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Evaluating the effects of trophic complexity on a keystone predator by disassembling a partial intraguild predation food web

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Summary

1. Many taxa can be found in food webs that differ in trophic complexity, but it is unclear how trophic complexity affects the performance of particular taxa. In pond food webs, larvae of the salamander *Ambystoma opacum* occupy the intermediate predator trophic position in a partial intraguild predation (IGP) food web and can function as keystone predators. Larval *A. opacum* are also found in simpler food webs lacking either top predators or shared prey.

2. We conducted an experiment where a partial IGP food web was simplified, and we measured the growth and survival of larval *A. opacum* in each set of food webs. Partial IGP food webs that had either a low abundance or high abundance of total prey were also simplified by independently removing top predators and/or shared prey.

3. Removing top predators always increased *A. opacum* survival, but removal of shared prey had no effect on *A. opacum* survival, regardless of total prey abundance.

4. Surprisingly, food web simplification had no effect on the growth of *A. opacum* when present in food webs with a low abundance of prey but had important effects on *A. opacum* growth in food webs with a high abundance of prey. Simplifying a partial IGP food web with a high abundance of prey reduced *A. opacum* growth when either top predators or shared prey were removed from the food web and the loss of top predators and shared prey influenced *A. opacum* growth in a non-additive fashion.

5. The non-additive response in *A. opacum* growth appears to be the result of supplemental prey availability augmenting the beneficial effects of top predators. Top predators had a beneficial effect on *A. opacum* populations by reducing the abundance of *A. opacum* present and thereby reducing the intensity of intraspecific competition.

6. Our study indicates that the effects of food web simplification on the performance of *A. opacum* are complex and depend on both how a partial IGP food web is simplified and how abundant prey are in the food web. These findings are important because they demonstrate how trophic complexity can create variation in the performance of intermediate predators that play important roles in temporary pond food webs.

Key-words: *Ambystoma*, *Anax*, food web, intraguild predation, predator–prey interactions, temporary ponds

Introduction

Although a considerable amount of work has examined how prey species perform in food webs differing in trophic complexity (e.g. presence/absence of intraguild interactions or number of predator species present; Polis *et al.* 1989; Borer 2002; Finke & Denno 2004; Carey & Wahl 2010), there is less empirical information describing how the performance of a particular predator species varies in food webs differing in trophic complexity. This is rather surprising because predators can be embedded within food webs that vary greatly in trophic complexity. For example, predators occupying the intermediate predator position in a partial intraguild predation (IGP) food web are embedded within a complex web of interactions involving top predators, prey species that are shared between predator species, and prey species that are not shared between predator species but they can also be found in less complicated food webs lacking other species present in partial IGP food webs (Daugherty, Harmon & Briggs 2007; Holt & Huxel

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2007). In this study, we examine how the simplification of a partial IGP food web via the removal of top predators and shared prey affects the performance of an intermediate predator species. To generalize our work while at the same time referring to particular species in a consistent manner, we designate species as intermediate predators, top predators, shared prey or unshared prey in less trophically complex food webs on the basis of the trophic position that a species occupies in the partial IGP food web.

Several lines of evidence suggest that the performance of intermediate predators should vary in food webs differing in trophic complexity. First, both empirical (Eubanks & Denno 2000; Dinter 2002; Onzo *et al.* 2005) and theoretical (Abrams & Matsuda 1996; van Baalen *et al.* 2001) studies indicate that growth and survival of predators in a simple food web (e.g. a single prey species and an intermediate predator) should be less than that observed in food webs where the predator has access to alternative prey species. Second, early theoretical work (Polis & Holt 1992; Holt & Polis 1997) on IGP demonstrates that the addition of top predators to a simple food web with intermediate predators and shared prey could cause the extinction of intermediate predators via predation and competition. Third, recent theoretical work (Daugherty, Harmon & Briggs 2007; Holt & Huxel 2007) suggests that the addition of prey not shared between top and intermediate predators in an IGP food web can alter the ability of intermediate predators to persist in the food web. Specifically, supplements of prey available exclusively to the top predator will lead to an increase in top predator population size enhancing the intensity of intraguild interactions, which will eventually drive the intermediate predator to extinction (Daugherty, Harmon & Briggs 2007; Holt & Huxel 2007). Over the short term, however, supplements of prey to top predators may satiate top predators and reduce consumption rates of top predators on intermediate predators (Abrams & Matsuda 1996). Fourth, a number of studies have demonstrated that the strength of interaction between two species (e.g. a predator and prey) can depend on the presence or absence of a third species (e.g. another species of predator; Sih, Englund & Wooster 1998; Relyea 2003). Although these lines of evidence suggest that the ability of intermediate predators to survive and grow should change across a broad gradient of food web complexity, no empirical study has examined the growth and survival of an intermediate predator across a large portion of this gradient.

