refer to Mylius et al. (2001).

With decreasing $\Phi$, juvenile predators increasingly depend on resource biomass and thus increasingly compete with consumers, while adult predators increasingly prey on consumers and thus become less resource dependent. These changing interactions alter the equilibrium properties of the IGP system. Figure 2 shows how the productivity thresholds that separate parameter regions with different types of equilibria shift to higher $R_{\text{max}}$ values when $\Phi$ is decreased from 0.5. Because consumers are competitively superior and hence in consumer-resource equilibrium impose a resource density that is insufficient for juvenile predators to achieve positive biomass production, invasion of intraguild predators is successful only if juvenile predators compensate their lower resource ingestion with ingestion of consumer biomass. Lower values of $\Phi$ imply that juveniles forage less on consumers and hence need higher consumer densities to attain positive biomass production. Because higher consumer densities occur at higher productivity levels, the predator invasion threshold $I_p$ shifts to higher $R_{\text{max}}$ values for lower values of $\Phi$. With decreasing values of $\Phi$, consumers hence increasingly impose a competitive bottleneck for juvenile predators, which limits invasion of the intraguild predator in the consumer-resource equilibrium.

The productivity threshold where the predator-resource equilibrium becomes stable against invasion by consumers ($I_p$) also shifts to higher $R_{\text{max}}$ values with decreasing values of $\Phi$. As shown by Mylius et al. (2001), this productivity threshold is determined by the predation pressure imposed on consumers, preventing successful consumer invasion. Since adult predators feed less on the resource with decreasing $\Phi$, higher productivity levels are needed to sustain predator densities that are sufficient to suppress the consumer’s growth rate below 0. Around $\Phi = 0.35$, $I_p$ merges with $E_c$, so that bistability between the predator-resource and the coexistence equilibrium no longer occurs.

For lower $\Phi$ values, juvenile predators forage more and more on resource and hence suffer increasingly from the competition by consumers. Predator persistence is then possible only if consumer densities are driven down by predation to such an extent that resource density is sufficiently high for juvenile predator growth. Consequently, for low $\Phi$ values, predators may be able to persist at a high density but fail to invade the consumer-resource equilibrium when at low density. This also implies that there are ranges of $R_{\text{max}}$ values, for which a coexistence equilibrium occurs as an alternative stable state of a consumer-resource equilibrium that the predator cannot invade. Figure 1 (right) shows for $\Phi = 0.3$ that invasion of predators occurs at slightly higher $R_{\text{max}}$ values than for $\Phi = 0.5$ and that all values of $R_{\text{max}}$ allowing for predator persistence also allow for invasion of the consumer-resource equilibrium by predators (see also the position of $I_p$ along the $R_{\text{max}}$ axis in fig. 2). For $\Phi = 0.1$ (fig. 3, left), however, there are $R_{\text{max}}$ values where predators can persist at high density, while these $R_{\text{max}}$ values do not allow invasion of the consumer-resource equilibrium by a low density of predators. In figure 3 (left), this is apparent from the fact that the curve representing coexistence equilibria starts out at the threshold value $I_p$ in the direction of lower $R_{\text{max}}$ values (fig. 3, top left). This initial part of the equilibrium curve represents unstable equilibria, separating the stable consumer-
resource equilibrium from a stable coexistence state. At a productivity threshold denoted by $E_p$, the predator equilibrium curve changes direction to higher $R_{max}$ values again (limit point or saddle node bifurcation) and continues as a curve representing stable coexistence equilibria. The point $E_p$ is the predator exclusion point and represents the minimal productivity level required for predators to persist in coexistence with consumers. The $\Phi$ value at which $E_p$ originates is shown in figure 2. For $\Phi$ values where the persistence boundary $E_p$ is positioned at lower productivity than the invasion boundary $I_c$, bistability occurs between the consumer-resource state and the coexistence state. Biologically, this means that for productivity levels where these two states co-occur, predators cannot invade the consumer-resource state because of the negative effect of competition on juveniles, but predators can maintain themselves when present at high density. This persistence is due to the predation of adult predators on consumers, which increases resource biomass for juvenile predators. For $R_{max}$ values exceeding $I_p$, a wide range of resource productivities exist for which coexistence is the only stable state (fig. 3, left). At $R_{max}$ values exceeding the consumer invasion threshold ($I_c$), consumers are excluded and a predator-resource equilibrium is the only stable state (fig. 3, left). The different combinations of equilibria are depicted in figure 2, in which the positions of the productivity thresholds along the $R_{max}$ axis for $0.5 \leq \Phi \leq 0.0$ are plotted. As shown in figure 2, decreasing the value of $\Phi$ toward 0 shifts the positions of $I_p$ and $I_c$ toward higher $R_{max}$ values, while the productivity threshold $E_p$ changes little over $R_{max}$. Ultimately, this results in the equilibrium configuration as illustrated in figure 3 (right) for $\Phi = 0$. Adults now prey solely on consumers, and juveniles forage only on the resource. Because of the competitive advantage of consumers, the predator invasion point disappeared, and the consumer-resource equilibrium is stable for all $R_{max}$ values.
As an alternative outcome of dynamics, a stable coexistence state exists. Since adults lack an alternative resource at $\Phi = 0$, consumers cannot be excluded from the coexistence state, which translates in the absence of the consumer invasion point ($I_c$). Therefore, for low $\Phi$ values, the only productivity threshold present is $E_p$, marking the lower limit of $R_{\text{max}}$ for which the intraguild predator persists (fig. 2).

