

# Predator size and phenology shape prey survival in temporary ponds

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**Abstract** Theoretical efforts suggest that the relative sizes of predators and their prey can shape community dynamics, the structure of food webs, and the evolution of life histories. However, much of this work has assumed static predator and prey body sizes. The timing of recruitment and the growth patterns of both predator and prey have the potential to modify the strength of predator–prey interactions. In this study, I examined how predator size dynamics in 40 temporary ponds over a 3-year period affected the survival of spotted salamander (*Ambystoma maculatum*) larvae. Across communities, gape-limited predator richness, but not size, was correlated with habitat duration (pond permanence). Within communities, mean gape-limited predator size diminished as the growing season progressed. This size reduction occurred because prey individuals grew into a body size refuge and because the largest of the predators left ponds by mid-season. Elevated gape-limited predation risk across time and space was predicted by the occurrence of two large predatory salamanders: marbled salamander larvae (*Ambystoma opacum*) and red-spotted newt adults (*Notophthalmus viridescens*). The presence of the largest

gape-limited predator, *A. opacum*, predicted *A. maculatum* larval survival in the field. The distribution of large predatory salamanders among ponds and across time is expected to lead to differing community dynamics and to generate divergent natural selection on early growth and body size in *A. maculatum*. In general, a dynamic perspective on predator size often will be necessary to understand the ecology and evolution of species interactions. This will be especially true in frequently disturbed or seasonal habitats where phenology and ontogeny interact to determine body size asymmetries.

**Keywords** Community dynamics · Growth/predation risk tradeoffs · Prey size refuge · Priority effects · Temporary ponds

## Introduction

Insights into the structure and functioning of communities and the evolution of life histories frequently are derived from the size distributions of interacting species (Peters 1983; Williams and Martinez 2000; Cohen et al. 2003; Loeuille and Loreau 2005; Thygesen et al. 2005). This field of research suggests that body size distributions can predict emergent properties of food webs, such as trophic-level abundances, food chain length, and the evolution of the life histories of interacting species. However, much of this research ignores the joint ontogeny of predators and prey that occurs over the course of a developmental season (Werner and Gilliam 1984; de Roos et al. 2003a). Experimental evidence suggests that ontogenetic changes in body size can alter the outcome of predator–prey interactions (Alford 1989; Wilbur and Fauth 1990). In some cases, the typical representation of size-dependent predation risk

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assumed in theoretical literature or represented in simplified experiments may not match the dynamics found in natural systems (Wilbur 1988; Skelly 2002). Because most studies occur as theoretical exercises or simplified experiments (for an early exception see Paine 1976), evidence from field systems is necessary to evaluate the premises upon which the growing body of predator–prey size theory is founded (Persson et al. 1996; Woodward and Hildrew 2002).

Body size asymmetries often determine the outcome of predator–prey interactions (Wilson 1975; Peters 1983; de Roos et al. 2003a) because the size of a predator's gape or capture apparatus frequently constrains its ability to handle large prey (Hambright 1991; Scharf et al. 2000). Therefore, a gape-limited predator for a focal prey species can be defined by the relative size differences between predator and prey given information about the size threshold above which prey can no longer be captured (Wilbur 1988; Wisinger 1992). In contrast, gape-unconstrained predators are defined as those taxa that can prey upon all size classes of a given species due to the predators' large size or specialized behavioral or morphological adaptations that allow them to take larger prey (e.g., venom). Predator gape size constraints can create a refuge for prey that grow rapidly to a body width or depth that is sufficient to render them invulnerable to predation (Wilson 1975; Paine 1976; Chase 1999; Day et al. 2002). On the other hand, high initial predation risk associated with this rapid growth or high densities of gape-unconstrained predators may select for slower growth (Skelly and Werner 1990; Abrams and Rowe 1996). Most organisms decrease their growth rates when exposed to reliable cues of predation risk as a consequence of adopting behaviors that reduce detection by predators and thereby decrease instantaneous predation risk (Skelly and Werner 1990; Lima 1998; Benard 2004). These risk-reducing behaviors frequently include decreased foraging activity and the increased use of low-risk and low-resource microhabitats. However, in some cases, individuals forage more frequently and grow rapidly under threat of predation (Crowl and Covich 1990; Walters and Juanes 1993; Chase 1999; Urban 2006). When the relative risks from gape-limited predators outstrip the risks from gape-unconstrained predators, the optimal strategy can be to adopt riskier foraging behaviors that support growth into a size refuge, decrease cumulative predation risk, and produce future increases in size-correlated fecundity (Urban 2007).

When both the predator and prey grow at different rates or arrive in the habitat at different sizes, the predicted outcome becomes more complicated. Divergent growth rates between predators and prey can demarcate varying periods of prey vulnerability and invulnerability (Wilbur 1988). The interactions between prey and predator may shift between competition and predation depending on how pri-

ority effects, environmental conditions, genetic variation, and behavioral responses alter their relative growth rates (Wilbur 1988; de Roos et al. 2003a). A growing predator also can elicit alternative growth strategies in prey. Depending on the strength and shape of growth–risk relationships, prey individuals are predicted to evolve either a slow or a rapid growth strategy (DeAngelis et al. 1985). An intermediate strategy is not expected because a prey individual that grows at approximately the same rate as its gape-limited predator does not reach a body size refuge but still experiences the negative effects associated with elevated growth (here assumed to be due to a positive growth–risk relationship) (Urban 2006). Hence, variation in the relative growth rates and/or initial sizes of predators and prey can lead to highly divergent predictions of community and evolutionary dynamics.