We evaluated the effect of trophic complexity on the performance of an intermediate predator, larval *Ambystoma opacum*, which is known to have an important keystone effect on assemblages of larval anurans (Morin 1995; Chalcraft & Resetarits 2003). To do this, we conducted an experiment where we focused on disassembling (or simplifying) one of the more trophically complex food webs in which we have encountered larval *A. opacum* in nature. We have observed predaceous marbled salamander (*A. opacum*) larvae in natural pond food webs that vary in trophic complexity (Fig. 1). The most trophically complex food web in our study is best described as partial IGP (Fig. 1a). We disassembled a partial IGP food web by independently removing the top predator and a prey species shared by top and intermediate predators to create three simplified food webs that we refer to as the multiple predator food web (Fig. 1b), the multiple prey food web (Fig. 1c) and the simple food web (Fig. 1d).

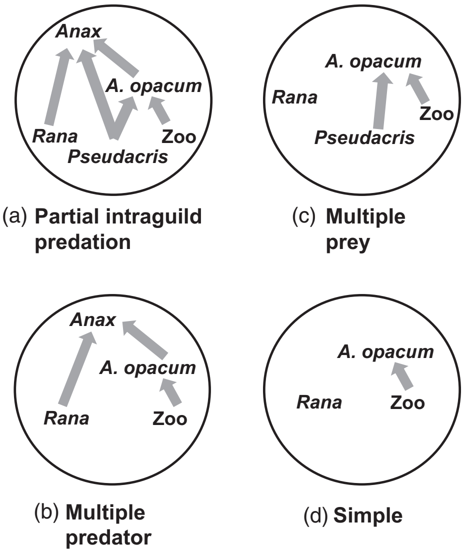

Fig. 1. Examples of natural food webs in which *Ambystoma opacum* can be found in eastern North Carolina. In each food web, the following letters stand for; *A. opacum* = *Ambystoma opacum*, *Rana* = Overwintered *Rana* tadpoles, *Pseudacris* = *Pseudacris crucifer* tadpoles and Zoo = Zooplankton. Each circle represents a food web in our study with solid arrows describing the feeding relationships within each food web; trophic complexity, in terms of the number of species and trophic links present, decreases as *Anax* and shared prey are removed from the partial intraguild predation (IGP) food web. Although simpler than the partial IGP food web, the multiple predator food web is more trophically complex than the multiple prey food web because it has more trophic links.

It has been suggested that one needs information on the long-term population dynamics of species involved in intraguild interactions to directly assess predictions from IGP theory (Briggs & Borer 2005). Consequently, we cannot explicitly test predictions of IGP theory because we focused on the response of a particular life-history stage (larval) of an intermediate predator to a change in trophic complexity. Nonetheless, prior work has demonstrated that the survival and growth of individuals during the larval stage of the intermediate predator (*A. opacum*) that we studied can play an important role in adult demography (Scott 1994) and population regulation (Taylor & Scott 1997; Taylor, Scott & Gibbons 2006).

We expect that simplifying a partial IGP food web by removing shared prey will result in lower growth and survival of *A. opacum* owing to lower resource availability. We also expect that simplifying a partial IGP food web by removing top predators will enhance intermediate predator survival but the effect on growth will depend on the relative importance of a variety of different mechanisms. For example, the loss of top predators from partial IGP food webs could (i) increase intermediate predator growth if the presence of top predators scares intermediate predators into foraging less

(Crumrine & Crowley 2003; Rudolf & Armstrong 2008); (ii) decrease intermediate predator growth if the presence of top predators alleviates intraspecific competition among intermediate predators by thinning the population size of intermediate predators and/or (iii) enhance intermediate predator growth if top predators are important interspecific competitors with intermediate predators. Although we expect the loss of top predators and shared prey to affect intermediate predator growth in an additive fashion, we expected that their combined loss would affect intermediate predator survival in a non-additive way. We expected a non-additive effect on intermediate predator survival because shared prey presence could detract top predators from consuming as many intermediate predators.

The effect of food web complexity on intermediate predator performance could depend on the abundance of prey present. For example, the elimination of top predators from a partial IGP food web with a high abundance of prey may have a greater impact on intermediate predators when the food web has a high abundance of prey as more top predators are supported in food webs with more prey (Finke & Denno 2005). In the absence of larger population sizes of top predators in food webs with more prey, we expect food web simplification to affect intermediate predator performance to a greater extent when few prey are present because top predators will be less likely to be satiated in food webs with a low abundance of prey. Given that predator satiation reduces the overall mortality risk of intermediate predators, the mortality risk of intermediate predators will change the most following the loss of top predators in food webs with a low abundance of prey.

We also expect that the loss of shared prey from food webs will have a greater impact on intermediate predators when few prey are present. If food webs have a high abundance of prey available, intermediate predators should not suffer from the loss of shared prey because there are lots of other resources to eat. Consequently, we evaluated the effects of food web simplification on intermediate predator performance in partial IGP food webs that had either a low or high abundance of total (shared and unshared) prey available.

