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CONSEQUENCES OF STAGE-STRUCTURED PREDATORS: CANNIBALISM, BEHAVIORAL EFFECTS, AND TROPHIC CASCADES

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Abstract. Cannibalistic and asymmetrical behavioral interactions between stages are common within stage-structured predator populations. Such direct interactions between predator stages can result in density- and trait-mediated indirect interactions between a predator and its prey. A set of structured predator–prey models is used to explore how such indirect interactions affect the dynamics and structure of communities. Analyses of the separate and combined effects of stage-structured cannibalism and behavior-mediated avoidance of cannibals under different ecological scenarios show that both cannibalism and behavioral avoidance of cannibalism can result in short- and long-term positive indirect connections between predator stages and the prey, including "apparent mutualism." These positive interactions alter the strength of trophic cascades such that the system's dynamics are determined by the interaction between bottom-up and top-down effects. Contrary to the expectation of simpler models, enrichment increases both predator and prey abundance in systems with cannibalism or behavioral avoidance of cannibalism. The effect of behavioral avoidance of cannibalism, however, depends on how strongly it affects the maturation rate of the predator. Behavioral interactions between predator stages reduce the short-term positive effect of cannibalism on the prey density, but can enhance its positive long-term effects. Both interaction types reduce the destabilizing effect of enrichment. These results suggest that inconsistencies between data and simple models can be resolved by accounting for stage-structured interactions within and among species.

Key words: community stability; consumer–resource dynamics; food webs; intraspecific predation; paradox of enrichment; predator-dependent functional response; predator interference; size structure.

INTRODUCTION

Reliable predictions of how communities respond to environmental influences require an understanding of how the interaction of intra- and interspecific processes shape population and community dynamics. Most individuals undergo considerable size changes during their growth period and different size cohorts commonly coexist (Polis 1984). This size structure creates size-structured interactions, in which the type and strength of the interaction with other members in the community (conspecific or heterospecific) depend on the relative size of the individuals involved (Polis 1984, Rudolf 2006, 2007*b*). However, the community dynamics resulting from the interaction of intra- and interspecific size-structured interactions are not well understood.

Cannibalism is a prevalent feature of size-structured populations in both aquatic and terrestrial food webs (Fox 1975*a*, Polis 1981, Wagner and Wise 1996, Persson 1999, Woodward and Hildrew 2002, Persson et al. 2003, Woodward et al. 2005*b*). Cannibalism has a strong impact on population dynamics because it introduces a trophic structure and feedback loops within a population (Claessen et al. 2004), and because it affects the behavioral interactions between size classes (Sih 1981, Rudolf 2006). Cannibalistic stages and their conspecific prey are often distinct functional groups that occupy different trophic levels in the food web. This difference in trophic position of cannibals and conspecific prey in relation to other species creates different trait- (behavioral) and density- (cannibalistic) mediated indirect interactions (TMII and DMII, respectively), even in systems with one predator and one prey species (Rudolf 2006) (Fig. 1A–C). For example, the consumption of small predators by large conspecifics will reduce the predation pressure on the prey of the small predators, resulting in a positive DMII between large predators and heterospecific prey (Fig. 1C). A similar positive indirect interaction can result from changes in predator behavior. To avoid aggressive or lethal interactions with larger conspecifics, smaller individuals commonly change their activity schedule, habitat use, or foraging activity, as observed in insects (Sih 1981, Van Buskirk 1992), isopods (Leonardsson 1991), fish (Biro et al. 2003), and amphibians (Rudolf 2006). This change in behavior can reduce the per capita consumption rate of small predators in the presence of large conspecifics (Sih 1981, Rudolf 2006) (Fig. 1B). In systems with three species, such TMII and DMII can have a strong impact

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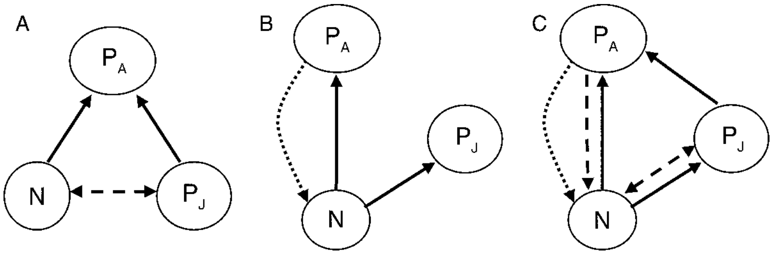

FIG. 1. Food web topologies and their possible cannibalistic-mediated (dashed arrows) and behavioral-mediated (dotted arrows) indirect interactions between adult (P_A) and juvenile (P_J) predators and the prey (N). Solid lines indicate predation; double-headed arrows indicate reciprocal interactions. (A) Cannibalistic-mediated indirect interaction between conspecific and heterospecific prey mediated through adult predators (Eq. 1); (B) behavior-mediated indirect interaction between heterospecific prey and adult predators without cannibalism mediated through altering the behavior of juvenile predators (Eq. 3); (C) both behavioral- and cannibalistic-mediated indirect interactions between predator stages and prey (see Fig. 1A, B) with additional density-mediated indirect interactions between adult predators and prey through consumption of juvenile predators (Eq. 5).

on the effects of predation on community structure (Werner and Peacor 2003, Preisser et al. 2005) and determine the effects of enrichment on communities (Krivan and Schmitz 2004). Indirect interactions between multiple stages of a size-structured predator and their prey could have a similarly strong impact on communities. However, because at least two functional groups (i.e., the small and the large stage of a species) belong to the same species and are directly coupled through growth transitions and reproduction, the long-term dynamics cannot be readily derived from three-species systems that lack such feedback loops between functional groups. Furthermore, in cannibalistic populations both DMII and TMII are likely to act simultaneously. However, it is still poorly understood how the separate and combined effects of these two indirect interactions types (i.e., DMII and TMII resulting from cannibalism) between different predator stages and their prey affect the dynamics and structure of food webs.

Another interaction type that has been neglected is the indirect interaction between conspecific and heterospecific prey (Fig. 1A). Heterospecific and conspecific prey share a common predator, which creates the potential for indirect interactions between both prey types. Changes in the abundance of conspecific prey can indirectly affect the density of the heterospecific prey by altering the predation pressure of the heterospecific prey and vice versa (Fox 1975*b*, Orr et al. 1990, Leonardsson 1991, Rudolf 2007*a*). In three-species systems such indirect interactions are commonly called "apparent competition" when the predation rate for one prey increases with an increase in the density of the other prey or "apparent mutualism" when the predation rate for one prey decreases with an increase in the density of the other prey (Holt 1977), and have important effects on community dynamics (Holt and Lawton 1993, Abrams and Matsuda 1996, Bonsall and Hassell 1997, Rudolf and Antonovics 2005).

The analysis presented here extends current theory by asking how the separate and combined impact of cannibalism and nonlethal behavioral (i.e., antipredator) interactions between predator stages affect the structure and dynamics of communities. For this purpose, I analyzed three different models. These models represent different ecological scenarios (Fig. 1A–C), and at the same time allow me to isolate and investigate the individual and combined short- and long-term effects of both interaction types. In particular, I asked how cannibalistic interactions between predator stages and behavioral avoidance of cannibalism alter the relationship between a predator and its prey, how they alter the effect of bottom-up and top-down cascades on species abundances, and how they affect the stability of the system. I show that for most ecological scenarios cannibalistic interactions between predator stages and behavioral avoidance of cannibalism can lead to positive short- and long-term indirect interactions between different predator stages and their prey. These indirect interactions can reduce the destabilizing effect of enrichment and alter the dynamics of trophic cascades. Furthermore, the behavioral avoidance of cannibalism is likely to enhance the positive effect of cannibalism on the prey density.

CANNIBALISTIC-MEDIATED INDIRECT INTERACTIONS BETWEEN JUVENILE PREDATORS AND PREY

First, I examine a scenario in which juvenile predators are on the same trophic level as the prey (Fig. 1A) to analyze the individual consequences of the cannibalistic (lethal) interaction between both predator stages on the dynamics of a simple predator–prey system. Such a scenario applies to species with a large size difference between stages or ontogenetic switch in diet, as for example, in newts (Kats et al. 1994), or species with egg cannibalism (Schellhorn and Andow 1999) or hyper- and/or autoparasitoids (Mills and Gutierrez 1996, Schreiber et al. 2001, Bogran and Heinz 2002). Consider a simple Rosenzweig-McArthur type predator–prey model including two predator stages, adults (P_A) and juveniles (P_J), and one prey species without size structure (N). In nature, cannibalism and predation

TABLE 1. Model parameter definitions.

