Interactions Between the Salamander Siren Intermedia and the Keystone Predator Notophthalmus Viridescens

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INTERACTIONS BETWEEN THE SALAMANDER
SIREN INTERMEDIA AND THE KEYSTONE PREDATOR
NOTOPHTHALMUS VIRIDESCENS[1]

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Abstract. Is the ability to function as a keystone predator a property of a species or an emergent property of the community? We addressed this question in a temporary-pond community where the broken-striped newt *Notophthalmus viridescens dorsalis* is known to act as a keystone predator on larval anurans.

We independently manipulated the initial density of adult *Notophthalmus* (two or four) and the presence or absence of one adult *Siren intermedia* in a set of 20 artificial ponds to determine if this additional predator affected the ability of *Notophthalmus* to function as a keystone predator. Each pond received a diverse assemblage of larval anuran prey: a spring-breeding assemblage of 275 *Rana utricularia*, 100 *Pseudacris crucifer* and 25 *Bufo americanus* tadpoles, and a summer assemblage of 200 *Hyla chrysoscelis* and 150 *Gastrophryne carolinensis* tadpoles. Two additional ponds received neither predator, to assay the outcome of competition among the tadpoles.

The effect of the salamander *Siren* on *Notophthalmus* survival and fecundity depended on the density of *Notophthalmus*. At low newt density *Siren* had no effect on survival, but at high newt density competition reduced the survival and growth rates of *Notophthalmus*. The density of *Notophthalmus* and the presence of *Siren* interacted to determine the fecundity of *Notophthalmus*. At low newt density *Siren* reduced *Notophthalmus* reproductive success by preying on larvae. At high newt density *Siren* indirectly enhanced reproductive success by reducing survival of adults, thus releasing larvae from intraspecific competition and cannibalism. *Notophthalmus* density had no effect on adult *Siren* survival or growth rate in this experiment, but other evidence indicates that competition with *Notophthalmus* reduces the growth rates of *Siren*.

Notophthalmus acted as a keystone predator on the assemblage of spring-breeding anurans; it increased the number of metamorphs of the weak competitor *Pseudacris crucifer* by releasing them from interspecific competition. *Siren* preyed on tadpoles in a nonselective manner. An additive model was sufficient to describe the effects of *Siren* and initial density of *Notophthalmus* on the structure of the tadpole assemblage.

In our system of experimental ponds, the strong interaction between *Siren* and *Notophthalmus* density did not extend its effects to lower trophic levels, and the direct and indirect effects of *Siren* did not alter the role of *Notophthalmus* as a keystone predator.

Key words: amphibian ecology; competition; complex interactions; density dependence; experimental field study; indirect effects; keystone predator; North Carolina; Notophthalmus; predation; Siren; temporary ponds.

INTRODUCTION

Predators play a major role in determining the structure of aquatic communities (Paine 1966, Morin 1981, Kerfoot and Sih 1987). Predators can reduce the abundance of prey directly (Gause 1934) or alter the abundance and distribution of prey species via indirect effects (Kerfoot and Sih 1987), which may be either negative or positive. Predators can indirectly decrease the relative abundance of prey species by allowing other species that are inferior competitors, but resistant to predation, to multiply (Dodson 1974, Kerfoot 1975, Morin 1981), or indirectly increase their abundance by reducing densities of superior competitors (Paine 1966, Dayton 1971, 1975, Stein and Magnuson 1976, Morin 1981, 1983). The discovery that predators can reverse the outcome of competitive interactions, the "keystone predator" concept of Paine (1966), has provided important insight into the role of predators in maintaining species diversity in natural communities. However, little experimental work has examined whether the role of the keystone predator changes with alterations in community structure, such as the presence of additional predators or the complexity of the prey assemblage.

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Many communities contain multiple predators, and because interactions among predators are likely to generate indirect effects that cascade to lower trophic levels (e.g., Kerfoot and Sih 1987, Kneib 1988), top predators can assume an especially important role in the determination of community structure (Paine 1966, 1980, Morin 1981, 1983, Sprules and Bowerman 1988). Here we describe the ecological interactions between two common predatory salamanders, one of which (*Notophthalmus viridescens*) is known to be a keystone predator in temporary pond communities (Morin 1981, 1983), and examine the effects of their interaction on an assemblage of larval anuran prey. The results specifically address whether the effects of this keystone predator are altered by a second predator, or whether its role is robust to such an interaction.