Materials and methods

STUDY SYSTEM

Larvae of *A. opacum* are common in ephemeral ponds in the eastern United States and can function as keystone predators of larval anurans (Morin 1995; Chalcraft & Resetarits 2003). *A. opacum* lays eggs in dry portions of fishless ponds during the fall and typically metamorphoses late in the spring. A breeding pond for *A. opacum* does not need to be completely dry during oviposition (Petranka 1998; Lannoo 2005), and we have found *A. opacum* larvae in ponds in eastern NC and south-eastern VA that contain larvae of other species (e.g. dragonfly naiads and Ranid frogs) that were oviposited into the pond prior to the fall. Larval aeschnid naiads (primarily *Anax* spp.) consume *A. opacum*, but *A. opacum* can only consume the very early instars of larval *Anax*. Both *Anax* and *A. opacum* consume macroinvertebrates and small larval anurans during the spring (e.g. *Pseudacris*), but *A. opacum* are unable to eat some of the larger prey (e.g. overwintered *Rana* spp. tadpoles) that *Anax* can eat (Van Buskirk 1988; Wilbur & Fauth 1990; Morin 1995; Chalcraft & Resetarits 2003). Feeding trials indicate that larval *A. opacum* eat zooplankton (primarily *Daphnia* spp. and copepods), while later instar *Anax* do not (Davenport & Chalcraft, unpublished data). *A. opacum* will consume zooplankton throughout their larval period (Petranka 1998). Throughout their larval period, larval *A. opacum* and overwintered *Rana* tadpoles are both susceptible to *Anax* because neither species reaches a size refuge to avoid consumption by *Anax* (Relyea & Yurewicz 2002; Davenport, personal observation). In eastern NC, the most trophically complex food web in which we have found larval *A. opacum* included *Anax*, spring-deposited tadpoles (primarily *Pseudacris crucifer*), overwintered tadpoles (primarily *Rana sphenocephala*) and zooplankton. We have also encountered *A. opacum* in natural ponds representing the simplified food webs that we consider here. We focus on growth (mass at metamorphosis) and survival of larval *A. opacum* because these characteristics have previously been found to play an important role in adult demography (Scott 1994) and population regulation (Taylor & Scott 1997; Taylor, Scott & Gibbons 2006) of *A. opacum* populations.

EXPERIMENTAL DESIGN

We assessed growth and survival of 12 larval *A. opacum* embedded within a partial IGP food web, and in three simpler food webs that arise from the independent removal of top predators (two late instar *Anax* individuals) and shared prey (*P. crucifer*; Fig. 1). These manipulations produced three food webs that were trophically simpler than the partial IGP food web in the sense that they contained fewer species and fewer trophic links. The multiple predator food web and multiple prey food web had the same number of species present, but the number of trophic links is greater in the multiple predator food web. The simple food web had the fewest number of species present and trophic links. We simplified two separate partial IGP food webs that differed in total prey abundance. These manipulations produce a total of eight treatments: four treatments differing in food web complexity with a low abundance of total prey and four treatments differing in food web complexity with a high abundance of total prey (Table 1).

Our experiment was conducted in mesocosms: modified 1100-L cattle tanks designed to mimic natural ponds in eastern NC (Morin 1983; Wilbur 1997; Resetarits & Fauth 1998). Mesocosms are useful in studying the ecology of larval amphibians because they allow the experimenter to create many identical and independent experimental units to which they can apply treatments of interest (Morin 1989; Wilbur 1989). Studies conducted in natural ponds have identified that the same processes found to be important to the ecology of larval amphibians in mesocosms are also important in natural ponds (e.g. Petranka 1989; Scott 1990; Resetarits & Fauth 1998; Rubbo, Shea & Kiesecker 2006).

We arranged 32 mesocosms into four spatial blocks of eight at the West Research Campus of East Carolina University and performed all field procedures described below on a block-by-block basis. Mesocosms were filled with well water on 31 January to 2 February 2007, and each received 1 kg of hardwood leaf litter on 9 February 2007 to provide a natural refuge and nutrient source for the pond food web. Each mesocosm was equipped with a screen-covered standpipe to allow water overflow during rain events without the loss of study organisms. Furthermore, mesocosms were covered with a fibreglass mesh lid to contain experimental animals and to prevent the colonization of unwanted organisms.

Table 1. Abundances of organisms present in each of the eight food webs considered in our study. All abundances represent number of individuals/mesocosm except for zooplankton. Abundance for zooplankton represents volume of inoculum

		Top predator	Intermediate predator	Shared prey	Prey not shared by *Anax*	Prey not shared by *Ambystoma opacum*
Treatment	Prey abundance	*Anax*	*A. opacum*	*Pseudacris crucifer*	*Rana*	Zooplankton (mL)
Partial IGP	Low	2	12	200	5	450
Multiple predator		2	12	0	5	450
Multiple prey		0	12	200	5	450
Simple		0	12	0	5	450
Partial IGP	High	2	12	600	15	1350
Multiple predator		2	12	0	15	1350
Multiple prey		0	12	600	15	1350
Simple		0	12	0	15	1350

IGP, intraguild predation.