Parameterization and validation of size-based community models requires comparative studies of size-dependent interactions through time among communities that differ in top predators (Persson et al. 1996). Moreover, studies that examine communities across a large geographic area can support broader generalizations than those derived from a few local communities (Paine 1980). Here I evaluate the relationship between gape-limited predator size and the survival of spotted salamander (*Ambystoma maculatum*) larvae in 40 temporary ponds distributed across three sites along a latitudinal gradient over a 3-year period. A finely resolved temporal dataset on the sizes and densities of gape-limited and gape-unconstrained predators and their *A. maculatum* prey allowed me to address three questions about the structure of predation risks across space and time in a temporary environment. First, does pond permanence – i.e., the duration of annual inundation – predict variation in gape-limited predator diversity and size? More permanent ponds are expected to support greater overall species richness because species requiring both short and long development times can persist (Schneider and Frost 1996). Therefore, it is reasonable to expect that more permanent ponds will support a greater density of large gape-limited predators by providing habitat for larger bodied species that require longer development periods. Second, how does mean predator size change within a developmental season? A typical assumption in theoretical work is that predator size (both gape-limited and gape-unconstrained) remains constant or increases over the course of the growing season (Day et al. 2002; Cohen et al. 2003; Urban 2006). Although this generally may be true for individual predators, differences in growth rates, priority effects, and life history strategies among species could cause deviations from the expected pattern. Third, does *A. maculatum* survival depend on the size of gape-limited predators? Large gape-limited predators are expected to reduce prey survival during the early stages of prey growth.

## Methods

### Natural history and site description

*Ambystoma maculatum* is a relatively large (up to 33 g) terrestrial salamander found in eastern North America. Adults move from uplands into temporary ponds to breed each spring. In the southern New England states (USA), females lay eggs in late March to early April, and hatchlings hatch as small aquatic larvae (0.007–0.021 g) by the end of May. *Ambystoma maculatum* larvae make ideal study organisms for research on size-dependent predation risks because they must grow rapidly to reach a sufficient size to ensure metamorphosis before the ponds dry out in summer (Schneider and Frost 1996; Urban 2004). In the process, larvae can increase their body size by 20-fold over several months (M.C. Urban, unpublished data). Metamorphosis occurs above a size threshold when a pond dries or with the onset of cool autumn temperatures.

I sampled 40 ponds (range of areas 66–8,300 m<sup>2</sup>) from three sites that are each separated by approximately 80 km along a latitudinal gradient in the southern New England states (total gradient: 160 km). These sites included a southern location in Northford, Connecticut (CT) near the Long Island Sound coast, an intermediate location at Yale-Myers Research Forest in Union, CT, near the border with Massachusetts, and a northern location in Chesterfield, New Hampshire, in the southwest corner of the state. At each site, 12 or more ponds were identified as breeding sites for *A. maculatum* within a spatially defined and censused tract of undisturbed forest. Pond hydroperiods ranged along a gradient from temporary (dried by mid-June) to semi-permanent (occasional year-round inundation). However, no ponds were so permanent that they supported stable fish populations.

Prior work has shown that both the size and density of gape-limited predators decline from south to north among these sites (Urban 2006). In contrast, gape-unconstrained predation risk remains relatively constant along the same gradient. Common garden experiments have revealed that *A. maculatum* larvae forage more frequently and grow faster in regions characterized by intense predation risk from the gape-limited marbled salamander (*Ambystoma opacum*) predator (Urban 2006).

### Sampling

Each pond was sampled at least every 2 weeks from the initiation of *A. maculatum* hatching in late May or early June until a pond dried or no larvae were collected in two subsequent surveys. I sampled prey and predator populations by sweeping all habitat areas in each pond with a 17 × 25-cm dip net with a 1.4-mm mesh. Effort was set proportional to

pond area (approximately one 0.8-m sweep per 20 m<sup>2</sup>) and varied with hydrological changes in pond area over the course of the season. For logistical reasons, five ponds with total inundated areas over 3000 m<sup>2</sup> in the spring were sampled with fixed effort (approx. 120 sweeps) before drying decreased their areas to levels that allowed area-proportional sampling. Prey and potential predators of *A. maculatum* were collected and preserved in 70% ethanol. Predators were identified to genus (invertebrates) or species (vertebrates) under a stereoscope (magnification 7–30×) using appropriate literature (Merritt and Cummins 1996; Petranka 1998). Because sweep length was standardized (length 0.8 m), species abundances divided by number of dip net sweeps were used as an estimate of species densities. Pond permanence was measured as the number of days from the initiation of *A. maculatum* breeding until the last date that a pond was observed with water. Ponds that retained water throughout the season were assigned the length of the maximum regional growing season (from breeding date until early autumn).