In the coexistence state at $\Phi = 0.0$, equilibrium patterns with increasing productivity largely resemble those of a three-species linear food chain (Oksanen et al. 1981), where top predators regulate biomass of consumers and thus release the consumer’s control over resource biomass. Consumer densities therefore stay constant with changing values of $R_{\text{max}}$, leading to bottom-up regulation of resource biomass in equilibrium, which increases with increasing $R_{\text{max}}$. Under these conditions, predation by adult predators acts as the main structuring force, and consumers are top-down regulated by adult predators, which nullifies the potentially strong competition between juvenile predators and consumers. This cultivation by adult predators increases food availability for juvenile predators and enables their coexistence with the consumer (Walters and Kitchell 2001). In the alternative, consumer-resource equilibrium, strong competition for resources between juvenile predators and consumers translates into a juvenile competitive bottleneck, which restricts maturation and thereby marginalizes the predatory interactions between consumers and adults. Under such conditions interspecific competition is the main structuring interaction in the community leading to predator exclusion.

To allow for coexistence in basic IGP systems, consumers should be superior in resource consumption to offset the negative effects of predation (Holt and Polis 1997). When this assumption is not met, the intraguild predator can invade at lower resource densities compared with the consumer and a predator-resource equilibrium is the exclusive outcome of system dynamics (Diehl and Feissel 2000). In the case of life-history omnivory with a complete niche shift, however, adult predators require consumer biomass to reproduce. This assumption ensures that invasion of the intraguild predator is possible only with consumers present and also prohibits consumer exclusion. Resource competition now takes place between juvenile predators and consumers. When relaxing the assumption of consumer competitive dominance, juvenile predators no longer suffer from competition, and the intraguild predator can invade the consumer-resource equilibrium at $\Phi = 0.0$. This results in the equilibrium patterns as shown in figure 4. Here, the maximum ingestion rate of the predator ($M_p$) is set to 3.5, which ensures that juvenile predators can attain a positive growth rate at a lower $R_{\text{max}}$ value than required by consumers. Compared with basic IGP (fig. 1, left), there is a large scope for coexistence between consumers and intraguild predators. Similar to when consumers are superior resource competitors (fig. 3, right), equilibrium patterns in the coexistence equilibrium resemble those of a three-species linear food chain. Whereas IGP clearly operates as juvenile predators feed exclusively on resource, the ontogenetic niche shift of the intraguild predator results in a type of dynamics that closely resemble the classical pattern of a linear food chain.