Each of the eight treatments was randomly assigned to one mesocosm within each spatial block. Abundances of organisms added to a mesocosm assigned to a particular treatment (Table 1) are within the range of abundances observed within natural pond communities (Petranka 1989; Morin 1995; Relyea 2000). Inoculations of zooplankton to mesocosms were initially made on 8 February 2007 and then repeated every month for the remainder of the experiment. Inoculations were obtained by concentrating several sweeps of a fine mesh net in a natural pond into a bucket of water. Large invertebrates were removed from the inoculations as they could function as additional predators or prey resources. Zooplankton samples were collected on 24 June 2007 to ensure differences between low- and high-inoculation treatments were present. The average abundance of zooplankton in mesocosms designated to have a low abundance of prey (mean ± 1 SE = 58·29 ± 5·09 individuals per litre) was half the abundance observed in mesocosms designated to have a high abundance of prey (mean ± 1 SE = 108·42 ± 8·81 individuals per litre). *Anax*, overwintered *R. sphenocephala* tadpoles, and *A. opacum* were collected from the Croatan National Forest on 12–22 February 2007 and randomly assigned to the appropriate (based on treatment assigned to the mesocosm) mesocosms on 19–24 February 2007. Larval *A. opacum* added to mesocosms had an average mass of 4·27 g (SE ± 0·61 g). Larval *Anax* introduced into mesocosms were in their final instar, and their mean head width was 6·6 mm (SE ± 2·17 mm). Newly hatched *P. crucifer* were obtained by hatching eggs from amplexing pairs of *P. crucifer* adults on 20 February 2007 and added to mesocosms on 2 March 2007. The densities of shared prey (Table 1) in this study are well within the realm of densities observed in nature (Fauth & Resetarits 1991; Morin 1995).

Mesocosms were monitored daily, and metamorphosed salamanders (individuals with complete absorption of the gills) and frogs (defined by emergence of at least one forelimb) were captured and returned to the laboratory, where we recorded wet mass (*g*) and date of collection of each individual. *A. opacum* mass at metamorphosis was represented by the mean mass of all salamanders that successfully metamorphosed from a particular mesocosm. *A. opacum* survival was measured as the log (+0·01) of the proportion of individuals that survived to metamorphosis. The log transformation of proportion of *A. opacum* surviving not only assured statistical assumptions were met (see below) but has biological meaning because it is a measure of instantaneous per capita mortality rates. We did not include *A. opacum* larval period as a response variable because we collected larvae after hatching and could not accurately determine hatching dates. The size of larval dragonflies increased by the end of the experiment, but growth rates did not differ between treatments with *Anax* present. Seven larval dragonflies metamorphosed prior to the end of the experiment. Metamorphosed dragonflies were replaced within 24 h with a larval *Anax* that was comparable in size to the larval *Anax* that had just metamorphosed. Mesocosms were drained between 26 and 27 June 2007, and remaining leaf litter was searched meticulously for any surviving organisms. The wet mass (*g*) of all remaining larval amphibians and larval dragonflies was recorded, and all remaining animals were released at the site of capture.

STATISTICAL ANALYSES

We evaluated the effect of food web complexity on *A. opacum* mass at metamorphosis and survival by conducting a factorial ANOVA that specified the main and interactive effects of (i) *Anax* presence/removal and (ii) shared prey presence/removal. We performed a separate factorial ANOVA for treatments that had a low abundance of prey and for treatments that had a high abundance of prey because the abundances of shared prey did not vary independently of total prey abundance. Logistical constraints prevented us from designing an experiment that would have separated the independent and interactive effects of top predator removal, shared prey removal and total prey abundance. Although we cannot evaluate the interactive effects of shared prey removal from partial IGP food webs and unshared prey abundance, we can evaluate the interactive effects of top predator removal and unshared prey abundance by focusing on the loss of top predators from the multiple predator food web which lack shared prey. We evaluated the independent and interactive effects of top predator removal and the abundance of unshared prey in food webs lacking shared prey with a factorial ANOVA. The exclusion of food webs with shared prey in this analysis restricts the scope of inference of these results to a narrower range of environments differing in food web complexity (i.e. a simple food web and the multiple predator food web vs. the four different food webs described in Fig. 1), but it does provide some insight into how the loss of top predators can affect intermediate predators in food webs that differ in prey abundance.

We analysed *Rana* survival (log of the proportion of individuals that survived to the end of the experiment) with a factorial ANOVA that included the factors *Anax* removal, *P. crucifer* removal and *Rana* density. The ANOVA included all two-way and three-way interactions between the factors. We were not able to compare response variables for *P. crucifer* between the two food webs (the partial IGP food web and the multiple prey food web) in which *P. crucifer* was present owing to the fact that no *P. crucifer* survived in any ponds lacking *Anax*.

We performed Kolmogorov–Smirnov tests to evaluate the distribution of residuals for all analyses and Levene's tests to evaluate the homogeneity of variance assumption. We did not find significant departures in the observed distribution of residuals from that expected by a normal distribution ($P > 0{\cdot}15$), and we did not find evidence for extreme heteroscedasticity in variances among treatment groups ($P > 0{\cdot}731$). Block effects (and all interactions involving block effects) were originally included in all analyses. These results, however, are not presented here for simplicity, and their inclusion does not alter the interpretation of results as presented here. All statistical analyses were considered statistically significant when $P < 0{\cdot}05$.