### Predator definition and measurement

A predator species of *A. maculatum* larvae was defined by its ability to consume *A. maculatum* or similar amphibian larvae (Stenhouse 1985; Schneider 1997; Petranka 1998; Brunkhurst 2004; Urban 2004) and was assigned to either the gape-limited or gape-unconstrained functional category as indicated in the literature (Stenhouse 1985; Wilbur and Fauth 1990; Wissinger 1992; Wilbur 1997). Gape-limited predators cannot capture larger individuals of the focal prey species, whereas gape-unconstrained predators can capture a prey species throughout the prey's entire size ontogeny. Gape-limited predators included salamanders, fish, and small libellulid dragonfly larvae. Salamanders and fish often are gape-limited because they hunt by suctioning prey items through their mouths (Pough et al. 2001; van Wassenbergh et al. 2006). Small libellulid dragonflies also are limited in their ability to prey upon large individuals because they cannot readily handle prey larger than their labium widths (Wissinger 1992). In contrast, gape-unconstrained predators of *A. maculatum* larvae have morphological adaptations that enable them to grasp prey larger than themselves (e.g., stiff prementum in aeshnid dragonfly larvae, Wilbur 1997) or deliver immobilizing and necrotic venom (*Dytiscus*, Formanowicz 1982). A gape-limited predator individual was not counted unless its gape or labium surpassed the minimum head width of *A. maculatum* hatchlings (2.0 mm). *A. maculatum* head width is the morphological feature that generally prevents its capture by gape-limited predators (M.C. Urban, personal observation). In additional analyses, I defined predator densities based on calculated predator:prey size thresholds (see next section).

Gape-limited predator size was measured as the maximum cross-sectional dimension of each predator's gape or labium (for dragonfly larvae) with a digital caliper (nearest 0.1 mm). A maximum of ten individuals of each predator species, haphazardly selected from the homogenized sample of all available individuals, was measured for each pond on each sampling date. All individuals of a particular species were measured in samples of less than ten individuals. The mean predator size for each pond was calculated as the average of each predator taxon's mean size weighted by their field abundance. Some amphibian adults and metamorphs were not preserved due to low population numbers in the field. Red-spotted newt (*Notophthalmus viridescens*) adults only were preserved in 2004 and in a supplementary collection in 2005. *N. viridescens* sizes for 2002–2003 were assigned the mean size from the appropriate pond, when available, or the site mean calculated from the 2004 and 2005 collections across all dates. Sizes measured over all dates could be used because *N. viridescens* adult gape sizes did not change significantly over time (Urban 2006). Four metamorphic individuals of the predatory *A. opacum* larvae also were noted in the field but not preserved. The sizes of these individuals were estimated from the mean size for each site and capture date.

#### Predator:prey size thresholds

The predator:prey size threshold was estimated as the maximum prey head width consumed by a predator of a specific gape or labium width. The size thresholds for *A. opacum* larvae and *N. viridescens* adults in the region were estimated to be  $0.37 \pm 0.13$  and  $0.37 \pm 0.17$  SD, respectively (Urban 2006). For libellulid dragonflies, I used the estimated mean size threshold of 0.8 obtained for those species collected in my study (Wissinger 1992). These size thresholds were then applied to the mean size of *A. maculatum* larvae to determine whether gape-limited predators of specific sizes posed a threat. Prey size was estimated as the maximum head width for field-collected *A. maculatum* larvae. For large samples, a maximum of 20 haphazardly selected prey individuals were measured.

#### Statistical analyses

Standard linear regressions were used to analyze mean predator richness and gape size across all years versus pond permanence. I employed restricted maximum likelihood linear mixed-effects models to analyze data on predator size and density through time because predator metrics were likely to be non-independent within seasons and across years and thus needed to be treated as repeated measures on the same subject (pond) (von Ende 2001). Unless noted, the simpler model of random intercepts was chosen over a

more complex model with random slopes and intercepts after comparing Akaike Information Criterion (AIC) values (Crawley 2002). Decisions to include interactions also were made based on minimum AIC. When interactions were significant, I also analyzed results by independent factor/covariate levels to gain insights about the interaction.

A mixed-effects analysis of covariance (ANCOVA) model with pond entered as a random effect was used to evaluate changes in predator gape sizes through time and across sites. I also analyzed site-specific regressions for three types of ponds: (1) *A. opacum* present (with or without *N. viridescens* adults), (2) *N. viridescens* adults present (*A. opacum* absent) and (3) neither predatory salamander present. Because too few entries were available for a meaningful statistical sample of ponds with both *A. opacum* and *N. viridescens* present, and the patterns reflected those of *A. opacum*-only rather than *N. viridescens*-only ponds, I combined this pond type with the *A. opacum* category. I set the predator gape size in samples in which no predator gapes had been measured (because all predators were below 2 mm) to the predetermined detection limit of 2 mm. This algorithm fosters a more conservative evaluation of predator size effects because setting these values to zero or excluding them tended to increase the magnitude of size-dependent relationships revealed in the study. As *A. maculatum* larvae grow over the course of a season, many gape-limited predators no longer pose a threat to their survival. Therefore, I also evaluated the temporal dynamics of the densities of gape-limited predators only with gape or labium sizes sufficient to pose threats to *A. maculatum* larvae (hereafter size-dependent predator densities) in a mixed-effects ANCOVA model. Size-dependent predator densities were calculated for each sampling date and each pond as the density of gape-limited predators that posed a threat to *A. maculatum* larvae after taking into account the gape size of the predators, *A. maculatum*'s head width, and the size refuge threshold estimated for each predator species. Predator densities and gape sizes were ln-transformed after failing tests for normality and homogeneity of variances (Sokal and Rohlf 1995).