Natural history

Amphibians are an important component of temporary-pond communities in the Sandhills Region and Coastal Plain of North Carolina. Large temporary ponds in these regions are capable of supporting up to 5 species of salamanders and 16 species of anurans (J. E. Fauth, *unpublished data*). Salamanders are the dominant vertebrate predators in these temporary ponds. The most ubiquitous is the broken-striped newt, *Notophthalmus viridescens dorsalis* (Caudata: Salamandridae), which occurs in virtually all natural and man-made bodies of water. *Notophthalmus* adults are effective colonizers of new ponds, and persist in dried ponds by hiding in moist mud and beneath plant debris. When ponds refill, *Notophthalmus* enter the water column to feed on small aquatic prey (Hamilton 1940, Bishop 1941, Taylor et al. 1988). *Notophthalmus* functions as a keystone predator in temporary ponds; by selectively preying on the competitively dominant species, it reverses the outcome of competition among anuran tadpoles (Morin 1981, 1983). At high density, *Notophthalmus* is capable of excluding a number of insect and amphibian species from temporary ponds by consuming all their eggs and larvae (Morin 1983; H. M. Wilbur, *personal communication*; J. E. Fauth, *personal observation*).

Several other species of salamanders may coexist with *Notophthalmus* in temporary ponds of the Sandhills and Coastal Plain (Morin 1983). The lesser siren, *Siren intermedia intermedia* (Caudata: Sirenidae), is one of the largest and most abundant salamanders in this region and occurs with *Notophthalmus* in many natural ponds (J. E. Fauth, *unpublished data*). *Siren* is an obligately paedomorphic salamander that is restricted to the aquatic environment, but persists in temporary ponds by estivating in the mud when a pond dries (Gehlbach et al. 1973). When a pond refills, *Siren* emerges from its mucus-lined cocoon and feeds on the aquatic insects and larval amphibians that recolonize the pond. *Siren* occupies a high trophic position in temporary ponds, feeding on many smaller predators,

including aquatic invertebrates and larval *Notophthalmus* (J. E. Fauth and W. J. Resetarits, *unpublished data*). *Siren* cannot feed on adult *Notophthalmus* because of the extreme toxicity of adult *Notophthalmus* to vertebrates (Brodie et al. 1974).

Many species of insects and amphibians breed after rainstorms fill temporary ponds; use of such ephemeral habitats as oviposition sites may be an effective predator-avoidance strategy (Wilbur 1980, Resetarits and Wilbur 1989). When temporary ponds dry up, virtually all predators either emigrate or die from desiccation. *Notophthalmus* and *Siren* are unique predators because they circumvent the predator-avoidance strategy of many temporary-pond species by persisting in the dry pond basin, thus allowing them to prey on the eggs and larvae of even the earliest colonists. Because they affect prey species early in the development of the temporary-pond community, these predators are likely to have profound effects on community structure, as illustrated by the keystone-predator role played by *Notophthalmus* (Morin 1983).

MATERIALS AND METHODS

Field methods

The experiment was conducted in an array of 22 artificial ponds (cattle-watering tanks 1.5 m in diameter), in an open field at the Duke Zoology Field Station, Durham, North Carolina, in 1986. Our method of reconstructing pond communities closely followed that of Morin (1981, 1983). The interior of each tank was painted with an inert epoxy enamel to prevent leaching of toxic ions from the galvanized metal and to provide a fresh surface for colonization by periphyton. Tanks were filled to a depth of 50 cm (volume: ≈1000 L) with city tap water on 1–3 March. Occasional additions of water maintained a constant water level throughout the experiment, and screened drainpipes prevented overflow.

On 8 and 17 March, 0.5-kg packets of litter collected from the margin of a temporary pond were added to each tank. Pond litter provided spatial heterogeneity, chemical buffering of the water, resting stages of microorganisms, and a source of nutrients for the aquatic food web. Fifteen washed stems of an aquatic macrophyte (*Myriophyllum* sp.) were planted in three clumps in the litter to provide additional structural complexity. The experimental ponds were inoculated three times (8, 11, and 13 March) with carefully randomized 1-L pond water suspensions, collected with a 400-μm mesh net from several temporary ponds in Scotland, Richmond, and Durham counties. These inocula ensured the establishment of a diverse aquatic community. We also introduced additional macroinvertebrates as alternative prey for the salamanders on 16 March: two gravid amphipods (Amphipoda: Gammaridae), five pairs of adult isopods (Isopoda: Asellidae), four small snails (Gastropoda: Lymnaeidae), and

nine large snails (Gastropoda: Planorbidae). Snails and isopods reproduced rapidly in the experimental ponds. Tightly fitting lids of fiberglass windowscreening prevented unwanted colonization by insects and ovipositing treefrogs, and retained experimental organisms.

We experimentally manipulated two factors: the presence or absence of one adult *Siren*, and the density of adult *Notophthalmus* (two or four). All combinations of these two factors were replicated five times in a total of 20 ponds. Two additional ponds served as predator-free controls to assay the outcome of competition among tadpoles in the absence of predators. Ponds were placed in five spatial blocks to account for unknown physical gradients at the site. The two predator-free ponds were randomly assigned to blocks 1 and 5. All treatments were randomly assigned to positions within a block.