Results

SIMPLIFICATION OF PARTIAL INTRAGUILD PREDATION FOOD WEBS WITH A LOW ABUNDANCE OF UNSHARED PREY

Simplifying food web complexity by removing *Anax* from food webs with a low abundance of unshared prey caused an increase in *A. opacum* survival ($F_{1,\ 12} = 21{\cdot}38$, $P < 0{\cdot}001$; Fig. 2). The removal of *Anax* from a food web with a low abundance of prey did not cause *A. opacum* to metamorphose at a different size ($F_{1,\ 7} = 4{\cdot}13$, $P = 0{\cdot}088$; Fig. 2). In contrast, simplifying food webs via the removal of shared prey from food webs with a low abundance of prey did not affect *A. opacum* survival ($F_{1,\ 12} = 1{\cdot}09$, $P = 0{\cdot}317$; Fig. 2) or *A. opacum* mass at metamorphosis ($F_{1,\ 7} = 1{\cdot}49$, $P = 0{\cdot}261$; Fig. 2). The interaction between *Anax* removal and shared prey removal did not influence either *A. opacum* survival ($F_{1,\ 12} = 0{\cdot}04$, $P = 0{\cdot}843$; Fig. 2) or *A. opacum* mass at metamorphosis ($F_{1,\ 7} = 0{\cdot}16$, $P = 0{\cdot}701$; Fig. 2) in food webs with a low abundance of unshared prey. The average mass at metamorphosis of *A. opacum* in a mesocosm declined as the number of surviving *A. opacum* in a mesocosm increased ($r = -0{\cdot}824$, $P = 0{\cdot}001$, $N = 12$; Fig. S1, Supporting information).

SIMPLIFICATION OF PARTIAL INTRAGUILD PREDATION FOOD WEBS WITH A HIGH ABUNDANCE OF UNSHARED PREY

Similarly, the removal of *Anax* from food webs with a high abundance of prey caused an increase in *A. opacum* survival ($F_{1,\ 12} = 50{\cdot}78$, $P < 0{\cdot}001$; Fig. 3) but greatly reduced *A. opacum* mass at metamorphosis ($F_{1,\ 8} = 55{\cdot}72$, $P < 0{\cdot}001$; Fig. 3). Removal of shared prey from food webs with a high abundance of unshared prey did not affect *A. opacum* survival ($F_{1,\ 12} = 1{\cdot}74$, $P = 0{\cdot}212$; Fig. 3) but did decrease *A. opacum* mass at metamorphosis ($F_{1,\ 8} = 13{\cdot}02$, $P = 0{\cdot}007$; Fig. 3). The interactive effects of *Anax* removal and shared prey removal in food webs with a high abundance of prey did not influence *A. opacum* survival ($F_{1,\ 12} = 1{\cdot}44$, $P = 0{\cdot}253$; Fig. 3) but did influence *A. opacum* mass at metamorphosis ($F_{1,\ 8} = 9{\cdot}74$, $P = 0{\cdot}014$; Fig. 3). Specifically, *A. opacum* metamorphose at the same size when both *Anax* and shared prey are removed from a partial IGP food web as when *Anax* alone is removed from the partial IGP food web. This happens despite the fact that removal of shared prey alone from the partial IGP food web also causes *A. opacum* to metamorphose at smaller sizes.