Lastly, I explored a set of models that estimated the effects of gape-limited predator size and predator identity (*A. opacum*, *N. viridescens*) on *A. maculatum* survival in the field. *A. maculatum* survival was evaluated as the recruitment curve of the ln-transformed densities of hatchlings (approx. 1 week) and early larvae (approx. 3 weeks) versus their densities in the prior stage. These stages encompass the early time period when gape-limited predators pose the most substantial threat to *A. maculatum* larvae (see [Size-dependent predator densities](#) in [Results](#)). I used an ANCOVA to compare the changes in the recruitment dynamics of *A. maculatum* between ponds with and without *A. opacum*. The full model included the covariate of density from the previous stage and the factors year and site.

## Results

### Predator communities

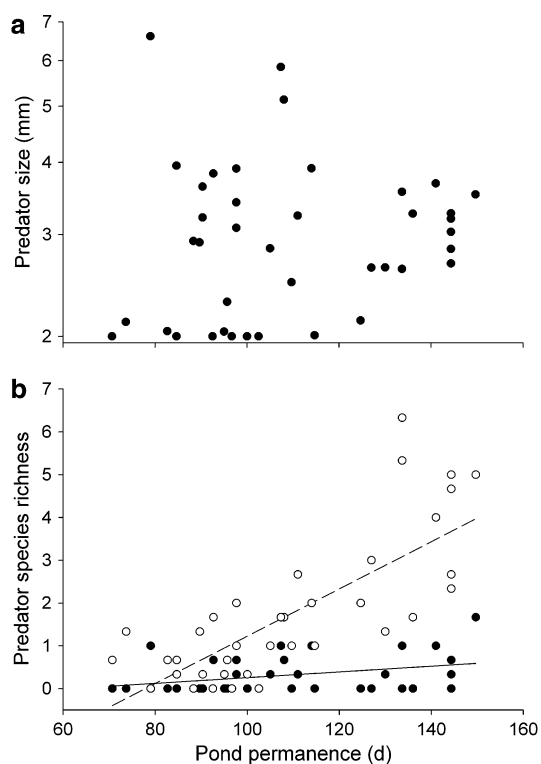
I collected 2818 predators over 3 years from 40 temporary ponds. The most abundant predator taxa were the caudates *Notophthalmus viridescens* adults and *Ambystoma opacum* larvae, the anuran *Rana clamitans*, odonate larvae, including *Sympetrum*, *Aeshna*, *Pachydiplax*, and *Leucorrhinia*, the coleopteran *Dytiscus*, the hemipterans *Lethocerus* and *Notonecta*, and the megalopteran *Chauliodes*. The largest gape-limited predators were the salamanders *A. opacum* and *N. viridescens* with median gape sizes of 8.07 and 6.21 mm, respectively.

In contrast to predictions, overall gape-limited predator size did not increase with pond permanence (Fig. 1a;  $F_{1,38} = 0.63$ ,  $P = 0.431$ ). However, both mean annual gape-limited and gape-unconstrained predator species richness increased with pond permanence (Fig. 1b;  $F_{1,38} = 5.84$ ,  $P = 0.021$ ;  $F_{1,38} = 54.85$ ,  $P < 0.001$ , respectively). The relationship between species richness and pond permanence was much stronger and less variable for gape-unconstrained predators (slope 0.055 species/days of permanence,  $R^2 = 0.59$ ) than for gape-limited predators (slope 0.007 species/days of permanence,  $R^2 = 0.13$ ).

### Gape-limited predator size dynamics and composition

Gape-limited predator size was explained by a significant interaction between site and time within season [Fig. 2,  $F_{3,279} = 4.97$ ,  $P = 0.002$ ; [Electronic Supplementary Material \(ESM\)](#)]. In contrast to predicted increases in predator size through time, the mean gape size of predators decreased with time at the southern and intermediate sites ( $F_{1,87} = 13.56$ ,  $P < 0.001$ ;  $F_{1,120} = 41.74$ ,  $P < 0.001$ ; [ESM](#)) but remained constant at the northern site ( $P = 0.34$ ).