Adult *Siren* were collected by dipnetting from two ponds in Scotland County, North Carolina, on 7 and 16 March. Individuals were weighed, measured (snout to posterior margin of vent [snout–vent length, SVL]), and added to experimental ponds on 20 March. Individuals of similar initial sizes were placed in the same block; this nonrandom distribution of *Siren* adults was intended to minimize within-block variation due to size. *Notophthalmus* were collected from one of the above ponds on 19 March, and were sexed, weighed, measured (SVL), and added to experimental ponds on 20 March. Either two or four adults were added, and a 50:50 sex ratio was established in each experimental pond. *Notophthalmus* courts and reproduces readily in artificial ponds (Morin et al. 1983, Wilbur et al. 1983). Both *Siren* (0.56 individuals/m²) and *Notophthalmus* densities (low density: 1.1 individuals/m²; high density: 2.2 individuals/m²) were within the range of densities encountered in nature (Gehlbach and Kennedy 1978, Harris et al. 1988; J. E. Fauth, *personal observation*).

We added two distinct assemblages of larval anurans to the experiment to mimic the breeding phenology of anurans in 1986. An assemblage of spring-breeding anuran tadpoles consisting of 25 *Bufo americanus,* 275 *Rana utricularia,* and 100 *Pseudacris* (=*Hyla*) *crucifer* hatchlings was added to all experimental ponds on 29 March. On 3 July, 127 d after the addition of the spring breeders, an assemblage of summer-breeding anurans consisting of 200 *Hyla chrysoscelis* and 150 *Gastrophryne carolinensis* tadpoles was added to the experimental ponds. By this time, all *Bufo* and *Pseudacris* had metamorphosed or died, but *Rana* tadpoles were still abundant in the tanks. These species of anurans are common components of temporary ponds in the Sandhills and Coastal Plain of North Carolina and, with the exception of *Gastrophryne,* the competitive relationships among them are well established (Morin 1983, Morin and Johnson 1988, Van Buskirk 1988, Alford 1989, Wilbur and Fauth 1990). *Rana* and *Bufo* are strong competitors, *Pseudacris* is a weak competitor, and *Hyla* is intermediate. *Gastrophryne* is a sur-

face filter-feeder with a rapid development rate, and seemed likely to be a strong competitor. If *Notophthalmus* acts as a keystone predator, *Pseudacris* should increase in relative abundance at the expense of *Bufo, Rana,* and *Gastrophryne.*

Ponds were searched for metamorphosing amphibians a minimum of three times per week and daily during peak periods of metamorphosis. Metamorphosis was defined by forelimb emergence in anurans and by gill resorption in *Notophthalmus.* Juvenile *Notophthalmus* were the offspring of the adults originally introduced into the artificial ponds. *Siren* are obligately paedomorphic so they never metamorphose. All amphibians recovered were identified, counted, measured (SVL), blotted dry on paper toweling, weighed to 0.1-mg precision, and released at their natal pond. Each individual's larval period was then calculated as the number of days since introduction into the experimental ponds. Ponds were drained and searched for survivors on 17–19 November, 8 d after the last metamorphic *Notophthalmus* was collected. At termination many ponds contained large populations of *Rana* tadpoles and *Notophthalmus* larvae that showed no sign of nearing metamorphic climax. If left in the ponds, these individuals would have overwintered and metamorphosed the following spring. Larval amphibians were preserved in formalin upon capture; adult *Notophthalmus* and *Siren* were anesthetized, weighed, and measured before preservation.

Statistical analyses

The independent units of statistical analysis were the means of population-level responses for individual ponds. The response variables were mean survival, mass, length of larval period, and growth rate (mean mass/mean larval period). These variables are known fitness components in several amphibians (Berven and Gill 1983, Smith 1987, Semlitsch et al. 1988) and are sensitive indicators of the intensity of competition (Wilbur 1988, Fauth et al. 1990). Low growth rates, long larval periods, and small mass at metamorphosis are associated with high levels of competition in amphibians (Wilbur 1980).

Our statistical model for testing the biological interactions between *Siren* and *Notophthalmus* density was an additive model:

$$R_{ijkl} = \mu + B_i + N_j + S_k + (I_{jk}) + E_l$$

where R_{ijkl} = the population mean response, μ = the grand mean, B_i = the effect of spatial blocks, N_j = the effect of *Notophthalmus* (j = 0, 2, or 4), and S_k = the effect of *Siren* (k = 0 or 1), and E_l is the residual error. We are interested in whether this additive model is sufficient to describe the main treatment effects, or whether an interaction term (I_{ijk}) is necessary. An interaction term could be generated by *Siren* affecting newt abundance or newt behavior, or by tadpoles re-

sponding differently to the two densities of newts when *Siren* is present.