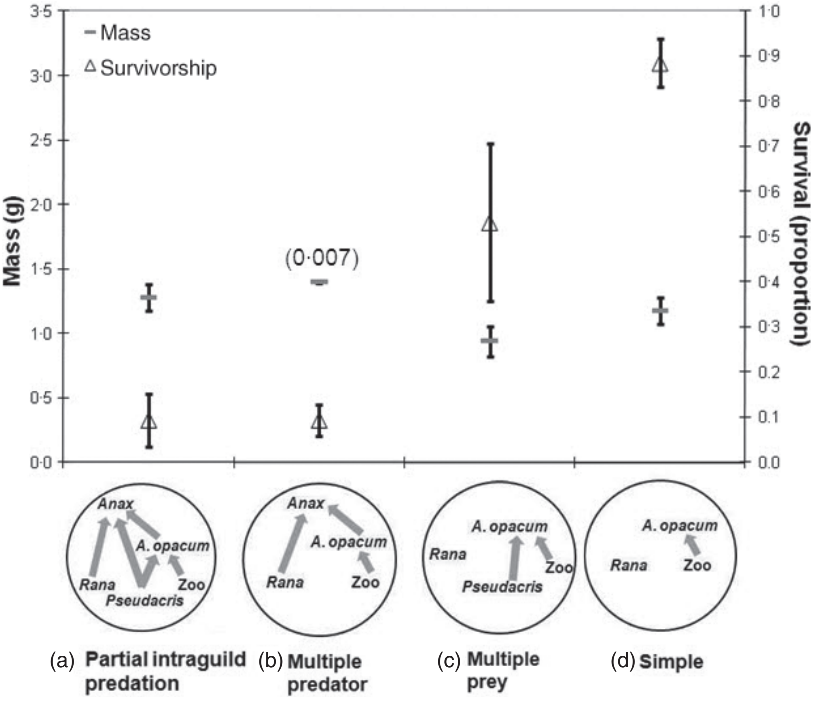

Fig. 2. Mean (± 1 SE) survival and mass at metamorphosis of *Ambystoma opacum* in food webs of varying complexity with a low abundance of prey. Means and standard errors are based on values (i.e. either total survival or average mass at metamorphosis of individuals within a pond) associated with an individual pond of a particular treatment. Numbers within parentheses represent the SE for a response variable in treatments, where the graphical depiction of the SE is smaller than the symbol size for the average response. $N = 4$ in all cases except for mean mass at metamorphosis in the multiple predator food web treatment ($n = 2$) and the partial intraguild predation food web treatment ($n = 1$). Sample sizes for these treatments were smaller because fewer ponds within these treatments produced surviving metamorphs.

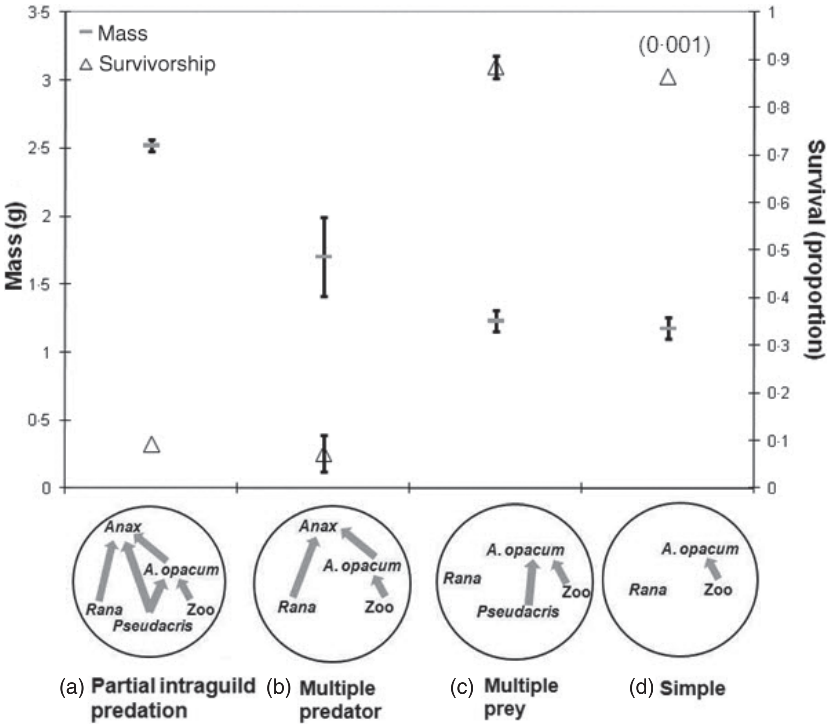

Fig. 3. Mean (± 1 SE) survival and mass at metamorphosis of *Ambystoma opacum* in food webs of varying complexity with a high (B) abundance of prey. Means and standard errors are based on values (i.e. either total survival or average mass at metamorphosis of individuals within a pond) associated with an individual pond of a particular treatment. Numbers within parentheses represent the SE for a response variable in treatments, where the graphical depiction of the SE is smaller than the symbol size for the average response. $N = 4$ in all cases except for mean mass at metamorphosis in the partial intraguild predation food web treatment with high prey abundance ($n = 2$). Sample sizes for these treatments were smaller because fewer ponds within these treatments produced surviving metamorphs.

Consequently, it appears that the effect of shared prey removal on *A. opacum* mass at metamorphosis is completely subsumed within the effect of *Anax* removal when both species are removed simultaneously. The average mass at metamorphosis of *A. opacum* in a mesocosm varied independently of the number of surviving *A. opacum* in a mesocosm (r = −0·158, P = 0·643, N = 11; Fig. S1, Supporting information).

EFFECTS OF PREY ABUNDANCE AND TOP PREDATORS IN FOOD WEBS LACKING SHARED PREY

Increasing the abundance of unshared prey in food webs lacking shared prey did not alter *A. opacum* survival ($F_{1, 12}$ = 0·37, P = 0·556) or *A. opacum* mass at metamorphosis ($F_{1, 8}$ = 1·36, P = 0·278). *Anax* removal from multiple predator food webs resulted in an increase in *A. opacum* survival ($F_{1, 12}$ = 34·53, P < 0·001) and a reduction in *A. opacum* mass at metamorphosis ($F_{1, 8}$ = 8·33, P = 0·02). The abundance of unshared prey did not alter the effect of *Anax* removal on either *A. opacum* mass at metamorphosis ($F_{1, 8}$ = 1·34, P = 0·280) or *A. opacum* survival ($F_{1, 12}$ = 0·27, P = 0·610).