A significant interaction was revealed between dominant predatory salamander type and time across the region ( $F_{3,279} = 11.27$ ,  $P < 0.001$ ) and within each site ( $P < 0.05$ ). The presence of either *A. opacum* or *N. viridescens* altered the magnitude and even the sign of the relationship between predator size and time (Fig. 3; [ESM](#)). For *A. maculatum* larvae in ponds with *A. opacum*, the mean overall predator gape size began at 6.0 mm in the spring and declined until mid-season at the southern and intermediate sites (slope  $-0.016$ ,  $F_{1,55} = 24.83$ ,  $P < 0.001$ ; slope  $-0.012$ ,  $F_{1,56} = 67.19$ ,  $P < 0.001$ , respectively). This decline in overall gape-limited predator size occurred despite the species-specific growth of predator gapes through time because *A. opacum* left ponds at mid-season. In ponds where only *N. viridescens* occurred, mean overall predator gape size in the spring was 3.8 mm and declined for both the intermediate and northern sites but at a slower rate than

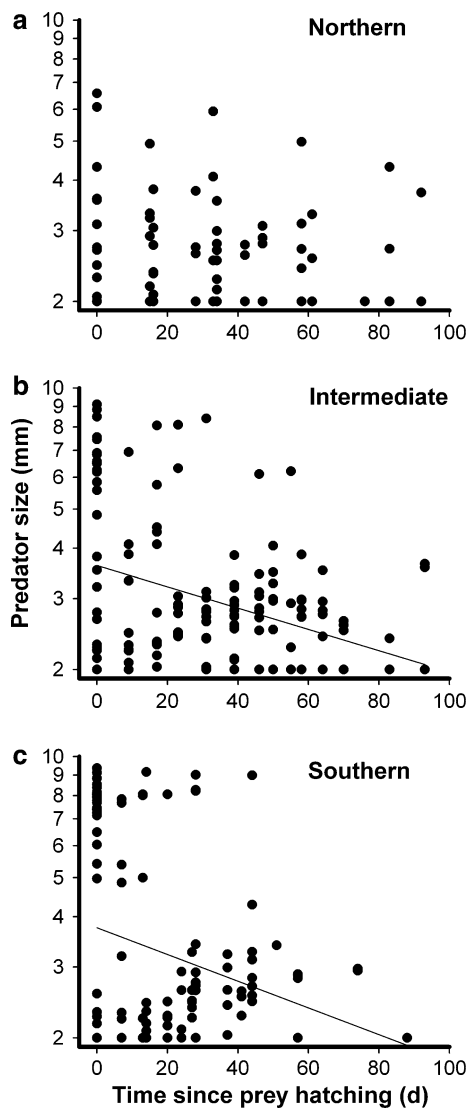


**Fig. 1** Predator size (**a**) and species richness (**b**) of gape-limited (filled circle) and gape-unconstrained (open circle) predators of *Ambystoma maculatum* larvae along a pond permanence gradient from 2002 to 2004. Mean values over a 3-year period for predator size, species richness, and pond permanence were analyzed. Lines indicate significant ( $P < 0.05$ ) regression slopes for gape-limited (solid line) and gape-unconstrained (broken line) predators. The relationship for predator size was tested using ln-transformed data. Permanence was measured as the number of days ( $d$ ) a pond held water following breeding by *A. maculatum* larvae, an event that closely follows the timing of spring ice-melt

that recorded for ponds inhabited by *A. opacum* (intermediate site: slope  $-0.005$ ,  $F_{1,38} = 9.38$ ,  $P = 0.004$ ; northern site: slope  $-0.004$ ,  $F_{1,23} = 4.37$ ,  $P = 0.048$ ). In ponds without salamanders, mean predator gape size was generally smaller at the beginning of the season (2.1 mm) and either increased slightly (southern site) or remained constant.

### Size-dependent predator densities

I also analyzed how gape-limited predator densities changed through time after including only those predators of a sufficient gape or labium size to prey upon the mean size of *A. maculatum* larvae with which they co-occurred. Size-dependent predator densities declined markedly over time: although they reached 1.0 individual per 10 m<sup>2</sup> during the first 2 weeks, no gape-limited predators of a sufficient size to pose a threat were detected after the fourth week of *A. maculatum* development. This result is both due to the metamorphosis and departure of predatory salamanders and the growth of *A. maculatum* into a size refuge from these gape-limited predators. Only the smallest predators remained the entire season,



**Fig. 2** Gape-limited predator gape size within a season for three sites – northern (a), intermediate (b), southern (c) – aggregated over a 3-year period. Lines indicate significant ( $P < 0.05$ ) regression slopes for ln-transformed size data determined with time within season as a covariate and year and pond as nested random effects. The relationship was not significant in (a)

and these predators never grew large enough to threaten the rapidly growing *A. maculatum* larvae. The full mixed-effects ANOVA model revealed a significant interaction between site and time ( $F_{2,240} = 6.40$ ,  $P = 0.002$ ). Significant declines in size-dependent predator densities occurred for the southern and intermediate sites, but not for the northern site (ESM). In contrast, gape-unconstrained predator densities remained constant throughout the season at all sites ( $P > 0.4$ ).