Predator treatments in this experiment were non-orthogonal; we had no estimate of the effect of *Siren* alone. Therefore we were not explicitly testing the additivity of the effects of these two predators with our design. Due to the limited number of tanks available, we were forced to choose between a complete factorial design with limited statistical power and a statistically powerful design that addressed a more specific question. We chose a design with sufficient power to have confidence in our results, and which reflected the distribution of the salamanders in nature. *Siren* has a more limited distribution in temporary ponds in North Carolina than does *Notophthalmus*. In temporary ponds where *Siren* occurs, *Notophthalmus* are always present, but at widely varying densities (J. E. Fauth, *unpublished data*).

We used multivariate analysis of variance (MANOVA) to analyze the relative abundances of metamorphs of the five anuran species. MANOVA provided a conservative test of the null hypothesis that treatments had no effect on the species composition of the anuran assemblage by simultaneously considering multiple correlated responses. Because the relative abundances sum to one and are thus linearly dependent, it was necessary to delete the relative abundance of one species from the analysis. Statistically the particular species chosen was inconsequential; *Bufo* was chosen because of its low initial abundance. MANOVA was also used to investigate whether the absolute abundance of survivors differed among treatments. Here the six-response vector consisted of the number of metamorphs of each anuran species plus the number of overwintering *Rana* tadpoles. This analysis tested the null hypothesis that treatments had no effect on the structure of the anuran assemblage. MANOVA was also used to test the effects of treatments on the vector of response variables (survival, mass at metamorphosis, length of larval period) as a measure of overall performance for each focal species (see Morin 1983). Analysis of variance (ANOVA) was used to analyze the individual response variables of each amphibian species, as well as the combined density of all surviving amphibians. ANOVA tested whether salamanders altered the total abundance of all surviving amphibians, and whether predator treatments had a significant effect on the performance of each focal species. Spatial blocks were initially considered fixed effects, but when preliminary analyses indicated that block effects and higher-order terms containing blocks were nonsignificant, block sums of squares were pooled as the error term in subsequent analyses. This treats blocks as random effects despite the fact that *Siren* were allocated to blocks according to size. Type III sums of squares were used in all analyses because they are not functions of cell counts, and are therefore suitable for unbalanced designs. Type III ss make each effect orthogonal to higher-level effects that contain the effect of interest, thus allowing main effects to be evaluated independently from their higher-order terms (SAS Institute 1985). Survival was angularly transformed to meet the assumptions of analysis of variance. All statistical analyses were performed using SAS (SAS Institute 1985).

RESULTS

Responses of adult Siren.—There were no effects of treatments on the responses of *Siren*: all individuals survived to the end of the experiment and their growth rates were similar in all treatments (mean growth rates 56.0 mg/d [0.15 mm/d] and 62.1 mg/d [0.16 mm/d] in treatments with low and high densities of *Notophthalmus*, respectively; $F_{1,9} = 0.06$, $P > .50$). This does not imply that *Notophthalmus* did not compete with *Siren*, only that no difference was observed between the responses to the two newt-density treatments.

Responses of adult Notophthalmus.—There was a highly significant *Siren* × *Notophthalmus* density interaction in a MANOVA of the survival and growth rate of adult *Notophthalmus* (Table 1), indicating that the effect of adding *Siren* depended on the initial density of *Notophthalmus*. Without *Siren* all *Notophthalmus* survived until the end of the experiment in low-density ponds. A single *Notophthalmus* died in a high-density pond, but growth rates were 59% below those in low-density ponds (ANOVA: $F_{1,8} = 4.33$, $P < .07$). When *Siren* was present *Notophthalmus* experienced no mortality at low density, but at high density survival was 25% lower (Fig. 1). Growth rates in high-density ponds were 62% below those at low density (ANOVA: $F_{1,8} = 6.36$, $P < .05$), despite the reduced survival. Growth rates at high density alone and low density with *Siren* were nearly identical (Fig. 1). Because *Siren* are incapable of preying on adult *Notophthalmus*, this reduction in growth is most likely due to interspecific competition. Based on comparison of *Notophthalmus* growth rates at low density with *Siren* and at high density alone, a single adult *Siren* appears to be the competitive equivalent of two adult *Notophthalmus*.

Notophthalmus *reproduction.* — *Notophthalmus* successfully reproduced in all but one experimental pond, which contained two adult male *Notophthalmus* at the end of the experiment. We assumed that a large immature male was incorrectly sexed as a female when the experiment began, so we excluded this pond from analyses of *Notophthalmus* reproduction.