**Discussion**

We formulated and analyzed an intraguild predation model that allowed us to vary the degree of resource overlap between juvenile and adult intraguild predators. In this way, the dynamics as described for classical IGP models, with no stage structure for the intraguild predator (here at $\Phi = 0.5$; Holt and Polis 1997; Mylius et al. 2001), can...
be linked to the dynamics of a system in which IGP is a consequence of a complete ontogenetic niche shift (here at $\Phi = 0.0$). In the latter configuration, juvenile and adult predators have nonoverlapping resource use, and resources of both life stages are essential and nonsubstitutable. Holt and Polis (1997) originally proposed that nonoverlapping resource use of juveniles and adult intraguild predators might reduce the likelihood of consumer exclusion and thereby enhance coexistence. Furthermore, Polis et al. (1989) conclude that IGP in many cases involves species that change food type at metamorphosis or by ontogenetic niche shifts, which is especially common in aquatic systems. In this study, we show that IGP as a result of such ontogenetic niche shifts can greatly alter the dynamics of classical IGP systems. Furthermore, it changes the conditions for which intraguild predator and prey can coexist, compared with IGP systems in which juvenile and adult predators have the same resource use (Holt and Polis 1997; Mylius et al. 2001).

Originally, IGP can persist in case of a delicate balance of competition and predation, which occurs when consumers are superior in resource competition to offset the negative effects of predation and when environmental productivity is intermediate (Polis et al. 1989; Holt and Polis 1997; Mylius et al. 2001; Amarasekare 2008). In low-productivity environments, resource competition dominates, allowing the superior consumer to outcompete the intraguild predator, while at high productivity, predation pressure becomes too high for consumer persistence. We show that a diet shift between juvenile and adult predators increases the scope of coexistence and totally prevents exclusion of the consumer at high productivity when the omnivorous feeding by the intraguild predator is completely divided between the juvenile and adult life stages (here at $\Phi = 0.0$; fig. 3, right). The inclusion of a diet shift in the life history of the intraguild predator therefore greatly increases the scope of coexistence between intraguild predators and intraguild prey. Coexistence, however, crucially depends on the assumption that adult predators require consumer biomass for reproduction and cannot persist on resource biomass alone. If consumers dominate resource competition, the coexistence state occurs next to a stable consumer-resource state, which cannot be invaded by predators (fig. 3, right). A competitively superior consumer is therefore able to prevent coexistence by imposing a bottleneck in the recruitment of the life-history omnivore. This contrasts with early studies on IGP, which for a variety of models show that the consumers should be superior resource competitors to allow for coexistence (Holt and Polis 1997; Borer et al. 2007). We furthermore show that this juvenile bottleneck does not occur when juvenile predators have a lower resource requirement than consumers (fig. 4). Note that this does not imply that the predator population as a whole is competitively superior to consumers, since adult predators are not involved in competition with consumers at all.

Whether consumer species are superior in resource competition compared with intraguild predators depends on the system considered. Vance-Chalcraft et al. (2007) showed in a meta-analysis that intraguild prey species are generally more effective at suppressing the shared resource compared with the intraguild predator, indicating that consumers are the dominant competitor. This effect, however, varied among different ecosystems (Vance-Chalcraft et al. 2007). It may also be argued that the feeding of life-history omnivores on different prey types results in morphological and behavioral trade-offs, and omnivores are therefore expected to be inferior resource feeders, compared with their specialist prey species (Werner and Gilliam 1984; Persson 1988).

Negative effects of competition on growth of life-history omnivores have been observed, especially in aquatic systems. Piscivorous fish that in early life stages compete with their prey for zooplankton or macroinvertebrates have been shown to suffer from reduced growth and development (Neill 1988; Persson and Greenberg 1990; Olson et al. 1995; Byström et al. 1998; Schröder et al. 2009). However, the effect of competition also depends on the amount of resource overlap, the time exposed to competition, and spatial factors such as habitat heterogeneity (Persson 1991). Considering this, young life-history omnivores might escape negative effects of competition. For example, piscivorous adult European perch (Perca fluviatilis) induce a behavioral response in their prey, juvenile individuals of roach (Rutilus rutilus), to spend more time in the littoral habitat as opposed to the pelagic zone of a lake (Persson 1991). This reverses the outcome of competition between juveniles because perch dominates competition in the more complex littoral zone, whereas roach dominates in the pelagic zone.

In the perch-roach system, as in many especially aquatic IGP systems, consumers and predators both grow considerably in body size, and size-dependent interactions may hence be important for both populations. For simplicity, we assumed that consumers do grow in body size but that the interactions of differently sized consumers are the same per unit biomass. In the appendix (available online), we present an extension of the current model in which the consumer population is also stage structured. This allows for different mass-specific feeding rates between juvenile and adult consumers and for predators to feed on either juvenile or adult consumers. In the appendix, we show that these extensions do not qualitatively change model predictions. Moreover, a consumer population in which juvenile and adult individuals have different feeding rates allows for enlarged coexistence possibilities of consumers.
and intraguild predators as a consequence of overcompensation in stage-specific biomass that can occur with an increase in consumer mortality (de Roos et al. 2007).