Populations and parameters	Definition
Populations	
N	population density of prey
P_A	population density of cannibalistic adult predators
P_J	population density of non-cannibalistic juvenile predators
Parameters	
m	density-independent maturation rate coefficient
μ_A, μ_J	density-independent mortality rate of adult and juvenile predators, respectively
e_n, e_c	conversion efficiency for heterospecific and conspecific prey, respectively
δ	conversion efficiency for prey-dependent maturation rate of predators
a_n, α	density-independent predation coefficient of adult and juvenile predators on prey
a_c	density-independent cannibalism coefficient
T_n, T_c	handling time for prey and juvenile predators, respectively
r	maximum instantaneous growth rate of the prey
K	carrying capacity of the prey population
γ	coefficient for interference effect of adult predators on α
ε	coefficient for interference effect of adult predators on a_c

rates are generally dependent on the relative abundances of both conspecific and heterospecific prey due to the time spent on handling each prey type (Fox 1975*b*, Orr et al. 1990, Leonardsson 1991, Rudolf 2007*a*). We can introduce this handling effect by assuming a standard Holling type II functional response (Holling 1959), which yields the functional response of the predator consuming the prey type i: $g_i(N, P_J) = a_iN/(1 + T_na_nN + T_ca_cP_J)$. Predators attack prey and juvenile conspecifics at a rate a_n and a_c respectively, and spend the time T_n and T_c handling each respective prey type. From this formulation it becomes immediately clear that cannibalism creates a functional response that is also dependent on the abundance of the small-predator stage (a predator-dependent functional response; Abrams and Ginzburg 2000). Interestingly, similar predator-dependent functional responses were invoked independently by Beddington (1975) and DeAngelis et al. (1975), except that they assumed a nonlethal behavioral interference between predators rather than cannibalism. The difference between behavioral interference and cannibalism is that with cannibalism, the density-dependent mortality of the predator is stage-structured and also dependent on the density of the prey. The dynamics of such a system (Fig. 1A) are given by

$$\frac{dN}{dt} = rN\left(1 - \frac{N}{K}\right) - \frac{a_nP_AN}{1 + T_na_nN + T_ca_cP_J} \tag{1a}$$

$$\frac{dP_J}{dt} = P_A\frac{e_na_nN + (e_c - 1)a_cP_J}{1 + T_na_nN + T_ca_cP_J} - (m + \mu_J)P_J \tag{1b}$$

$$\frac{dP_A}{dt} = mP_J - \mu_AP_A. \tag{1c}$$

A general description of the model parameters and variables is given in Table 1. This model assumes a logistic growth rate for the prey to allow for a comparison to previous models that examined the effect of enrichment (Rosenzweig 1971). One reason why cannibalism differs from standard density-dependent mortality is that individuals are consumed when they are killed and this results in positive (energy gain) and negative (mortality) aspect of cannibalism simultaneously. In this model, the net gain or loss due to cannibalism (resulting from the interaction of killing and energy gain) is given by ($e_c - 1$), with e_c indicating the energy gained from cannibalism (i.e., eating conspecifics). Note, that the energy gained through cannibalism is thus preserved and directly converted into reproduction. In the following, I assume that $0 < e_c \leq 1$ to avoid the biologically unrealistic situation where the predator can increases indefinitely in the absence of prey (i.e., if $e_c > 1$, an adult predator produces more than one offspring for each offspring it kills). Thus, the model accounts for three main aspects that are typical for cannibalistic systems (Claessen et al. 2004): (1) killing and (2) consumption of conspecifics, and (3) stage-structured interactions. The two scenarios examined below (Eqs. 3 and 5) account additionally for (4) intraspecific competition.

Although the foraging function of juvenile predators is not modeled explicitly in this scenario, for the sake of clarity, this does not imply that juveniles are not eating. It only assumes that the maturation rate of juveniles is not dependent on the adult or juvenile density. This could for example be the case in systems in which juveniles are feeding on an exclusive abundant resource, which is common in organisms with complex life cycles which commonly exhibit a major diet shift between juvenile and adult stage (Wilbur 1980). Systems in which juvenile predators and prey compete for a limited resource are analyzed elsewhere in detail (Rudolf 2007*b*).

Short-term dynamics.—An inspection of Eq. 1 shows that both conspecific and heterospecific prey experience "short-term apparent mutualism" (sensu Holt and Kotler 1987) because of cannibalism: increasing the density of juvenile predators increases the instantaneous net growth rate of the prey and vice versa (i.e., [$\partial N/dt \times$

$1/N]/\partial P_J > 0$; $[\partial P_J/dt \times 1/P_J)/\partial N > 0)$. Note, that this is a consequence of the realistic type II functional response. This will not be the case with a linear functional response (i.e., T_n, $T_c = 0$) which assumes that both predation and cannibalism rates are independent of each other.

Long-term dynamics.—The predator can successfully invade under the conditions that $e_n a_n K/\mu_A(1 + T_n a_n K) - \mu_J/m > 1$ (Appendix A). This condition shows that cannibalism is irrelevant for the invasion of the predator (van den Bosch et al. 1988). The explicit formulas of prey and predator equilibrium are somewhat cumbersome. The general effects of cannibalism and relation between the prey and predator densities, however, can be inferred from the isoclines of the prey and juvenile predators, respectively:

$$P_A = \frac{\left(1 - \frac{N}{K}\right)\frac{r}{a_n}(1 + T_n a_n N)}{1 - \left(1 - \frac{N}{K}\right) r\lambda \frac{a_c}{a_n} T_c} \tag{2a}$$

$$N = \frac{a_c(1 - e_c)\lambda P_A + (\mu_A + \mu_J\lambda)(1 + T_c a_c \lambda P_A)}{a_n[e_n - (\mu_A + \mu_J\lambda)T_n]} \tag{2b}$$

with the common factor $\lambda = \mu_A/m$. Eq. 2a is a parabola in N, while Eq. 2b is a straight line in P_A (Appendix B). Eqs. 2a and b imply that at relatively low prey density at equilibrium (i.e., as long as both isoclines intersect before the hump of the parabola), low cannibalism rates (a_c) can increase the predator population at equilibrium even if the energy gained from cannibalism is less than one (Appendix B). The range of cannibalism rates over which this positive effect occurs strongly increases with increasing energy gained from both prey types (e_c, e_n) and increasing attack rate on heterospecific prey (a_n).

Eqs. 2a and b also imply that increasing cannibalism rates (a_c) generally increases the prey equilibrium (Appendix B). This positive long-term effect of cannibalism on the equilibrium prey density is largely due to two terms in Eq. 2b. The positive effect of the first term, $a_c(1 - e_c)\lambda P_A$ is expected since it increases predator mortality. The positive effect of cannibalism in the second term, $T_c a_c \lambda P_A$, is a result of the indirect interaction between juvenile predators and prey created by cannibalism. It represents the time adult predators spend handling conspecifics, which reduces the predation rate on the heterospecific prey. The time predators spend handling both conspecific and heterospecific prey (T_c, T_n) has a positive effect on both predator and prey steady states as they reduce the overall maximal consumption rate of the predator. This means that cannibalism creates a positive long-term indirect effect between juvenile predators and the prey population.

Without cannibalism ($a_c = 0$) the prey equilibrium reduces to $\hat{N} = (m + \mu_J)\mu_A/a_n[e_n m - T_n\mu_A(m + \mu_J)]$, which indicates that the prey equilibrium does not increase with enrichment (i.e., increase in r or K; Fig. 2). However, with cannibalism in the system it can be shown from Eqs. 2a and b that any factor that increases the prey growth rate, r, or carrying capacity, K (i.e., enrichment of the prey resource), will increase both the predator density and the prey density (Fig. 2).

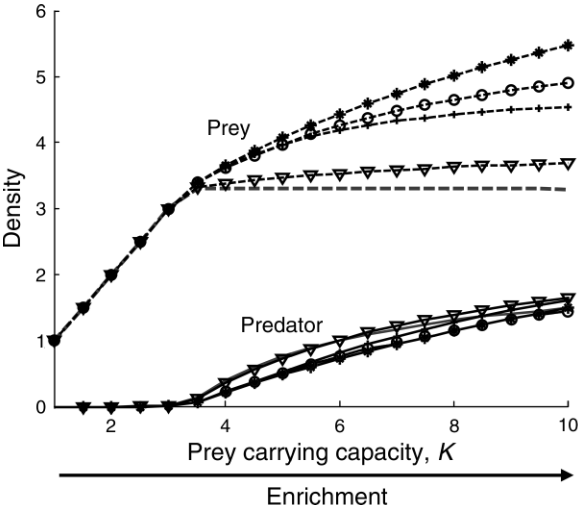

FIG. 2. Effect of enrichment (increase in the prey carrying capacity, K) on total predator (adults + juveniles) and prey equilibrium densities for systems where both predator stages consume the prey (Fig. 1C). Without cannibalism or direct behavioral interaction between predator stages (lines without symbols, a_c, γ, $\varepsilon = 0$); cannibalism only (open circles; $a_c = 0.5$, γ, $\varepsilon = 0$); behavioral interference only (open triangles; $a_c = 0$, $\gamma = 0.5$, $\varepsilon = 0.3$); and both cannibalism (asterisks; $a_c = 0.5$; $\gamma = 0.5$, $\varepsilon = 0.3$) and behavioral interference (plus signs; $a_c = 0.5$; $\gamma = 0.5$, $\varepsilon = 1.5$). The respective patterns are similar for the scenarios without juvenile predation. The other parameters were held constant at $r = 0.4$, $a_n = 0.4$, $e_n = e_c = 0.5$, $\alpha = 0.3$, $T_c = T_n = 0.8$, $m = 0.3$, $\mu_A = 0.2$, and $\mu_J = 0.1$. Parameters are defined in Table 1.