Reproduction in *Notophthalmus* was negatively density dependent. In the absence of *Siren*, *Notophthalmus* produced fewer offspring at high density than at low density (ANOVA: $F_{1,7} = 5.55$, $P < .05$). The effects of *Siren* depended on *Notophthalmus* density (Tables 2, 3). At low newt density *Siren* reduced the reproductive output (number of efts + larvae) of *Notophthalmus* by 64% ($F_{1,7} = 10.24$, $P < .02$). At high newt density, however, *Siren* did not affect reproductive output (Ta-
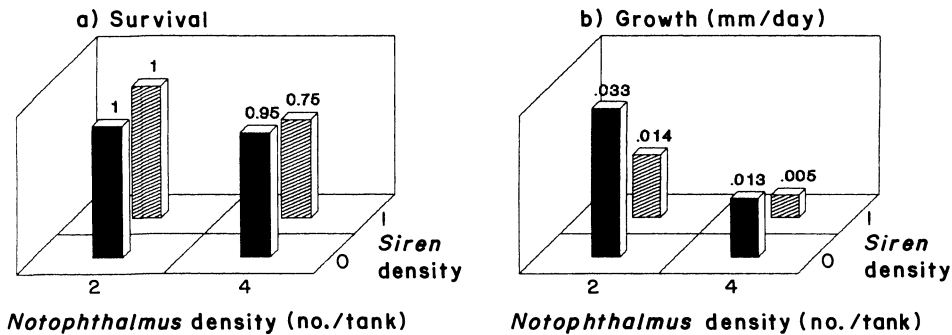
FIG. 1.   (a) Survival and (b) growth rates of adult *Notophthalmus* in the main experiment. The height of the bars reflects the magnitude of the mean population responses (values given at tops of bars).

ble 2). More efts emerged and they were smaller than those at high density alone, but the differences were not statistically significant. At high newt density the negative direct effect of *Siren* preying on larval *Notophthalmus* was offset by the positive indirect effect resulting from a reduction in adult *Notophthalmus* survival. The negative direct effect of *Notophthalmus* on its own reproductive output was stronger than the negative direct effect produced by *Siren*.

Anuran responses

Both *Siren* and *Notophthalmus* density significantly affected the total number of tadpoles that survived to metamorphosis (Table 4). Anuran survival was highest in the absence of predators, but declined sharply when *Notophthalmus* was present (Fig. 2). Two and four *Notophthalmus* had roughly equivalent effects, reducing the mean number of tadpoles that metamorphosed by 60% and 57%, respectively. When *Siren* were present

even fewer metamorphs emerged (Fig. 2). On average, 8.8 metamorphs emerged from ponds containing both predators, compared to 57 metamorphs from predator-free ponds. Lack of a significant interaction term in the ANOVA (Table 4) indicated that an additive model sufficiently described the dynamics of salamander predation on tadpoles.

Notophthalmus had a substantial impact on the composition of the anuran assemblage (Table 5). In the absence of predators, all five anuran species persisted in the experimental ponds. However, tadpoles of the hylids *Pseudacris crucifer* and *Hyla chrysoscelis* were present in lower frequencies than their initial proportions. These two species are the weakest competitors (Morin 1983, Wilbur 1987). Tadpoles of *Rana, Bufo,* and *Gastrophryne* were correspondingly more abundant. Addition of *Notophthalmus* to the experimental community caused a drastic shift in the composition of the anuran assemblage (Fig. 3). *Rana* became the

TABLE 1.   MANOVA and ANOVAs of adult *Notophthalmus* responses to treatments. Survival was angularly transformed to meet the assumptions of the analysis of variance.

MANOVA (survival, growth rate)			
Source of variation	df	Wilks' λ	*P*
Siren presence/absence	2,15	0.347	.0004
Notophthalmus density	2,15	0.227	.0001
Siren × *Notophthalmus* density	2,15	0.498	.0054
ANOVA of survival			
Source of variation	df	SS	*F*	*P*
Siren presence/absence	1	720.0	16.00	.0001
Notophthalmus density	1	1620.0	36.00	.0001
Siren × *Notophthalmus* density	1	720.0	16.00	.0001
Error	16	720.0		
Total	19	3780.0		
ANOVA of growth rate			
Source of variation	df	SS	*F*	*P*
Siren presence/absence	1	0.0009698	7.87	.0127
Notophthalmus density	1	0.0010175	8.26	.0110
Siren × *Notophthalmus* density	1	0.0001729	1.40	.2534
Error	16	0.0019713		
Total	19	0.0041315		

TABLE 2. Summary of treatment means for *Notophthalmus* efts and larvae.

Treatment		*Notophthalmus* response			
Siren	*Notoph-thalmus* density (no./ pond)	No. efts	Eft mass (g)	Eft larval period (d)	No. larvae
Absent	2	35.25	0.1744	188.3	8.25
	4	17.20	0.1661	192.7	1.00
Present	2	14.40	0.2681	184.1	3.00
	4	27.20	0.1480	190.2	8.20

clear dominant, and the proportion of *Pseudacris* greatly increased. Both species are resistant to predation by *Notophthalmus* (Morin 1983, 1986, Wilbur 1988, Wilbur and Fauth 1990); *Pseudacris* also benefits from reduced densities of competing tadpoles. At high *Notophthalmus* density the entire summer-breeding cohort (*Hyla* and *Gastrophryne*) was eliminated from the ponds. *Siren* had no statistically significant effects on the composition of the anuran assemblage (Table 5; Fig. 3) even though the total number of survivors was greatly reduced and several species were eliminated (Table 6).