#### Prey survival

The effects of mean gape-limited predator size and the presence of *A. opacum* and *N. viridescens* on *A. maculatum*

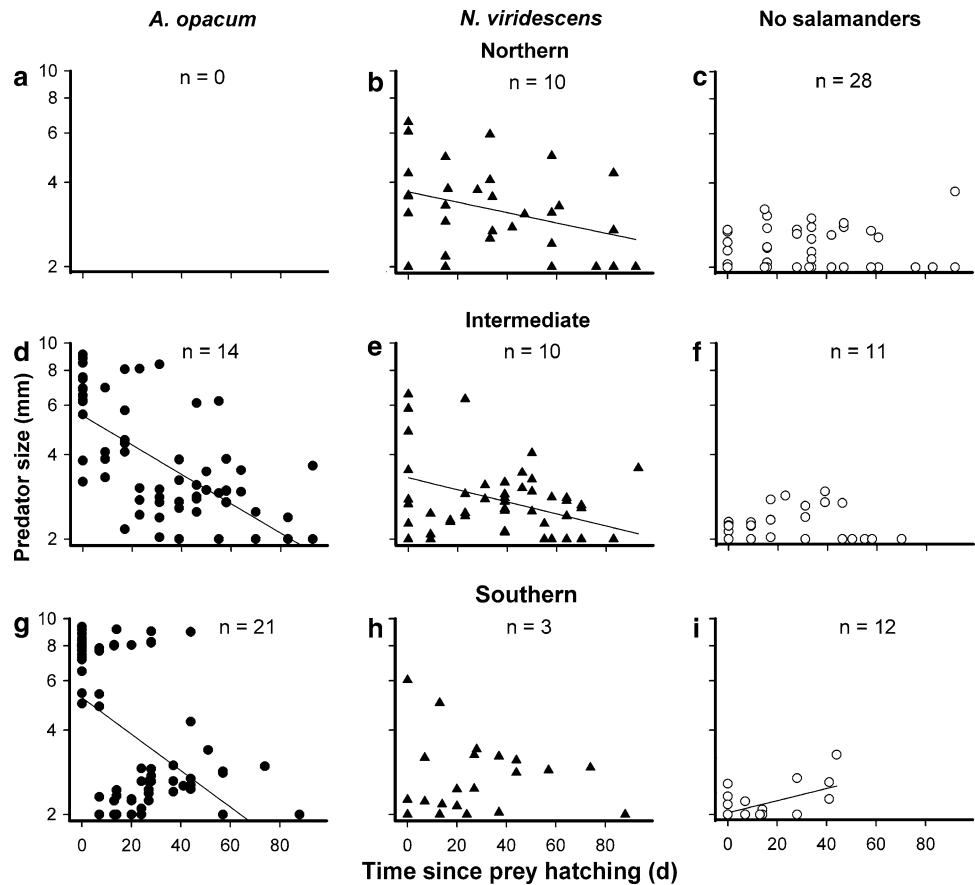
survival across two developmental stages were analyzed: from egg to hatchling, and from early-stage hatchling to mid-stage larva. Gape-limited predator size and the presence of *N. viridescens* were unrelated statistically to the survival of *A. maculatum* from egg to hatchling ( $P > 0.12$ ; ESM). However, the presence of *A. opacum* was associated significantly with decreased *A. maculatum* survival from egg to hatchling ( $F_{1,67} = 10.47$ ,  $P = 0.006$ ). Survival patterns consistent with intense predation by *A. opacum* during the prey's smallest and most vulnerable stage were illustrated at both the intermediate and southern sites (Fig. 4). However, gape-limited predator size and *A. opacum* and *N. viridescens* densities were not related statistically to *A. maculatum*'s survival at the next stage analyzed – from early-stage hatchling to mid-stage larva ( $P > 0.63$ ; ESM). Hence, much of the predation risk by gape-limited predators on *A. maculatum* is attributed to one species (*A. opacum*) and is confined to the early developmental stage immediately following hatching.

#### Discussion

Body size variation provides a prevailing axis by which ecologists seek to understand and predict the dynamics of interacting predators and their prey (Cohen et al. 2003; de Roos et al. 2003a; Paine and Trimble 2004). However, most studies of trophic interactions omit a dynamic perspective that accounts for predator–prey ontogeny and phenology. In habitats such as temporary ponds with strong effects of seasonality, the annual reassembly of communities creates a situation where priority effects and growth rates can readily shape the outcome of species interactions (Wilbur 1988; Alford 1989). In this study, the spatial and temporal dynamics of gape-limited predator distributions in temporary ponds created a heterogeneous and heretofore unexplored pattern of predation intensity and potentially divergent selection on prey growth. For the most part, only two predatory salamanders, *A. opacum* and *N. viridescens*, consistently attained a size that allowed them to prey upon *A. maculatum* hatchlings.

Semi-permanent and permanent ponds usually support higher species richness by maintaining species characterized by a more diverse set of developmental periods (Schneider and Frost 1996; Urban 2004). In this study, both gape-limited and gape-unconstrained predator species richness increased with pond permanence. The stronger relationship between gape-unconstrained predator richness and permanence versus that for gape-limited predator richness suggests a more intense selection for defenses against gape-unconstrained predators in more permanent ponds. Behaviors such as reduced foraging might be heavily favored in these more permanent environments where correlated

**Fig. 3** Gape-limited predator size within a season for northern (a, b, c), intermediate (d, e, f), and southern (g, h, I) site ponds with *A. opacum* (filled circle), *Notophthalmus viridescens* (filled triangle) and without predatory salamanders (open circle) over a 3-year period. Significant ( $P < 0.05$ ) regression relationships are indicated for ln-transformed size data. The number of pond-years ( $n$ ) used to construct each relationship is indicated above each subpanel