Rudolf (2007) studied an IGP model with a stage-structured intraguild predator and showed that coexistence is also possible in cases where intraguild predators are superior in resource competition, if the stage-structured predator is cannibalistic. While the condition that consumers should be superior competitors for the resource seems to hold for IGP systems lacking size structure (Holt and Polis 1997; Borer et al. 2007), the results presented here and the study performed by Rudolf (2007) suggest that this condition is not crucial for coexistence in systems where IGP is the result of an ontogenetic niche shift. Furthermore, a substantial degree of cannibalism in the predator population prevents predator-mediated exclusion of consumers and so enables coexistence with intraguild prey at high productivity (Crumrine 2005, 2010; Rudolf 2007). While these dynamics are comparable to the dynamics of the model presented here at $\Phi = 0.0$, the underlying mechanisms differ. In the model of Rudolf (2007), coexistence depends on the assumed density-dependent mortality (cannibalism) of intraguild predators, whereas in our model it depends on the assumption that consumers are an essential and nonsubstitutable resource for adult intraguild predators.

Other studies focusing on size-specific interactions within IGP systems conclude that life-history omnivory limits coexistence of predators and prey (Van de Wolfshaar et al. 2006) or increases coexistence only to a limited extent (Mylius et al. 2001). The manner in which size structure is implemented in those studies, however, differs from the way stage structure is incorporated here. Mylius et al. (2001) extended the basic IGP model with either a prey stage invulnerable to IGP or a predatory stage incapable of IGP. While this quantitatively increased the parameter space over which coexistence was possible, the general result of coexistence being limited to intermediate productivity levels remained valid (Mylius et al. 2001). Van de Wolfshaar et al. (2006) analyzed a physiologically structured population model with a size-structured predator and prey population. In that model, growth of both prey and predator was modeled food dependently, and foraging rates depended on the size of individuals. A positive feedback loop between foraging success of a predator on the resource early in life, more rapid growth in size, and hence higher foraging rates on consumers later in life resulted in rapid exclusion of consumers, especially at high resource productivities (Van de Wolfshaar et al. 2006). However, large adult intraguild predators in the model studied by Van de Wolfshaar et al. (2006) could still persist exclusively on resource biomass, which allowed the consumer to be excluded.

In short, this study shows that coexistence is promoted when consumer biomass is an essential resource for adult predators and when juveniles do not experience negative effects of competition. When all species coexist, equilibrium patterns resemble those of a three-species linear food chain where predator biomass is controlled bottom-up while consumer densities are top-down controlled by adult predators, which are the abundant predatory life stage (fig. 4). Furthermore, top-down control of consumers causes resource biomass to increase with productivity (fig. 3, right). Similar to classic IGP systems (here at $\Phi = 0.5$), the presence of a life-history omnivore in an IGP system leads to higher resource density at equilibrium, compared with resource density in the consumer-resource state (fig. 3, right).

The prediction of linear food chain dynamics in a stage-structured IGP system is supported by Persson et al. (1992), who found that biomass patterns of planktivorous and piscivorous fish in Scandinavian lakes agree with predictions of linear food chain theory in low to moderately productive lakes, even though these species are potentially involved in IGP interactions. While coexistence in basic IGP systems results from balanced competition/predation, our results show that in the case of life-history omnivory, such a balance leads to unstable coexistence. Potentially, both interactions might be equally strong; however, long-term dynamics converge to a state in which one of the interactions is far stronger than the other. In coexistence, predation by adult predators acts as the main force structuring the community, preventing competition between juveniles and consumers to occur. Coexistence is therefore a dynamical result that arises from the interaction between intraguild predators and prey, instead of resulting from a priori assumptions that weaken this interaction and, in this way, increase the scope of coexistence between intraguild predators and prey, for example, through spatial or temporal heterogeneity (Finke and Denno 2006; Janssen et al. 2007; Amarasekare 2008; Okuyama 2008) or additional resources for intraguild prey (Holt and Huxel 2007). As an alternative outcome of system dynamics, however, predators cannot persist because of the strong competition between juveniles and consumers. Now, the community is structured by interspecific competition, preventing predatory interactions between adults and consumers. So even though resource feeding by juvenile predators and predation on consumers by adult predators takes place continuously and simultaneously, only one of these two interactions determines community dynamics.