Extensive numerical simulations examining the long-term population dynamics over a large parameter space show that an increase in prey carrying capacity (K) and higher heterospecific attack rate (a_n) tends to destabilize the system while cannibalism (a_c) strongly increases the area of parameter space in which the system will return to a stable equilibrium after small perturbations (Fig. 3A shows a representative scenario). Increasing the handling time for heterospecific prey, T_n, reduces the stability region as expected from simpler models (Oaten and Murdoch 1975). However, T_c, the time spend handling conspecifics, has the opposite effect and increases the stability region of the system.

ADULT AND JUVENILE PREDATORS SHARE A PREY

Small predators sometimes share a prey with cannibalistic conspecifics (Persson et al. 2000, Rudolf 2006). This is often the case if the small stage is mobile and similar enough in their diet and ecology, such as in stream salamanders (Rudolf 2006), fish (Persson et al. 2000, Rettig and Mittelbach 2002), or arthropods (Polis 1984, Briggs et al. 2000). With cannibalism, this results in three distinct functional trophic levels: adult preda-

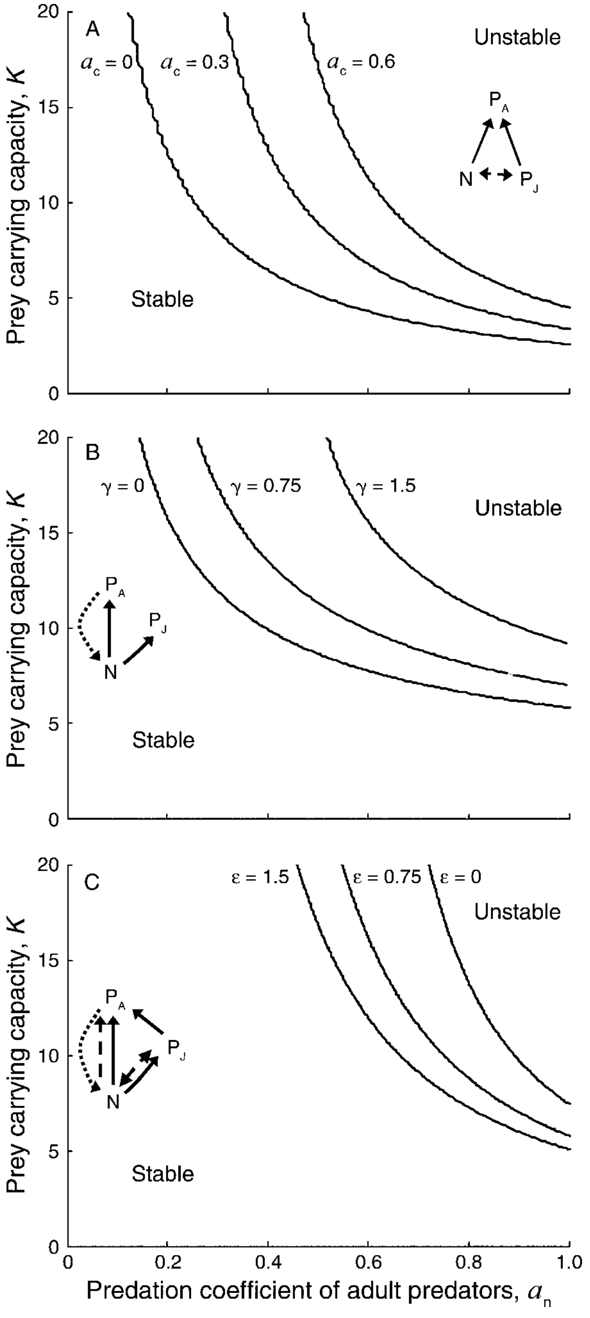

FIG. 3. Effect of carrying capacity (K) and predator attack rate (a_n) on the stability of different stage-structured predator–prey systems. In each panel, each curve identifies the demarcation in parameter space between stable equilibrium and unstable dynamics (oscillations) for various values of the parameter of interest. For systems in which only adult predators consume prey N, panel (A) shows the effects of cannibalism (Eq. 1, Fig. 1A). For systems in which both predator stages consume the common prey (N), panel (B) shows the behavioral interaction effect on predation rate of juvenile predators (Eq. 3, Fig. 1B), and panel (C) shows the behavioral interaction effect on the cannibalism rate of the predator (Eq. 5, Fig. 1C) ($\gamma = 0.5$, $a_c = 0.5$). Note that, for ease of comparison, panel (B) is shown with handling time added to Eq. 3. The stability plot corresponding to Eq. 3 without handling time is given in Appendix E. In panels (A) and (C), $\alpha = 0.3$. All other parameters were held constant at $T_n = T_c = 0.8$, $r = 0.4$, $\delta = 0.03$, $\mu_A = 0.2$, $\mu_J = 0.1$, and $e_n = e_c = 0.5$. Parameters are defined in Table 1.

tors, juvenile predators, and prey (Fig. 1B, C). To include predation by juvenile predators (P_J), the basic model (Eqs. 1a–c) can be extended by subtracting the mortality term $P_J\alpha(N, P_A, P_J)$ from the prey growth rate in Eq. 1a, with $\alpha(N, P_A, P_J)$ representing the functional response of juvenile predators. In such a system, both cannibalistic (lethal), and behavioral (i.e., behavior-mediated avoidance of cannibalism) interactions between predator stages are possible and can indirectly impact the prey population (Fig. 1C).

Behavior-mediated indirect interactions between adult predator and prey

First, I use this system to explore the individual effects of the behavioral avoidance of cannibalism in the predator on the predator–prey dynamics. Thus, to isolate the behavioral effects from the confounding lethal effects of cannibalistic interactions, cannibalism is eliminated by setting the cannibalism rate $a_c = 0$. Consequently, in this scenario juveniles respond behaviorally to adult predators, but adult predators are not "allowed" to cannibalize conspecifics.

Due to the risk of cannibalism, the presence and density of large predators commonly alters the behavior of small conspecifics, leading to a reduction of the predation rates of small predators (P_J) in proportion to the density of adult predators (P_A) given by $\alpha(N, P_A, P_J) = \alpha\beta(P_A)N$. The maximum attack rate of juvenile predators in the absence of adult conspecifics is given by α, and it decreases by $\beta(P_A)$ in the presence of adult predators, with the assumption that $0 < \beta(P_A) \leq 1$ and $d\beta/dP_A < 0$. Previous work (Krivan and Schmitz 2004) suggests that in three-species systems, $\beta(P_A)$ can be approximated by an exponential function, $\beta(P_A) = e^{-\gamma P_A}$, with γ indicating the strength of the behavioral effect of adults on juvenile predation rates.

If juvenile predators have no opportunity to compensate for this reduction in foraging activity, the behavioral response will also reduce their growth rate and thereby may increase the time to maturity (Rudolf 2006). Thus, the maturation rate, m, can indirectly be negatively affected by the density of adult predators. In the simplest scenario, the maturation rate is proportional to the number of consumed prey by some energy conversion coefficient, δ, and the maturation rate is given by $m = \alpha e^{-\gamma P_A}\delta N$. At low densities of adult predators ($P_A \approx 0$), juveniles mature at the maximum rate $\alpha N\delta$ which decreases with increasing adult density. If $\gamma = 0$, the maturation rate is not directly affected by adult predators, which could be the case if, for example, juveniles switch to another exclusive food resource, or if

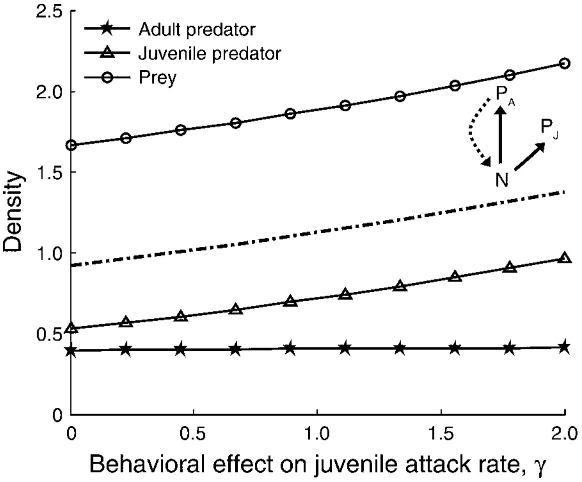

FIG. 4. Population densities in relation to the strength of the negative behavioral effect of adult predators on the attack rate of juvenile predators, γ. The line without symbols indicates the total predator population (adults plus juveniles). In this scenario, both adult and juvenile predators consume the common prey. Juvenile predators respond behaviorally to the presence of adult predators, but cannibalism is prevented in this scenario ($a_c = 0$; Fig. 1B). The other parameters are held constant at $r = 0.4$, $K = 8$, $a_n = 0.4$, $e_n = 0.5$, $\alpha = 0.3$, $\delta = 0.3$, $\mu_A = 0.2$, and $\mu_J = 0.1$. Parameters are defined in Table 1.