PERFORMANCE OF LARVAL ANURAN PREY IN FOOD WEBS DIFFERING IN TROPHIC COMPLEXITY

Survival of larval anurans differed between food webs. The effect of *Anax* on *Rana* survival depended on the density of *Rana* present (statistical interaction between *Anax* removal and *Rana* density: $F_{1, 24}$ = 6·33, P = 0·019). Specifically, the loss of *Anax* enhanced *Rana* survival when *Rana* density was high but reduced *Rana* survival when *Rana* density was low (Fig. S2, Supporting information). Independent of the synergistic effect between *Anax* presence and *Rana* density, there was a strong trend for *Rana* survival to increase as *Rana* density increased ($F_{1, 24}$ = 3·36, P = 0·079; Fig. S2, Supporting information). Neither the removal of *P. crucifer* nor any statistical interactions involving *P. crucifer* removal accounted for a significant amount of variation in *Rana* survival (all $F_{1, 24} \leq$ 0·47, $P \geq$ 0·500). *P. crucifer*, the shared prey, only survived to metamorphosis in the partial IGP food webs with a low abundance of prey (mean proportion surviving ± 95% CI = 0·05 ± 0·06) and a high abundance of prey (mean proportion surviving ±95% CI = 0·02 ± 0·03).

Discussion

We found that simplifying a partial IGP food web via the removal of top predators and shared prey can have detrimental effects on growth and survival of the intermediate predator, *A. opacum*. For *Ambystoma* larvae that do survive, individuals with higher mass at metamorphosis experience an earlier age at first reproduction, larger size at first reproduction, increased fecundity (larger clutch size for females) and a greater chance of surviving to their first reproductive event (Semlitsch, Scott & Pechmann 1988; Scott 1994). Simulation models incorporating data from natural populations of *A. opacum* indicate that variation in larval survival and mass at metamorphosis can have important consequences for the long-term dynamics of *A. opacum* populations (Taylor & Scott 1997; Taylor, Scott & Gibbons 2006). Both of these life-history responses clearly have significant consequences for the overall fitness of individual *A. opacum* and persistence of *A. opacum* populations.

Although the loss of top predators from a food web enhanced intermediate predator survival, the loss of shared prey did not affect intermediate predator survival or alter the effect that top predators have on intermediate predator survival. These observations reinforce the idea that top predators play a particularly important role in pond food webs (McPeek 1998; Chalcraft & Resetarits 2003). The results also suggest that competition for prey was not severe enough to cause intermediate predators to die. The fact that the loss of shared prey did not alter the impact of top predators on intermediate predator survival also suggests that alternative prey did not satiate predators as originally predicted. Although it is possible that a higher abundance of prey would have satiated top predators, the abundances of prey that we used are reflective of prey abundances found in nature. In this case, the loss of a top predator from a partial IGP food web has the same effect on intermediate predator survival as the loss of a top predator from a traditional IGP food web. This important finding indicates that the effect of shared and alternative prey on intermediate predator survival may only manifest in longer-term studies if alternative prey supports larger populations of top predators that exert more negative effects on intermediate predator survival (Daugherty, Harmon & Briggs 2007; Holt & Huxel 2007).

One of the most interesting results of our study is that food web simplification affected the growth of *A. opacum* differently in food webs that differed in total prey abundance. Simplification of a partial IGP food web had no effect on *A. opacum* size at metamorphosis when a low abundance of prey was present but reduced *A. opacum* size at metamorphosis when a high abundance of prey was present. The loss of either top predators or shared prey from a partial IGP food web with a high abundance of prey caused *A. opacum* to metamorphose at a smaller size, but the effect of shared prey loss on *A. opacum* growth was less than the effect of top predator loss. Removal of top predators and shared prey from partial IGP food webs with a high abundance of total prey had a non-additive effect on *A. opacum* mass at metamorphosis. The removal of both top predators and shared prey from a partial IGP food web resulted in *A. opacum* metamorphosing at a size that was comparable to that observed when only top predators were removed from the partial IGP food web. Given the importance of size at metamorphosis to the long-term dynamics of *A. opacum* (Taylor & Scott 1997; Taylor, Scott & Gibbons 2006), these findings indicate that food web simplification will have a greater impact on the long-term dynamics of intermediate predators when prey abundance is rather high vs. low.

One potential explanation for why we failed to detect statistically significant effects of food web simplification on *A. opacum* mass at metamorphosis in food webs with a low abundance of prey is that our design lacked statistical power. We evaluated the statistical power to detect treatment effects in food webs with a low abundance of prey that were as large as the treatment effects observed in food webs with a high abundance of prey. We found that the statistical power of the analyses on *A. opacum* mass at metamorphosis in food webs with a low abundance of prey was adequate (β of predator effect = 0·99, β of shared prey effect = 0·91 and β of predator × shared prey interaction = 0·78) to detect differences in *A. opacum* mass at metamorphosis that were as large as those observed in food webs with a high abundance of prey. Consequently, we conclude that the effects of food web simplification are stronger in food webs with a high abundance of prey than in food webs with a low abundance of prey.