In classical models of IGP, the type of resource dynamics and functional response, the relative competitive ability of intraguild prey (consumer) versus intraguild predator, and the relative efficiency of IGP (i.e., the energy transfer efficiency of the direct link from resource to intraguild pred-
ator compared with the indirect link via consumers) determine whether and which type of alternative stable states occur (Takimoto et al. 2007; Verdy and Amarasekare 2010). With semi-chemostat resource dynamics, two different scenarios are possible: either a consumer-resource equilibrium or a coexistence equilibrium occurs as an alternative stable state next to a stable predator-resource equilibrium (Verdy and Amarasekare 2010). Accordingly, we find a coexistence state next to a predator-resource state for the classical IGP model (at \( \Phi = 0.5 \)). However, for decreasing values of \( \Phi \), we find that the scenario changes from a coexistence and a predator-resource equilibrium to a coexistence and a consumer-resource equilibrium as alternative stable states. The latter combination can occur only in classical IGP systems with logistic resource growth and Type II consumer functional responses (Verdy and Amarasekare 2010). The occurrence of a coexistence equilibrium as an alternative stable state to a consumer-resource equilibrium implies that persistence of the intraguild predator is possible at lower productivity levels than the productivity that allows for predator invasion of the consumer-resource equilibrium. Thus, intraguild predators are subjected to an Allee effect, which in classical IGP models originates from the nonlinearities of the logistic resource growth and the Type II consumer functional response. In our system at \( \Phi = 0.0 \), however, a completely different mechanism is responsible for this Allee effect, since it represents a juvenile competitive bottleneck whose occurrence depends only on the assumption that consumers are superior resource competitors.

Our model prediction that an IGP system involving a life-history omnivore is, in coexistence, mainly structured by predation—despite a potential for mixed competition/predation interactions—is supported by long-term studies focusing on the interactions between the life-history omnivore perch (\( \text{Perca fluviatilis} \)) and its competing prey roach (\( \text{Rutilus rutilus} \), L. Persson and A. M. de Roos, unpublished manuscript). In this system, the potential for mixed interactions appears to be of minor importance for explaining long-term dynamics. Instead, interspecific predation of perch on roach and intraspecific processes such as competition and cannibalism are proposed to determine coexistence (L. Persson and A. M. de Roos, unpublished manuscript). During transient dynamics, however, competition between roach and juvenile perch may be relevant since roach can impose a bottleneck for perch recruitment (Byström et al. 1998). Similarly, the interaction between arctic char (\( \text{Salvelinus alpinus} \)) and brown trout (\( \text{Salmo trutta} \)) has generally been interpreted as driven by interspecific competition (Nilssson 1965; Jansen et al. 2002), whereas long-term data now suggest that the system is structured by predation only (Persson et al. 2007).

Results presented here also have implications for ecosystem management. In particular, strong predation by adult predators structuring a community may mask potentially strong competitive interactions between juveniles and consumers. Therefore, communities with the potential of mixed competition/predation interactions may seemingly respond to changes in productivity or exploitation as a linear food chain by, for example, revealing a trophic cascade with increasing exploitation of top predators. Negative effects of competition may remain hidden and become apparent only after the collapse of the predator. Depending on the competitiveness of juvenile predators, the community may shift to an alternative state from which predator recovery is impossible. Overexploitations of piscivorous fish stocks provide good examples of this phenomenon (Frank et al. 2005; Persson et al. 2007; Van Leeuwen et al. 2008; Casini et al. 2009). For example, overexploitation of cod in the Northwest Atlantic and Baltic Sea has led to an increase in prey fish densities and a community-wide regime shift. The recovery of the cod population may now be limited by the strong competitive interaction between prey fish and juvenile cod resulting from the community shift (Casini et al. 2009). For predator exploitation and recovery, it is hence important to consider realized as well as potential interactions between predators and their prey. From this ecosystem perspective, the strategy of culling prey to relax competition or increase adult food availability (Persson et al. 2007), which at first sight seems counterintuitive, starts to make sense.

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