they move to habitats without adult conspecifics. For simplicity, I only present the analytical results without predator satiation (i.e., T_n, $T_c = 0$), since a detailed numerical analysis showed that the general effects of the behavioral interaction are qualitatively similar with satiation (compare Figs. 3 and 4; Appendices D and E) but can be illustrated analytically much clearer in the simpler model. The predator–prey dynamics are given by

$$\frac{dN}{dt} = rN\left(1 - \frac{N}{K}\right) - a_n P_A N - \alpha e^{-\gamma P_A} N P_J \tag{3a}$$

$$\frac{dP_J}{dt} = P_A e_n a_n N - (\alpha e^{-\gamma P_A} \delta N + \mu_J) P_J \tag{3b}$$

$$\frac{dP_A}{dt} = \alpha e^{-\gamma P_A} \delta N P_J - \mu_A P_A. \tag{3c}$$

Short-term dynamics.—It follows from the formulation of Eq. 3a that increasing the interference between predator stages increases the short term growth rate of the prey by decreasing the total prey mortality. An increase in adult predator density, P_A, has a short-term positive effect on the prey growth if $(\partial(g+h)/\partial P_A)/N < 0$ (with $g = a_n P_A$, $h = \alpha e^{-\gamma P_A} P_J$), which is only true if $\gamma \alpha e^{-\gamma P_A} P_J > a_n$. In other words, it is only true if the product of the total mortality imposed by juvenile predators and the interference effect exceeds the predation rate of adults. This effect is strongest at low densities of adult predators and high densities of juvenile predators.

Long-term dynamics.—If the invasion conditions are met (Appendix A), the biologically relevant (i.e., $N \geq 0$) isoclines for the prey and juvenile predators are given by

$$P_A = \left(1 - \frac{N}{K}\right) \frac{r}{a_n + \mu_A (N\delta)^{-1}} \tag{4a}$$

$$N = \frac{1}{2}\left[\frac{\mu_A}{e_n a_n} + \sqrt{\left(\frac{\mu_A}{e_n a_n}\right)^2 + 4\frac{\mu_A \mu_J}{e_n a_n \delta \alpha} e^{\gamma P_A}}\right]. \tag{4b}$$

Eq. 4a is a humped-shaped function of N while Eq. 4b is an increasing function in P_A (Appendix C). Eqs. 4a and b imply that when small stages of the predator behaviorally avoid cannibalism, this can have a positive long-term effect on the prey abundance, but only if this interaction effect reduces the maturation rate of the predator (i.e., if the maturation rate is a negative function of P_A) (Fig. 4, Appendix C). The reason for this is that in this scenario, the prey partly benefits from a higher adult predator density because it decreases the recruitment rate of the juvenile predators into the reproductive adult stage. A stronger interference effect (γ) on the maturation rate has a positive effect on the prey equilibrium (Eqs. 4a and b, Fig. 4). Thus, the behavioral avoidance of cannibalism in the predator can result in a positive indirect long-term effect on the prey population, but only if the maturation rate is also affected by the behavioral interaction. Any factor that increases the maturation rate of the predator (i.e., increase in δ, α) reduces the magnitude of the positive effect of the behavioral interference for the prey density. Adding a type II functional response ($T_n > 0$) does not alter this pattern (Appendix D).

The behavioral avoidance of cannibalism, γ, can have a positive or a negative effect on the predator equilibrium depending on whether the predator isocline intersects before or after the hump with the prey isocline, respectively (Appendix C). Thus, factors that shift the hump of the prey isocline to the right (e.g., increase in prey carrying capacity, K) or the predator isocline to the left (e.g., decrease in predator mortality) will promote the positive effect of γ on the predator equilibrium density. The positive effect of γ on the predator density occurs as long as the resulting gain in offspring production (due to the decreases in the competition between adult and juvenile predators) exceeds the loss in offspring production (due to reduced maturation rates of juveniles).

In the presence of behavioral avoidance of cannibalism ($\gamma > 0$), enrichment of the system (i.e., increase in r or K) will result in an increase of *both* the prey and the predator equilibrium densities (Eqs. 4a and b, Fig. 2). If the maturation rate is independent of the adult predator density ($\gamma = 0$), only the predator density will increase with enrichment while the prey density remains constant. Numerical simulations showed that enrichment of the system eventually destabilizes the dynamics but only at very high values of K. This is a result of the stage-structured interaction in the predator. Similar to cannibalism, increasing the strength of the behavioral interference (γ) on the attack rate of juvenile predators will further increase the size of the stability region (Appendix E). Introducing a type II response generally decreases the stability of the system and slightly alters the shape of the stability region, but does not alter the general stabilizing effect γ (Fig. 3B). All general behavioral effects on the predator–prey system are robust and hold true even if the maturation rate is constant and independent on the prey density.

Interaction of cannibalism- and behavior-mediated indirect effects

In the final scenario, I allow cannibalism and behavior-mediated avoidance of cannibalism to be present simultaneously (Fig. 1C) to determine their combined impact on the predator–prey system and how both interaction types affect each other. Because we now allow for cannibalism in this scenario (i.e., $a_c > 0$), we first need to account for the fact that when juvenile predators alter their foraging behavior to avoid cannibalistic conspecifics this will necessarily also reduce the risk of being cannibalized. It is reasonable to assume that this decrease in cannibalism rates is proportional to the decreases in the functional response of the small predators: $a_c := a_c e^{-\varepsilon P_A}$ (Krivan and Schmitz 2004). The combined predator–prey model including both density- and trait-mediated indirect interactions can be written as

$$\frac{dN}{dt} = rN\left(1 - \frac{N}{K}\right) - \frac{a_n P_A N}{1 + T_n a_n N + T_c a_c e^{-\varepsilon P_A} P_J} - \frac{\alpha e^{-\gamma P_A} N P_J}{1 + T_n \alpha e^{-\gamma P_A} N} \tag{5a}$$

$$\frac{dP_J}{dt} = P_A \frac{e_n a_n N + (e_c - 1) a_c e^{-\varepsilon P_A} P_J}{1 + T_n a_n N + T_c a_c e^{-\varepsilon P_A} P_J} - \left(\frac{\alpha e^{-\gamma P_A}}{1 + T_n \alpha e^{-\gamma P_A} N} \delta N + \mu_J\right) P_J \tag{5b}$$

$$\frac{dP_A}{dt} = \frac{\alpha e^{-\gamma P_A}}{1 + T_n \alpha e^{\gamma P_A} N} \delta N P_J - \mu_A P_A. \tag{5c}$$

Short-term dynamics.—From the term $T_c a_c e^{-\varepsilon P_A} P_J$ in Eq. 5a, we can see that now the short-term effect of behavioral interference on cannibalism rates (ε) reduces the short-term apparent mutualism between juvenile predators and prey in the adult predation term (see Eq. 2) because it reduces the time adult predators spend handling conspecific prey. Depending on the strength of cannibalism (a_c) relative to the predation rate of juvenile predators (α), increasing the juvenile density can either have a positive or negative short-term effect on the growth rate of the prey. The general qualitative effects of cannibalism (a_c) and the effect of behavioral interference on juvenile consumption rate (γ) on the equilibrium population size and stability regions are similar to the models explored above.

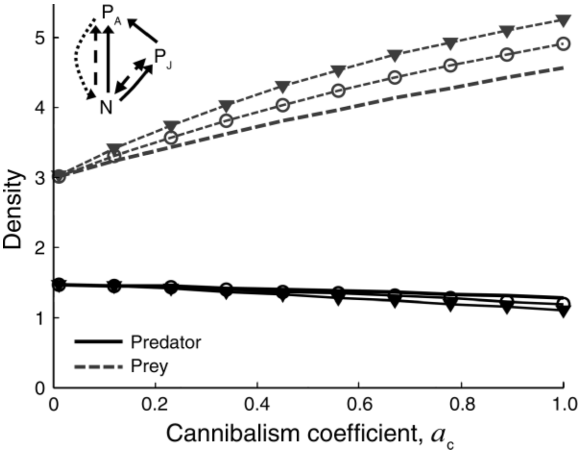

FIG. 5. Indirect effect of cannibalism for three different relations of the two behavioral interference coefficients γ (negative effect on per capita predation rate of juvenile predators) and ε (negative effect on per capita cannibalism rate): $\gamma - \varepsilon > 0$ (solid triangles); $\gamma - \varepsilon = 0$ (open circles); $\gamma - \varepsilon < 0$ (no symbol). For the respective combinations, $\varepsilon = 0.1$, 0.5, and 0.9. In all scenarios, both adult and juvenile predators share the common prey (Fig. 1B, C). The other parameters were held constant at $r = 0.4$, $K = 8$, $a_n = 0.4$, $e_n = e_c = 0.5$, $\alpha = 0.3$, $T_c = T_n = 0.8$; $\delta = 0.3$, $\mu_A = 0.2$, $\mu_J = 0.1$, and $\gamma = 0.5$. Parameters are defined in Table 1.