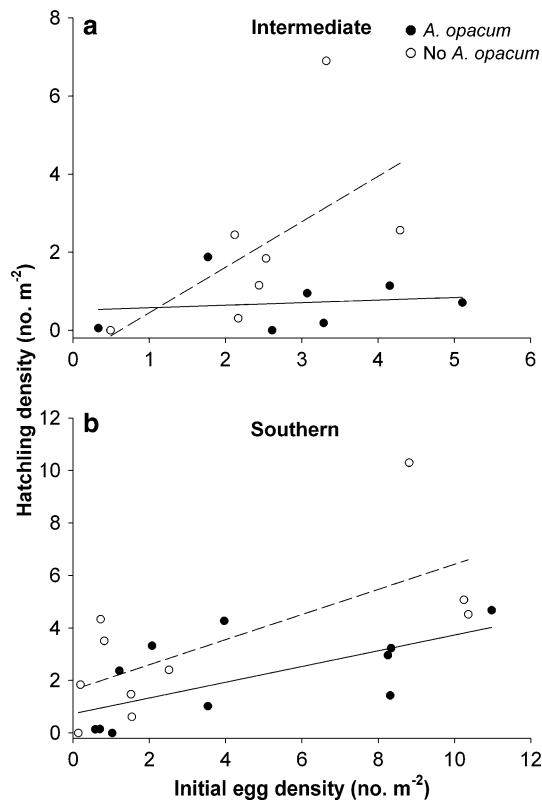


longer developmental periods still provide enough time for growth to critical life history stages (e.g., metamorphosis) before pond drying (Wellborn et al. 1996).

Conversely, more permanent ponds did not sustain larger gape-limited predators. Instead, the largest predators were those taxa that were able to exploit the periodicity of the temporary pond habitat in ways that differed from their prey base. The large predatory salamanders, *A. opacum* and *N. viridescens*, do not conform to the standard life history pattern of most temporary pond predators whereby recruitment occurs in early spring and juveniles emerge by late summer. Instead, *A. opacum* adults lay their eggs in the autumn in dry pond margins. Their larvae hatch following pond inundation, overwinter under ice cover, and emerge in the spring as relatively large and effective predators of newly recruited spring-breeding amphibians (Stenhouse 1985). Because of this early start, *A. opacum* attain sufficient size for metamorphosis earlier in the season than other amphibian larvae and tend to emerge as terrestrial juveniles by mid-July in the region. *Notophthalmus viridescens*, on the other hand, has a complex life cycle in which initially aquatic larvae become terrestrial juvenile efts before returning to ponds as aquatic adults. However, even at the adult stage, they frequently switch opportunistically between aquatic and moist upland microhabitats. *Notophthalmus*

*viridescens* adults generally migrate into ponds during the winter or early spring (Gill 1978; Alford 1989) and usually leave ponds for terrestrial habitats by mid-summer (M.C. Urban, unpublished data). An early exodus from ponds may remove parasites and reduce physiological stresses associated with pond drying (Gill 1978).

My results suggest that the phenology of predator species plays an important role in determining the outcome of predator–prey interactions in temporary ponds. Predatory salamanders with large proportionate effects on prey employed a life history strategy that did not constrain them to the same developmental time windows as their prey. *Ambystoma maculatum* larvae generally can outgrow other gape-limited predators, such as libellid larvae, that recruit and grow throughout the remainder of the season. Therefore, early arrival or arrival as adults by gape-limited predators in temporary ponds offers them the ability to take advantage of a seasonally abundant resource: high densities of small, easily captured prey. However, this strategy has consequences. Complete cohort failure has been recorded for overwintering *A. opacum* when ponds freeze completely, and winter temperature likely determines *A. opacum*'s northern range limits (M.C. Urban, unpublished data). Research in other systems also suggests an important role for both predator size and phenology on prey survival. For instance, prior



**Fig. 4** Significant linear regression relationships ( $P < 0.05$ ) between initial egg densities and hatchling densities for ponds at the intermediate (a) and southern (b) sites with (filled circle, solid line) or without (open circle, dashed line) *A. opacum*. Pond means were calculated for data available from 2002 to 2004. Note the change in the length of axes between sites

experimental work shows that while *N. viridescens* adults strongly affected prey survival, the strength of this relationship depended on the timing of prey recruitment relative to the arrival and departure of newts (Alford 1989). In both marine and freshwater systems, early arrival at a large size provides the opportunity for piscivores to prey upon small juvenile fishes (Keast 1985; Juanes and Conover 1995; Scharf et al. 2006), suggesting the generality of this mechanism in other aquatic taxa. Hence, the size-selective predators with the largest effects may be those species that differ phenologically from their prey. Changes in phenology, such as enforced by climate change, also could alter this contextual relationship and lead to the differential fitness of either the predator or the prey species (Durant et al. 2005). Preliminary evidence from this system indicates that mild winters are associated with denser and bigger-bodied *A. opacum* larvae in the spring.