The structure of the anuran assemblage was largely determined by the relative susceptibility of each species to predation and competition. In predator-free ponds survival of the strong competitors *Bufo* and *Rana* was high (Table 6; Fig. 3). However, few *Rana* metamorphosed; most remained as overwintering tadpoles. Few *Pseudacris* survived in ponds without predators. Survival of the summer cohort of tadpoles was mixed in the two predator-free ponds. In one pond both species persisted (survival: *Hyla*, 5.5%; *Gastrophryne*, 56%). In the other pond a diatom bloom occurred in late spring and persisted until the end of the experiment; only a single *Gastrophryne* emerged. In the absence of predators survival of all species except *Pseudacris* was relatively high, but the mean mass of the metamorphs was low (Table 6). *Pseudacris* benefitted from a moderate level of predation. In the absence of predators its survival was very low, and its overall abundance was negatively correlated with that of every other anuran species (Table 7; Fig. 3), indicating it was a poor competitor. However, *Pseudacris* was much more abundant in ponds where *Notophthalmus* reduced the densities of its competitors.

Although neither predator had a statistically significant effect on survival of *Bufo* (Table 7; Fig. 3), *Bufo* was eliminated from the experimental community when *Siren* was present. Likewise, the number of metamorphs of *Rana* was not affected by either predator, although *Siren* had a significant impact on the number of overwintering tadpoles (Tables 6 and 7). The tadpoles that survived in tanks with *Siren* were larger than those in tanks lacking *Siren* ($F_{1,14} = 7.49$, $P < .02$).

The effects of the two predators on the summer anuran cohort were also mixed (Table 6). Neither predator had a significant effect on survival of *Hyla*, which performed poorly in all treatments (Table 6). However, *Gastrophryne* performed well in one pond without predators (Table 6) but was virtually eliminated from ponds with *Notophthalmus* (Table 6 and 7).

A MANOVA on the six-response vector—consisting of the final abundance of each anuran species plus the number of overwintering *Rana* tadpoles—indicated that only *Siren* had a significant effect on the structure of the entire tadpole assemblage (Table 7). The effect of *Siren* was to reduce the total number of metamorphs (Table 4), especially *Pseudacris,* and to reduce the number of overwintering *Rana* tadpoles (Table 7). *Notophthalmus* did not affect the overall structure of the prey assemblage despite strong negative effects on *Gastrophryne* survival and positive effects on *Pseudacris* (Tables 6 and 7). Lack of a significant interaction term in the MANOVA indicated that the two factors—*Siren* presence and *Notophthalmus* density—acted in an additive manner in determining the structure of the prey assemblage. The possibility of a Type II error in the conservative MANOVA test is unlikely, since ANOVAs of the survival of individual prey species also failed to demonstrate a significant interaction.