Long-term dynamics.—When focusing on the behavioral avoidance of cannibalism it becomes clear that increasing the behavioral avoidance effect on cannibalism rates (ε) will have a negative long-term effect on the prey equilibrium (Fig. 5). The reason for this is that ε decreases cannibalism rates, and thus also decreases the positive cannibalism- (lethal) mediated indirect effect of juvenile predators on the prey. This long-term effect of ε increases with higher cannibalism rates (Fig. 5). In general, numerical simulation showed that increasing ε tends to decrease the stability region (Fig. 3C).

The combined effect of behavioral and cannibalism-mediated interactions between predator stages on the prey population is largely determined by how strong the behavioral interaction affects the predator maturation rate (i.e., γ) compared to the effect on the cannibalism rate (i.e., ε). It can be shown from Eqs. 5a–c that if $\gamma > \varepsilon$, then the behavioral interference will enhance the indirect positive long-term effect of cannibalism on the prey equilibrium (Fig. 5 shows a representative example). However, if $\gamma < \varepsilon$, then the behavioral interference between predator stages will reduce the positive long-term effect of cannibalism (Fig. 5). The magnitude of these effects increases at higher maturation rates (i.e., larger δ). The positive effect of cannibalism rates on the predator equilibrium density is strongly reduced with

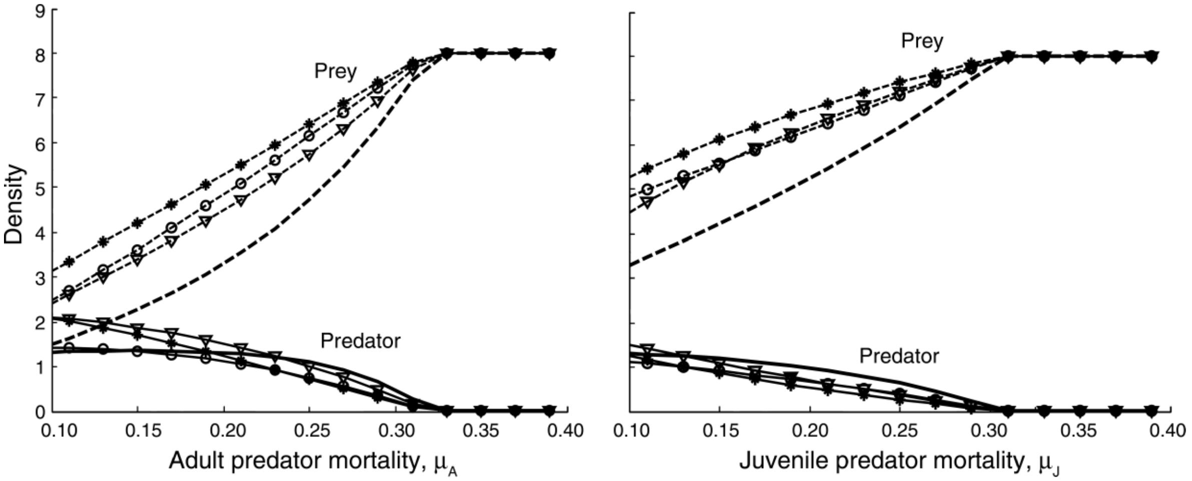

FIG. 6. Effects of changes in adult and juvenile predator mortality on prey and total (juvenile + adult) predator equilibrium densities for systems without predator interaction, i.e., no cannibalism or behavioral interaction between stages (lines without symbols, a_c, γ, $\varepsilon = 0$); systems with cannibalism only (open circles; $a_c = 0.5$, γ, $\varepsilon = 0$); systems with behavioral interference only (triangles; $a_c = 0$, γ, $\varepsilon = 1.5$); and systems with both cannibalism and behavioral interference (asterisks; $a_c = 0.5$; γ, $\varepsilon = 1.5$). In all scenarios, both adult and juvenile predators consume the common prey, N (Fig. 1B, C). All other parameters were held constant at $K = 8$, $r = 0.4$, $a_n = 0.4$, $e_n = e_c = 0.5$, $\alpha = 0.3$, $T_c = T_n = 0.8$, $\delta = 0.3$, $\mu_A = 0.2$, and $\mu_J = 0.1$. Parameters are defined in Table 1.

increasing attack rate (α) of small predators and disappears with increasing behavioral interference.

If both behavioral avoidance of cannibalism and cannibalism are present, enrichment generally results in a stronger increase in prey abundance but reduced the predator abundance at equilibrium compared to systems with only one interaction type (Fig. 2). The behavioral interaction reduces the effect of enrichment on the prey equilibrium but increases the predator equilibrium compared to systems with cannibalism only if $\gamma < \varepsilon$ (Fig. 2), in other words, if adult predators have a much stronger impact on the behavior and development of their conspecific than on their heterospecific prey.

The two positive indirect interactions between predator stages and prey also alter the effect of changes in predator mortality on equilibrium prey density. Increasing juvenile or adult predator mortality has a smaller long-term effect on prey density with cannibalism or behavioral avoidance of cannibalism, especially at high predator mortalities (Fig. 6 shows a representative example). Increasing the mortality of adult predators (μ_A) has by far the smallest effect on prey density when both interaction types are present (Fig. 6). The positive effect of increasing predator mortality on the predator density expected for predators with saturating functional response, an allee effect, is strongly reduced or eliminated by cannibalism and disappears in the presence of behavioral interactions.

DISCUSSION

The theoretical predictions derived here suggest that size-structured cannibalism and behavioral avoidance of cannibalism in a stage-structured predator can create short- and long-term positive indirect interactions between different predator stages and their prey. Such indirect interactions can increase a system's stability and alter the strength of trophic cascades and as a consequence the dynamics of the system are driven by the interaction of bottom-up and top-down effects. These results emphasize the importance of incorporating stage-structured interactions within and among populations in community ecology.

Behavioral and lethal consequences of cannibalism

Similar to multiple species systems, the interactions between size-structured populations are complex and there are many ways in which a size-structured predator and its prey can interact. This study examined three scenarios that differed in the life history of the species and the size-structured interactions. The general patterns that result from the lethal effects of cannibalism were robust to changes in the interactions of juvenile predators and prey. Thus the results should apply to a variety of different predator–prey systems. One of the important differences between the different scenarios, however, was the difference in the presence or absence of behavioral avoidance of cannibalism. There are several types of cannibalism in natural populations and the specific form will determine if there are behavior-mediated consequences of cannibalism. For example in systems with egg cannibalism (Schellhorn and Andow 1999, Cottrell 2005) or when cannibalism results from hyper- or autoparasitism (Mills and Gutierrez 1996, Hunter et al. 2002), conspecific victims are immobile and will thus not respond behaviorally to the presence of cannibals. In such systems it will be sufficient to focus on the lethal effects of cannibalism to predict the dynamics of predator–prey systems. However, in systems where small individuals are mobile they generally alter their behavior in response to conspecifics as observed in a variety of species including isopods, fish, insects, chameleons, and stream salamanders (Sih 1982, Leonardsson 1991, Persson and Eklov 1995, Biro et al. 2003, Keren-Rotem et al. 2006, Rudolf 2006). If this behavioral change also reduces feeding rates, this change in behavior often has negative effects on developmental rates of conspecific victims (Murdoch and Sih 1978, Ziemba and Collins 1999, Taylor et al. 2001, Rudolf 2006). This is likely to be the case if small individuals increase their refuge use or reduce their overall foraging activity in the presence of cannibals (Van Buskirk 1992, Claus-Walker et al. 1997, Rudolf 2006). However, if individuals can compensate for the reduced consumption rate, for example when small individuals shift to new habitats with alternative resources (Persson and Eklov 1995, Biro et al. 2003, Bystrom et al. 2003, Keren-Rotem et al. 2006), their developmental rates might be unaffected. In this case, the change in behavior will alter the predation rates, but might not affect developmental rates (Persson and Eklov 1995). The present study indicates that it is not only important to account for the lethal effects of cannibalism, but that it is equally important to determine and account for the consequences of the behavioral responses to cannibalism to reliably predict the dynamics of such predator–prey systems. Neglecting these behavioral effects can lead to qualitatively and quantitatively erroneous predictions on how environmental influences or anthropogenic disturbances affect the dynamics and structure of communities.