In this study, only the largest gape-limited predators had strong effects on prey survival (e.g., Kurzava and Morin 1994). The presence of *A. opacum*, but not *N. viridescens*, explained early declines in *A. maculatum* hatchling density. The difference between these two predators is likely based

on *A. opacum* being larger gaped than *N. viridescens* when *A. maculatum* hatch and *A. opacum* larvae continuing to grow while *N. viridescens* adult body sizes remain relatively constant (Urban 2006). Survival differences across time and ponds were consistent with the observed period of *A. maculatum* vulnerability to *A. opacum* predators. Decreased prey densities in ponds with *A. opacum* occurred at the two more southern sites; however, the magnitude of this effect appeared to be strongest at the intermediate site (Fig. 4). The reasons for this pattern are not yet fully understood, but it could indicate the potential for different evolved reactions to predator occurrence between the two sites (Urban 2006). Differences in adaptations could occur because gape-limited predation risk, especially from *A. opacum*, is rarer and more variable among ponds at the intermediate site, suggesting the possibility of greater maladaptation due to gene flow from predator-free ponds (Urban and Skelly 2006).

Overall, evidence from my study indicates that the distribution of size-selective predators can provide accurate predictions for variation in prey abundances among temporary ponds. Similar effects of size-limited predators have been observed in other systems. *Notophthalmus viridescens*, one of the species highlighted in my study for its contribution to gape-limited predator size variation, is a keystone predator in similar temporary pond communities (Fauth and Reseta-rits 1991). In freshwater lakes, the presence of size-selective planktivorous fish predicts the composition and size of the zooplankton community (Brooks and Dodson 1965). In both marine and freshwater systems, gape-limited piscivores can alter prey behavior, growth and mortality (Walters and Juanes 1993; Persson et al. 1996). The classic keystone predator *Pisaster* only has strong and prolonged effects on the composition of rocky intertidal communities if its prey are at a sufficiently small size (Paine 1976; Paine and Trimble 2004). Taken together, results from my study and others indicate that natural gradients of size-dependent predation risk across space and time often can provide important insights into the biological determinants of local community composition and prey species abundances. However, general insights require that sufficient information is known about the predator species' phenology, size ontogeny, and its dynamic morphological constraints on the capture of large prey. Without this knowledge, the relative sizes of species may not predict the actual strength of the interactions. For example, gape-unconstrained predators of varying sizes successfully captured even the largest *A. maculatum* larvae by using adaptations such as venom (dytiscid beetles) or strong labia (aeshnid dragonfly larvae) that eliminate the need to engulf prey completely in order to subdue them. Also, the strong effects of predator and prey ontogeny revealed in my study suggest that adult body size – the usual explanatory variable in size-based predictions (Peters



1983) – may be remarkably uninformative about potential interaction strengths without any knowledge of the joint size trajectories of predators and prey.

The categorization of predators as gape-limited or gape-unconstrained presents a simple dichotomy that ignores many potentially relevant natural history details. Gape-unrelated effects of predator body size, such as the avoidance of small prey based on optimal foraging strategies and the increased predation rates of larger predators due to elevated metabolic demands, will affect predator–prey interactions (Schoener 1971; Wilson 1975; Peters 1983). Other size-unrelated predator traits, such as different foraging strategies, habitat choices, and environmental contexts (e.g., structural complexity), also can play important roles in determining predation rates (Huey and Pianka 1981; Gotceitas and Colgan 1989; Lima and Dill 1990). While predator gape-limitation can be used to produce generalizable predictions that may be applicable to a variety of natural situations, these predictions ultimately require experimental validation.

Most modeling frameworks of predator–prey interactions ignore prey size structure. Models that do incorporate ontogenetic shifts in prey body size generate novel predictions, including the stability of predator–prey interactions (Abrams and Walters 1996), enhanced prey abundances, an emergent Allee effect for predators (de Roos et al. 2003b), and disruptive selection on prey growth (DeAngelis et al. 1985; Day et al. 2002; Urban 2007). Field patterns for *A. maculatum* demonstrated a restricted duration of gape-limited predation confined to early developmental periods. In the context of community dynamics, a shorter window of vulnerability to predation due to a size refuge or the phenology of predators may promote their persistence in the face of otherwise intense predation risk (Paine 1976). In the context of evolutionary theory, high gape-limited predation threats are expected to promote the evolution of rapid growth in prey so that they can escape into a size refuge (DeAngelis et al. 1985; Day et al. 2002; Urban 2007). This strategy involves trading off declines in initial survival with the benefit of higher cumulative survival. However, theoretical predictions assume constant gape-limited predator densities through time in contrast to what was observed in this study. A reduced period of vulnerability to gape-limited predators may favor a strategy of slow growth to wait out the gape-limited predator's impending departure before engaging in risky foraging strategies to promote rapid growth. Conversely, a reduction in risky foraging behavior and subsequent growth are expected when gape-unconstrained predation threats are more intense than those from gape-limited predators, regardless of the timing of gape-limited predator threats (Urban 2007).

A focus on predator foraging traits has contributed greatly to our understanding of ecological, microevolutionary, and macroevolutionary patterns (Reznick et al. 1996;

Schmitz 1998; McPeck and Brown 2000; McPeck 2004). My results demonstrate that the phenology and growth dynamics of gape-limited predators may provide additional insights into the ecology and evolution of prey life histories. Such efforts are increasingly necessary in order to predict the effects of community perturbations initiated by the anthropogenic addition or deletion of top predators, the impacts of size-selective harvest, and changes to the global climate.

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