DISCUSSION

In order for the keystone predator effect to occur, there must be asymmetric competition among the potential prey species, and the predator must selectively consume the dominant competitor (Paine 1966, Morin 1981). Asymmetries in the competitive relationships among the larval anurans used in this experiment were described in previous studies (Morin 1983, Wilbur and Alford 1985, Wilbur 1987, Morin and Johnson 1988, Van Buskirk 1988, Alford 1989) and were apparent in our experiment. In the absence of predators the relative
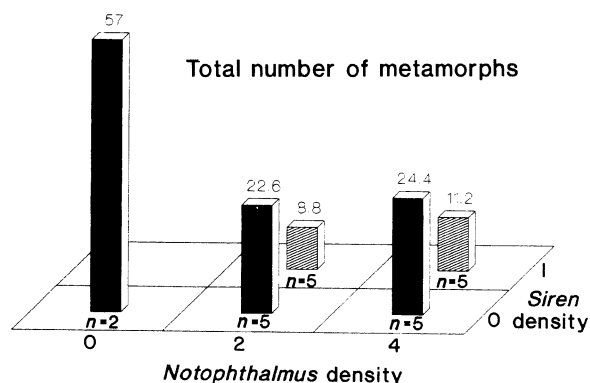
FIG. 2. Total number of anuran metamorphs as a function of predator treatments. The height of the bars reflects the magnitude of the mean population responses, which are given above the bars. Numbers below the bars indicate the total number of populations represented.
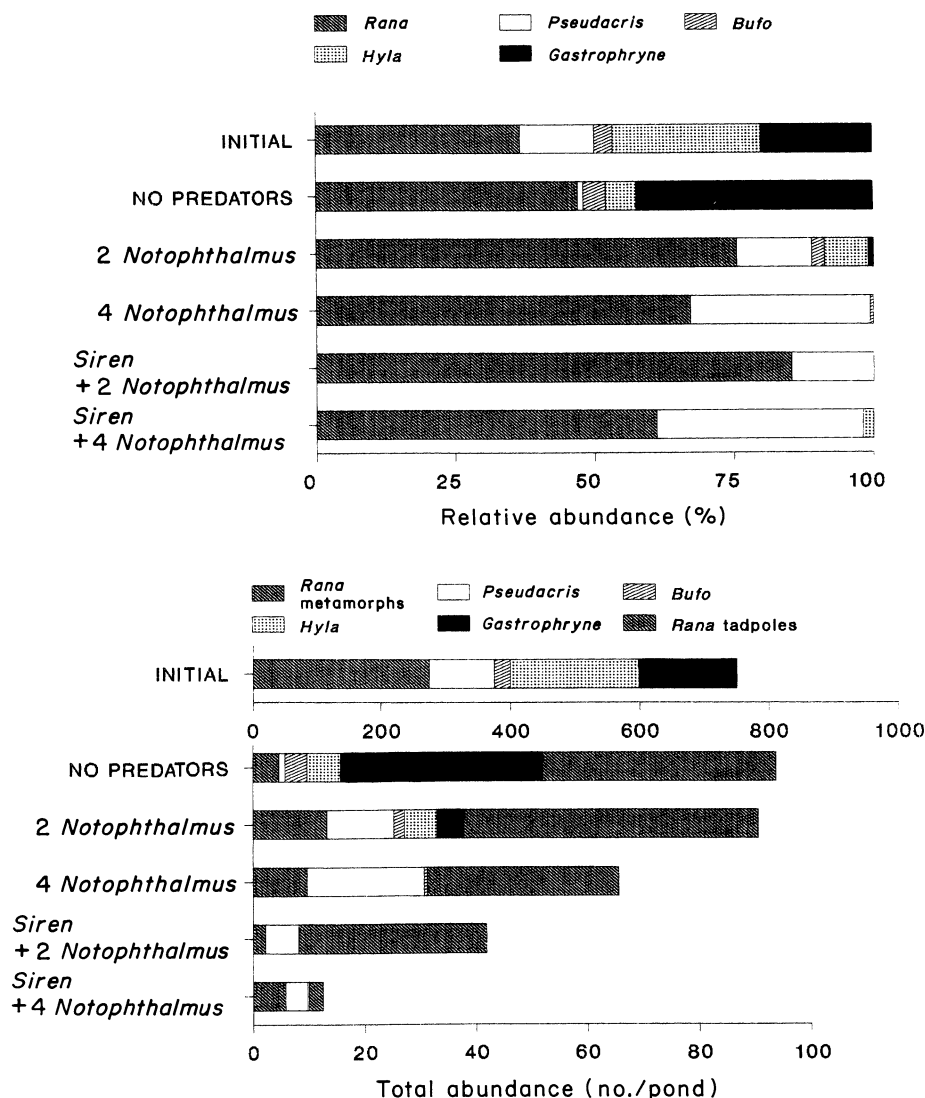
FIG. 3. (a) Species composition of the anuran assemblage. Values are the relative abundance of five anurans in the initial introduction of hatchlings and in the communities of metamorphosing frogs and overwintering tadpoles from the predator treatments. Each bar represents the mean of five replicate populations, except the bars for the no-predator treatment (which represents two populations) and the initial composition. (b) Absolute abundances of the species in the anuran assemblage. For the five treatments (lower section of figure), the *Rana* data are divided into metamorphs (leftmost position on each bar) and overwintering tadpoles (rightmost position on each bar). Note different abundance scales for initial condition and for the five treatments.

abundance of the strong competitors *Rana utricularia, Bufo americanus,* and *Gastrophryne carolinensis* increased, at the expense of the weaker competitors *Pseudacris crucifer* and *Hyla chrysoscelis.* The role of *Notophthalmus* as a keystone predator, described by Morin (1981, 1983), was also observed in our experiment. When newts were present the relative abundance of the weakest competitor, *Pseudacris crucifer,* increased at the expense of the competitive dominants *Gastrophryne, Hyla,* and *Bufo.*

Notophthalmus was a keystone predator in our experiment, as well as in those of Morin (1981, 1983),

Wilbur (1987), and Alford (1989), despite radical differences in the total densities (750, 1200, 1760, and 1760 tadpoles per pond in high-density treatments, respectively) and species richness (5, 6, 4, and 4 species, respectively) of the anuran assemblages. In each experiment *Notophthalmus* preyed selectively on the competitive dominants (*Scaphiopus holbrooki, Rana utricularia, Bufo* sp., and/or *Gastrophryne*), allowing competitively inferior species (generally hylids) to increase in relative abundance. This suggests that *Notophthalmus* will be a keystone predator whenever the precondition of asymmetric competition among its lar-

TABLE 3. Summary of ANOVAs of population mean responses of *Notophthalmus* efts and larvae.