Stage-structured indirect interactions

There is increasing evidence that size-structured indirect interactions have important consequences for the dynamics of communities. For example, the strength of competitive interactions within and between stages can be altered via indirect size-structured interactions (Hamrin and Persson 1986, Persson and Greenberg 1990, Yasuda et al. 2004). The results presented here show that stage-structured cannibalism can create a positive indirect interaction between juvenile predators and heterospecific prey comparable to "apparent mutualism" (Holt 1977). Similarly, adult predators were also found to have an indirect positive effect on the prey abundance mediated through behavioral interference with juvenile conspecifics. Thus, the model predicts that both direct interaction types between predator stages can result in positive short-term (i.e., within generation) and long-term indirect effects on the prey. This is consistent with the dynamics observed in several laboratory and field experiments that demonstrate that such short- and long-term positive indirect effects can result from the interaction between predator stages on prey survival (Sih 1981, Leonardsson 1991, Persson et al. 2003, Crumrine 2005, Rudolf 2006). These positive indirect interactions counteract the general negative effects of the predator on the prey density. Consequently, they strongly alter the dynamics of food webs by changing the effect of trophic cascades. This demonstrates the strong impact of size-structured cannibalism on the dynamics of communities.

While the basic mechanisms creating the "apparent mutualism" between conspecific and heterospecific prey are similar to three species systems (i.e., reduction in predation/cannibalism rates), the long term population dynamics of the system differ between cannibalistic and three-species system. The reason for this is that conspecific prey and predator have coupled dynamics through growth transition and reproduction. In three-species systems, decreasing the natural mortality rate of the alternative prey can decrease the mortality and thus density of the other prey species (Abrams and Matsuda 1996). In contrast, while cannibalism has a general positive effect on the heterospecific prey mortality, decreasing the natural mortality rate of conspecific prey will not lead to a long term decrease in the mortality rate of the heterospecific prey.

The mechanisms underlying the positive indirect effects of adult predators on the prey are similar to three-species systems where positive indirect interactions between a predator and its prey arise when a predator consumes or behaviorally reduces the predation rate of another predator species (Soluk and Collins 1988, Crumrine and Crowley 2003, Vance-Chalcraft and Soluk 2005). Interestingly, despite the fact that both predator stages belong to the same species, size-structured cannibalism and the behavioral avoidance of cannibalism in a predator can result in long-term dynamics that are somewhat analogous to predatory interactions in three-species food chains (Abrams et al. 1996, Krivan and Schmitz 2004), with the difference that only two species are involved. However, unlike in three-species systems, the effect of behavioral avoidance of cannibalism in the predator completely depends on the behavioral effect on the maturation rate of the predator. If the maturation rate is not affected, behavioral interactions that only affect the juvenile attack rate have no effect on the prey density or trophic cascades because the equilibrium density of the prey is independent of the attack rate of juvenile predators. This is consistent with previous theoretical studies in size-structured systems that have demonstrated the importance of density-dependent effects on developmental rates for population and community dynamics (reviewed in de Roos et al. 2003).

Another novel finding of this study is that when both interaction types act simultaneously the behavioral effect of adult predators on juvenile predators will always reduce the positive short-term effect of juvenile predators on the prey but is likely to enhance the positive cannibalism-mediated effects on the long term if the maturation rate is affected. This suggests that predictions made on short term experiments where both interactions are not estimated separately are likely to make erroneous predictions about the long-term effects (e.g., Leonardsson 1991, Gerber and Echternacht 2000, Crumrine 2005, Finke and Denno 2006). It has been shown in three or more species systems that behavior-mediated indirect interactions can either enhance or reduce the effect of density-mediated interactions (Peacor and Werner 1997, Crumrine and Crowley 2003, Krivan and Schmitz 2004). This study suggests for the first time that a similar relationship of behavioral and lethal effects of cannibalistic interactions between predator stages can be expected in two species systems, but that enhancement is more likely. It will be interesting to extend the present analysis to more detailed individual based models that explicitly account for the specific size changes and energetic of size-structured interactions (de Roos and Persson 2001). In general the results presented here show that size-structured interactions lead to dynamics that can differ profoundly from unstructured models without cannibalism. This suggests that some of the classical concepts derived from those unstructured models cannot be applied to predict the dynamics of natural communities in which size-structured cannibalism is very frequent (Polis 1981, Persson 1999, Woodward and Hildrew 2002, Woodward et al. 2005*b*).

Top-down and bottom-up cascades in size-structured system

Classical food web theory predicts that adjacent trophic levels should not be positively correlated across a productivity gradient (Oksanen et al. 1981, Leibold et al. 1997). However, this prediction is often not met in natural systems in which both trophic levels frequently increase with increasing productivity (McQueen et al. 1986, Ginzburg and Akcakaya 1992, Leibold et al. 1997). To overcome this inconsistency of data and theory, recent studies have incorporated more realism into the simple models (Ginzburg and Akcakaya 1992, Abrams 1993, Leibold 1996, Krivan and Schmitz 2004, Vos et al. 2004). However, the importance of intraspecific stage structure within populations has received relatively little attention despite its omnipresence in food webs. Here I show that intraspecific interactions between stages of a predator provide a simple mechanism that could also explain the observed positive correlation between both predator and prey.

The effect of cannibalism in this study is expected and consistent with previous models of cannibalism (Kohlmeier and Ebenhoh 1995, van den Bosch and Gabriel 1997). However, this is the first study to demonstrate that the behavioral avoidance of cannibalism can create a similar positive correlation if the change in behavior affects the developmental rate of the predator. Different species within a trophic level often vary considerably in the degree of cannibalism and the spatial or temporal overlap of stages (Polis 1981, Gerber and Echternacht 2000, Rudolf 2007*a*) and therefore also differ in the interaction strength between stages. This study suggests that such species-specific differences in the strength of stage-structured interactions between predator stages and prey could explain the variation in the strength of trophic cascades found across food webs (Leibold et al. 1997, Schmitz et al. 2000).

Stage-structured cannibalism creates at least two distinct functional groups (cannibals and victims) and thus increases the functional and trophic (structural) diversity within the predator–prey system. In multispecies systems, such an increase in species diversity within and among trophic levels alters the dynamics of the system (Abrams 1993, Leibold 1996). This poses the questions to whether the effects of size-structured interactions simply results from separating the predator into different stages. Chase (1999) showed that allowing the prey to grow into an invulnerable size class can alter the effect of enrichment and result in an increase in both predator and prey densities. A similar response was observed when part of the prey population showed a predator-induced defense creating two different groups within the prey population (Vos et al. 2004). However, in the present study and a comparable one (e.g., Mylius et al. 2001), simply separating the predator population into different stages did not alter the effect of enrichment in the absence of intraspecific interactions. Thus, it is the functional diversity resulting from cannibalism and stage-structured interactions that creates the observed positive correlation between the predator and prey density across a productivity gradient.

While there are other mechanisms that can contribute to this positive correlation of predator and prey abundance, stage-structured intraspecific interactions are highly frequent in most organisms (e.g., Fox 1975*a*, Polis 1981, Persson 1988, Persson et al. 2000, Yasuda et al. 2001, Woodward and Hildrew 2002, Biro et al. 2003, Woodward et al. 2005*b*, Keren-Rotem et al. 2006), and the results presented here suggest that they can explain this positive correlation. Indeed, it is interesting to note that most studies that record a positive correlation between adjunct trophic levels were carried out in aquatic food webs (Ginzburg and Akcakaya 1992, Leibold et al. 1997). In aquatic food webs, the majority of species have distinct size classes and cannibalism is very common at different trophic levels. For example, in one of the few sufficiently detailed studies that reports a positive correlation between adjunct trophic levels of fish, zooplankton, and phytoplankton, all of the 10 fish species examined were cannibalistic, and a significant part of the zooplankton biomass were also cannibalistic species (Mills and Schiavone 1982). Furthermore, it has been shown that small fish commonly change their behavior in response to larger conspecifics (Persson and Eklov 1995, Biro et al. 2003). Besides giving valuable new insights into the dynamics of natural communities, these results are especially important for applied management of natural systems because they demonstrate that we cannot ignore the size-structured interactions within species if we want to predict how environmental influences such as enrichment or anthropogenic harvesting affect the dynamics and structured of natural communities.