The simplification of partial IGP food webs had complex effects on intermediate predator growth in food webs with a high abundance of prey, indicating our initial hypothesis about an additive response to top predator and shared prey loss was incorrect. We believe that simplifying partial IGP food webs with a high abundance of prey resulted in smaller salamanders because the removal of top predators and shared prey from a partial IGP food web resulted in the loss of two important processes that interact synergistically to promote *A. opacum* growth. One process involves top predators providing a growth benefit to surviving intermediate predators in food webs with a high abundance of prey by reducing the number (survival) of intermediate predators that have to compete for prey (Figs 3 and S1, Supporting information). The beneficial effects on the growth of surviving prey by predators thinning prey population size have been reported in other studies as well (Van Buskirk & Yurewicz 1998; Relyea 2002, 2007). Nonetheless, the absence of a difference in mass at metamorphosis for salamanders in different food webs with a low total abundance of prey (Figs 2 and S1, Supporting information) indicates that top predators did not have a beneficial thinning effect on salamander growth when the abundance of total prey is low. Resource availability may be so limiting in food webs with a low abundance of prey that the decrease in the number of salamanders presented by thinning is insufficient to alleviate the stress of low food availability. A second process promoting intermediate predator growth in partial IGP food webs with a high total abundance of prey is the availability of shared prey reducing competition among intermediate predators. The loss of shared prey from a partial IGP food web with a high abundance of prey increased competition which resulted in smaller *A. opacum* in the multiple predator food web (Fig. 3). The availability of shared prey did not appear to be sufficient to reduce competition in the absence of thinning by top predators, however, because salamanders metamorphosed at the same size in the simple food web and the multiple prey food web (both of which lacked top predators; Fig. 3). Consequently, we conclude that thinning the population size of intermediate predators augments the beneficial effects of shared prey availability when total prey abundance is high. The simplification of a partial IGP food web with a low abundance of prey had no effect (or at least weaker effects than in food webs with a high abundance of prey) on intermediate predator growth because predator thinning and the amount of shared prey present were insufficient to ameliorate strong competition for a low amount of resources. Our results indicate that the way in which a partial IGP food web is simplified can have important effects on intermediate predator growth. The loss of top predators, however, has the most striking effect because their removal represents the loss of two processes that enhance intermediate predator growth while the loss of shared prey results in the loss of one process.

Our finding that simplification of a partial IGP food web and total prey abundance interact synergistically to affect *A. opacum* performance suggests that among pond variation in food web complexity and prey abundance can generate source and sink habitats for *A. opacum* metapopulations. Source ponds (partial IGP food webs) may be contributing to the persistence of *A. opacum* populations by providing larger, more fecund salamanders to colonize or rescue nearby sink ponds (simplified food webs in our study) that produce smaller individuals that will not survive long after metamorphosis (Petranka 1989; Scott 1990). If sink ponds (simple food webs) produce smaller individuals that do live to reproduce, then the sink populations will still likely have lower population growth rates (compared to source population growth rates) unless they gain migrants from source populations. Dispersal between ponds of various qualities is thought to be responsible for causing fluctuations in the size of amphibian populations (Semlitsch *et al.* 1996; Marsh & Trenham 2001; Smith & Green 2005).

Our results also suggest that food web complexity may facilitate the ability of a predator species to fulfil a keystone role in ecological food webs by preventing keystone predators from becoming overabundant and consuming everything. *A. opacum* is a known keystone predator that enhances survival of competitively inferior larval anurans by selectively consuming competitively dominant larval anurans (Morin 1995; Chalcraft & Resetarits 2003). With keystone predators at high abundances, however, the beneficial effects of keystone predators on competitively inferior prey can be diminished as competitively inferior prey have a greater probability of being consumed (Morin 1983). We suggest that *A. opacum* is more likely to operate in a keystone manner in trophically complex food webs, where top predators (such as *Anax*) reduce *A. opacum* overall abundance.

Although the short-term nature of our study (<1 generation of the study animals) prevents us from directly testing the equilibrial conditions predicted by IGP theory, our findings build on the results of others that have demonstrated the importance of larval survival and growth on fitness and population dynamics of *A. opacum*. In particular, our results shed important light on how the simplification of a partial IGP food web will affect populations of an intermediate predator, *A. opacum*. Our study supports the argument (Daugherty, Harmon & Briggs 2007; Holt & Huxel 2007) that intermediate predators are more likely to persist over a broader range of conditions with top predators when there is a sufficient abundance of alternative prey available to predators. In our case, however, the availability of shared prey did not enhance the survival of intermediate predators by reducing the consumptive effect of top predators on intermediate predators. Instead our empirical data provides the novel contribution that in partial IGP food webs, shared prey support intermediate predator growth rates when top predators are present by augmenting the beneficial effects of thinning by top predators on intermediate predators.

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Supporting Information

Additional Supporting Information may be found in the online version of this article.

Fig. S1. The relationship between *A. opacum* survival and *A. opacum* mass at metamorphosis in food webs differing in trophic complexity.

Fig. S2. Mean proportion of *Rana sphenocephala* surviving (±1 SE) in eight food webs differing in trophic complexity (presence/removal of the top predator, *Anax*, and presence/removal of shared prey, *Pseudacris crucifer*) and total prey abundance.

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