Stage-structured interactions and the stability of food webs

Classical models predict that increasing the productivity of predator–prey systems will destabilize the population dynamics (i.e., "paradox of enrichment" [Rosenzweig 1971]). While there is some support for this effect in laboratory experiments (e.g., Luckenbill 1974, Bohannan and Lenski 1997), it is hardly ever observed in nature (Jensen and Ginzburg 2005). There is increasing evidence that size-structured interactions strongly influence how communities respond to enrichment (see de Roos et al. [2003] for a review). For example, Abrams and Quince (2005) showed that with a stage-structured prey, increasing prey growth can increase the stability of a two-species system. In three-species systems with intraguild predation, separating a predator population into a predatory and non-predatory stage increases the stability region of a three-species system along a productivity gradient (Mylius et al. 2001). In the models presented here, increasing productivity also tends to destabilize stage-structured predator–prey systems, but increasing cannibalism strongly stabilizes the system. While there are examples where cannibalism can destabilize population dynamics (Claessen et al. 2004), the observed stabilizing effect is in agreement with previous comparable predator–prey models (Kohlmeier and Ebenhoh 1995, van den Bosch and Gabriel 1997, Claessen et al. 2000, Schreiber et al. 2001). This prediction is also consistent with experimental studies in which protozoan food webs with cannibalistic predators were more stable than systems with non-cannibalistic predators (Holyoak and Sachdev 1998). An interesting novel finding of this study is that the behavioral avoidance of cannibalism in a stage structured predator can also strongly decrease the destabilizing effect of enrichment. Thus, since both cannibalism and the corresponding behavioral interactions often cooccur, such direct stage-structured interactions between stages should strongly stabilize food webs, and counteract any potential destabilizing effects resulting from competition between cohorts (de Roos et al. 2003). In turn, this also means that any factor that alters the abundance of the cannibalistic stage of the predator population (e.g., through invasive predators or anthropogenic harvesting) can have profound impacts on the stability of the community.

Conclusions

Recent studies have demonstrated that the dynamics of size-structured systems are often fundamentally different from predictions of simple models of homogeneous populations (Chase 1999, de Roos et al. 2003, Abrams and Quince 2005). However, despite the omnipresence of size-structured interactions, their impacts for community dynamics are still poorly understood (e.g., Woodward et al. 2005*a*). The present study shows that we need to account for intraspecific interactions between predator stages if we want to make reliable predictions on how communities respond to natural or human generated environmental influences. To date, most data on food webs simply record the number of individuals within a species. Yet, there is increasing evidence that we need data on the size- or stage-structure within a population and the specific size-structured interactions within and across species. Incorporating this information will greatly improve our understanding of how differences in life histories and intraspecific processes in predators determine the dynamics of predator–prey interactions and natural communities.

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LITERATURE CITED

Abrams, P. A. 1993. Effect of increased productivity on the abundances of trophic levels. American Naturalist 141:351–371.

Abrams, P. A., and L. R. Ginzburg. 2000. The nature of predation: prey dependent, ratio dependent or neither? Trends in Ecology and Evolution 15:337–341.

Abrams, P. A., and H. Matsuda. 1996. Positive indirect effects between prey species that share predators. Ecology 77:610–616.

Abrams, P. A., B. A. Menge, and G. G. Mittelbach. 1996. The role of indirect effects in food webs. Pages 371–395 *in* G. A. Polis and K. O. Winemiller, editors. Food webs: integration of patterns and dynamics. Chapman and Hall, New York, New York, USA.

Abrams, P. A., and C. Quince. 2005. The impact of mortality on predator population size and stability in systems with stage-structured prey. Theoretical Population Biology 68: 253–266.

Beddington, J. R. 1975. Mutual interference between parasites or predators and its effect on searching efficiency. Journal of Animal Ecology 44:331–340.

Biro, P. A., J. R. Post, and E. A. Parkinson. 2003. From individuals to populations: prey fish risk-taking mediates mortality in whole-system experiments. Ecology 84:2419–2431.

Bogran, C. E., and K. M. Heinz. 2002. Host selection by the heteronomous hyperparasitoid *Encarsia pergandiella*: multiple-choice tests using *Bemisia argentifolii* as primary host. Entomologia Experimentalis et Applicata 103:11–21.

Bohannan, B. J. M., and R. E. Lenski. 1997. Effect of resource enrichment on a chemostat community of bacteria and bacteriophage. Ecology 78:2303–2315.

Bonsall, M. B., and M. P. Hassell. 1997. Apparent competition structures ecological assemblages. Nature 388:371–373.

Briggs, C. J., S. M. Sait, M. Begon, D. J. Thompson, and H. C. J. Godfray. 2000. What causes generation cycles in populations of stored-product moths? Journal of Animal Ecology 69:352–366.

Bystrom, P., L. Persson, E. Wahlstrom, and E. Westman. 2003. Size- and density-dependent habitat use in predators: consequences for habitat shifts in young fish. Journal of Animal Ecology 72:156–168.

Chase, J. M. 1999. Food web effects of prey size refugia: Variable interactions and alternative stable equilibria. American Naturalist 154:559–570.

Claessen, D., A. M. de Roos, and L. Persson. 2000. Dwarfs and giants: cannibalism and competition in size-structured populations. American Naturalist 155:219–237.

Claessen, D., A. M. de Roos, and L. Persson. 2004. Population dynamic theory of size-dependent cannibalism. Proceedings of the Royal Society of London Series B-Biological Sciences 271:333–340.

Claus-Walker, D. B., P. H. Crowley, and F. Johansson. 1997. Fish predation, cannibalism, and larval development in the dragonfly *Epitheca cynosura*. Canadian Journal of Zoology 75:687–696.

Cottrell, T. E. 2005. Predation and cannibalism of lady beetle eggs by adult lady beetles. Biological Control 34:159–164.

Crumrine, P. 2005. Size structure and substitutability in an odonate intraguild predation system. Oecologia 145:132–139.

Crumrine, P. W., and P. H. Crowley. 2003. Partitioning components of risk reduction in a dragonfly–fish intraguild predation system. Ecology 84:1588–1597.

DeAngelis, D. L., R. A. Goldstein, and R. V. O'Neill. 1975. A model for tropic interaction. Ecology 56:881–892.

de Roos, A. M., and L. Persson. 2001. Physiologically structured models: from versatile technique to ecological theory. Oikos 94:51–71.

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.

Finke, D., and R. Denno. 2006. Spatial refuge from intraguild predation: implications for prey suppression and trophic cascades. Oecologia 149:265.

Fox, L. R. 1975*a*. Cannibalism in natural populations. Annual Review of Ecology and Systematics 6:87–106.

Fox, L. R. 1975*b*. Factors influencing cannibalism, a mechanism of population limitation in the predator *Notonecta hoffmanni*. Ecology 56:933–941.

Gerber, G. P., and A. C. Echternacht. 2000. Evidence for asymmetrical intraguild predation between native and introduced *Anolis* lizards. Oecologia 124:599.

Ginzburg, L. R., and H. R. Akcakaya. 1992. Consequences of ratio-dependent predation for steady-state properties of ecosystems. Ecology 73:1536–1543.

Hamrin, S. F., and L. Persson. 1986. Asymmetrical competition between age classes as a factor causing population oscillations in an obligate planktivorous fish species. Oikos 47:224–232.

Holling, C. S. 1959. Some characteristics of simple types of predation and parasitism. Canadian Entomologist 91:385–398.

Holt, R. D. 1977. Predation, apparent competition, and the structure of prey communities. Theoretical Population Biology 12:197–229.

Holt, R. D., and B. P. Kotler. 1987. Short-term apparent competition. American Naturalist 130:412–430.

Holt, R. D., and J. H. Lawton. 1993. Apparent competition and enemy-free space in insect host–parasitoid communities. American Naturalist 142:623–645.

Holyoak, M., and S. Sachdev. 1998. Omnivory and the stability of simple food webs. Oecologia 117:413–419.

Hunter, M. S., T. R. Collier, and S. E. Kelly. 2002. Does an autoparasitoid disrupt host suppression provided by a primary parasitoid? Ecology 83:1459–1469.

Jensen, C. X. J., and L. R. Ginzburg. 2005. Paradoxes or theoretical failures? The jury is still out. Ecological Modelling 188:3–14.

Kats, L. B., J. A. Breeding, K. M. Hanson, and P. Smith. 1994. Ontogenetic changes in California newts (*Taricha torosa*) in response to chemical cues from conspecific predators. Journal of the North American Benthological Society 13:321–325.

Keren-Rotem, T., A. Bouskila, and E. Geffen. 2006. Ontogenetic habitat shift and risk of cannibalism in the common chameleon (*Chamaeleo chamaeleon*). Behavioral Ecology and Sociobiology 59:723.

Kohlmeier, C., and W. Ebenhoh. 1995. The stabilizing role of cannibalism in a predator–prey system. Bulletin of Mathematical Biology 57:401–411.

Krivan, V., and O. J. Schmitz. 2004. Trait and density mediated indirect interactions in simple food webs. Oikos 107:239–250.

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.

Leibold, M. A., J. M. Chase, J. B. Shurin, and A. L. Downing. 1997. Species turnover and the regulation of trophic structure. Annual Review of Ecology and Systematics 28: 467–494.

Leonardsson, K. 1991. Effects of cannibalism and alternative prey on population-dynamics of *Saduria entomon* (Isopoda). Ecology 72:1273–1285.

Luckenbill, L. S. 1974. The effects of space and enrichment on a predator–prey system. Ecology 55:1142–1147.

McQueen, D. J., J. R. Post, and E. L. Mills. 1986. Trophic relationships in fresh-water pelagic ecosystems. Canadian Journal of Fisheries and Aquatic Sciences 43:1571–1581.

Mills, E. L., and A. J. Schiavone. 1982. Evaluation of fish communities through assessment of zooplankton populations and measures of lake productivity. North American Journal of Fisheries Management 2:14–27.

Mills, N. J., and A. P. Gutierrez. 1996. Prospective modelling in biological control: an analysis of the dynamics of heteronomous hyperparasitism in a cotton-whitefly–parasitoid system. Journal of Applied Ecology 33:1379–1394.

Murdoch, W. W., and A. Sih. 1978. Age-dependent interference in a predatory insect. Journal of Animal Ecology 47:581–592.

Mylius, S. D., K. Klumpers, A. M. de Roos, and L. Persson. 2001. Impact of intraguild predation and stage structure on simple communities along a productivity gradient. American Naturalist 158:259–276.

Oaten, A., and W. W. Murdoch. 1975. Functional response and stability in predator–prey systems. American Naturalist 109: 289–298.

Oksanen, L., S. D. Fretwell, J. Arruda, and P. Niemela. 1981. Exploitation ecosystems in gradients of primary productivity. American Naturalist 118:240–261.

Orr, B. K., W. W. Murdoch, and J. R. Bence. 1990. Population regulation, convergence, and cannibalism in *Notonecta* (Hemiptera). Ecology 71:68–82.

Peacor, S. D., and E. E. Werner. 1997. Trait-mediated indirect interactions in a simple aquatic food web. Ecology 78:1146–1156.

Persson, L. 1988. Asymmetries in competitive and predatory interactions in fish populations. Pages 203–218 *in* B. Ebenman and L. Persson, editors. Size-structured populations: ecology and evolution. Springer-Verlag, Berlin, Germany.

Persson, L. 1999. Trophic cascades: abiding heterogeneity and the trophic level concept at the end of the road. Oikos 85: 385–397.

Persson, L., P. Bystrom, and E. Wahlstrom. 2000. Cannibalism and competition in Eurasian perch: population dynamics of an ontogenetic omnivore. Ecology 81:1058–1071.

Persson, L., A. M. de Roos, D. Claessen, P. Bystrom, J. Lovgren, S. Sjogren, R. Svanback, E. Wahlstrom, and E. Westman. 2003. Gigantic cannibals driving a whole-lake trophic cascade. Proceedings of the National Academy of Sciences (USA) 100:4035–4039.

Persson, L., and P. Eklov. 1995. Prey refuges affecting interactions between piscivorous perch and juvenile perch and roach. Ecology 76:70–81.

Persson, L., and L. A. Greenberg. 1990. Juvenile competitive bottlenecks: the perch (*Perca fluviatilis*)–roach (*Rutilus rutilus*) interaction. Ecology 71:44.

Polis, G. A. 1981. The evolution and dynamics of intraspecific predation. Annual Review of Ecology and Systematics 12: 225–251.

Polis, G. A. 1984. Age structure component of niche width and intraspecific resource partitioning: Can age groups function as ecological species? American Naturalist 123:541–564.

Preisser, E. L., D. I. Bolnick, and M. F. Benard. 2005. Scared to death? The effects of intimidation and consumption in predator–prey interactions. Ecology 86:501–509.

Rettig, J. E., and G. G. Mittelbach. 2002. Interactions between adult and larval bluegill sunfish: positive and negative effects. Oecologia 130:222–230.

Rosenzweig, M. L. 1971. Paradox of enrichment: destabilization of exploitation ecosystems in ecological time. Science 171:385–387.

Rudolf, V. H. W. 2006. The influence of size-specific indirect interactions in predator–prey systems. Ecology 87:362–371.

Rudolf, V. H. W. 2007*a*. The influence of cannibalism and size-structure on the dynamics of aquatic communities. Dissertation. University of Virginia, Charlottesville, Virginia, USA.

Rudolf, V. H. W. 2007*b*. The interaction of cannibalism and omnivory: consequences for community dynamics. Ecology 88:2697–2705.

Rudolf, V. H. W., and J. Antonovics. 2005. Species coexistence and pathogens with frequency-dependent transmission. American Naturalist 166:112–118.

Schellhorn, N. A., and D. A. Andow. 1999. Cannibalism and interspecific predation: role of oviposition behavior. Ecological Applications 9:418–428.

Schmitz, O. J., P. A. Hamback, and A. P. Beckerman. 2000. Trophic cascades in terrestrial systems: a review of the effects of carnivore removals on plants. American Naturalist 155: 141–153.

Schreiber, S. J., N. J. Mills, and A. P. Gutierrez. 2001. Host-limited dynamics of autoparasitoids. Journal of Theoretical Biology 212:141–153.

Sih, A. 1981. Stability, prey density and age/dependent interference in an aquatic insect predator, *Notonecta hoffmanni*. Journal of Animal Ecology 50:625–636.

Sih, A. 1982. Foraging strategies and the avoidance of predation by an aquatic insect, *Notonecta hoffmanni*. Ecology 63:786–796.

Soluk, D. A., and N. C. Collins. 1988. Synergistic interactions between fish and stoneflies: facilitation and interference among stream predators. Oikos 52:94–100.

Taylor, R. C., J. C. Trexler, and W. F. Loftus. 2001. Separating the effects of intra- and interspecific age-structured interactions in an experimental fish assemblage. Oecologia 127:143–152.

Van Buskirk, J. 1992. Competition, cannibalism, and size class dominance in a dragonfly. Oikos 65:455–464.

Vance-Chalcraft, H. D., and D. A. Soluk. 2005. Multiple predator effects result in risk reduction for prey across multiple prey densities. Oecologia 144:472.

van den Bosch, F., A. M. de Roos, and W. Gabriel. 1988. Cannibalism as a life boat mechanism. Journal of Mathematical Biology 26:619–633.

van den Bosch, F., and W. Gabriel. 1997. Cannibalism in an age-structured predator–prey system. Bulletin of Mathematical Biology 59:551–567.

Vos, M., A. M. Verschoor, B. W. Kooi, F. L. Wackers, D. L. DeAngelis, and W. M. Mooij. 2004. Inducible defenses and trophic structure. Ecology 85:2783–2794.

Wagner, J. D., and D. H. Wise. 1996. Cannibalism regulates densities of young wolf spiders: evidence from field and laboratory experiments. Ecology 77:639–652.

Werner, E. E., and S. D. Peacor. 2003. A review of trait-mediated indirect interactions in ecological communities. Ecology 84:1083–1100.

Wilbur, H. M. 1980. Complex life-cycles. Annual Review of Ecology and Systematics 11:67–93.

Woodward, G., B. Ebenman, M. Emmerson, J. M. Montoya, J. M. Olesen, A. Valido, and P. H. Warren. 2005*a*. Body size in ecological networks. Trends in Ecology and Evolution 20: 402–409.

Woodward, G., and A. G. Hildrew. 2002. Body-size determinants of niche overlap and intraguild predation within a complex food web. Journal of Animal Ecology 71:1063–1074.

Woodward, G., D. C. Speirs, A. G. Hildrew, and C. Hal. 2005*b*. Quantification and resolution of a complex, size-structured food web. Advances in Ecological Research 36:85–135.

Yasuda, H., E. W. Evans, Y. Kajita, K. Urakawa, and T. Takizawa. 2004. Asymmetric larval interactions between introduced and indigenous ladybirds in North America. Oecologia 141:722.

Yasuda, H., T. Kikuchi, P. Kindlmann, and S. Sato. 2001. Relationships between attack and escape rates, cannibalism, and intraguild predation in larvae of two predatory ladybirds. Journal of Insect Behavior 14:373.

Ziemba, R. E., and A. C. Collins. 1999. Development of size structure in tiger salamanders: the role of intraspecific interference. Oecologia 120:524–529.

APPENDIX A

Derivations of the conditions for predator invasion and persistence (*Ecological Archives* E088-186-A1).

APPENDIX B

Figures showing the effect of changes in the cannibalism rate on predator and prey isoclines and equilibrium population densities (*Ecological Archives* E088-186-A2).

APPENDIX C

Effect of changes in the strength of the behavior-mediated avoidance of cannibals on prey and predator isoclines (*Ecological Archives* E088-186-A3).

APPENDIX D

Effect of the strength of behavior-mediated avoidance of cannibals on the equilibrium population densities of both predator stages and the prey (*Ecological Archives* E088-186-A4).

APPENDIX E

Effect of behavior-mediated avoidance of cannibals on the stability of the predator–prey system without handling time (*Ecological Archives* E088-186-A5).