	Response variables									
	Reproductive output (no. efts + no. larvae)		No. efts		Mass efts		Eft larval period		No. larvae	
Source of variation	F	P	F	P	F	P	F	P	F	P
Siren presence/absence	0.70	NS	0.77	NS	0.91	NS	0.86	NS	0.05	NS
Notophthalmus density	0.05	NS	0.18	NS	2.64	NS	2.15	NS	0.05	NS
Interaction	8.07	*	6.24	*	2.01	NS	0.06	NS	2.01	NS

* $P < .05$; NS = $P \geq .05$.

val anuran prey is fulfilled. What if the precondition is not met, and the larval anurans are equal competitors, such as the *Rana utricularia* and *Bufo americanus* used by Wilbur and Fauth (1990)? In this case *Notophthalmus* preyed on each species in proportion to its representation in predator-free control ponds and so did not alter the composition of the anuran assemblage (Wilbur and Fauth 1990).

Not all predators of larval anurans are keystone predators. Morin (1983) discovered that larval *Ambystoma tigrinum* entirely eliminated an assemblage of larval anurans consisting of 1200 individuals of six species from experimental pond communities. Under identical conditions *Notophthalmus* acted as a keystone predator (Morin 1983). In a second study conducted in experimental ponds, Van Buskirk (1988) found that naiads of two odonate species (*Anax junius* and *Tramea carolina*) preyed selectively on tadpoles of the weak competitors *Pseudacris triseriata* and *Hyla* (=*Pseudacris*) *crucifer*. The combined effects of the two odonates were additive; either alone or in concert the odonates decreased survival of *Pseudacris* and *Hyla* and enhanced survival of the strong competitor *Bufo americanus* (Van Buskirk 1988).

In our experimental ponds *Siren* did not act as a keystone predator. *Siren* preyed on tadpoles in a nonselective manner, reducing densities of species in proportion to their abundance. However, the structure of the anuran assemblage (as measured by the vector of the absolute abundances of metamorphs) was determined principally by the presence or absence of *Siren*, irrespective of the density of *Notophthalmus*. Those anuran larvae that survived predation metamorphosed

earlier and at larger size than in the no-predator control. Both shorter larval period and larger size at metamorphosis have been linked to increased fitness in amphibians (Smith 1987, Semlitsch et al. 1988). In our experimental ponds *Notophthalmus* established the composition of the anuran assemblage, and *Siren* set the total abundance of larval anurans.

We found that interactions between the predators depended on the density of *Notophthalmus*. At low density *Siren* had no effect on survival of adult newts, but at high density survival was significantly reduced. Competition is the most likely causal mechanism for the reductions in survival and growth, because adult *Notophthalmus* are invulnerable to vertebrate predation by virtue of their powerful tetrodotoxin (Brodie et al. 1974). We expected to find that interactions between *Siren* and *Notophthalmus* density would uniquely determine prey abundance because competition between the salamanders decreased the number of adult *Notophthalmus* present. Surprisingly, we found no evidence in the responses of the larval anurans for an interactive effect of the predators, presumably because the tadpoles are vulnerable to predation by *Notophthalmus* for only a short time (Alford 1989, Wilbur and Fauth 1990). Van Buskirk (1988) found that larval odonates had an additive effect on the abundance of their tadpole and zooplankton prey, even though interactions between the predators reduced the density of one of the odonate species in the two-predator communities. He ascribed the additive effect to predation on tadpoles occurring before interactions between the odonates reduced predator densities. A similar mechanism likely operated in our experiment. Adult *No-*

TABLE 4. ANOVA of total abundance of metamorphosed anurans. Model $R^2 = 0.96$.

Source of variation	df	SS	F	P
, Block	4	3011.50	6.59	.0476
Siren presence/absence	1	911.25	7.97	.0477
Notophthalmus density	2	1750.05	7.65	.0429
Block × *Siren* presence/absence	4	1350.50	2.95	.1596
Block × *Notophthalmus* density	5	5548.70	9.71	.0235
Siren × *Notophthalmus* density	1	0.45	0.00	.9530
Error	4	457.30		
Total	21	12 289.32		

TABLE 5. MANOVA of species composition of the tadpole assemblage. Values are the angular transformations of the relative abundances of *Rana utricularia, Pseudacris crucifer, Hyla chrysoscelis, Gastrophryne carolinensis.*

Source	df	Wilks' λ	F	P
Siren presence/absence	4,14	0.91117	0.34	.8457
Notophthalmus density	8,28	0.22896	3.81	.0038
Siren × *Notophthalmus* density	4,14	0.75082	1.16	.3691

tophthalmus are not preyed upon by *Siren,* and therefore reductions in adult *Notophthalmus* densities were probably due to long-term competitive interactions, whereas tadpoles were vulnerable to newt predation for only a brief period.

The direct and indirect effects of *Siren* did nothing to alter the role of *Notophthalmus* as a keystone predator in this system. In each instance a simple additive model was sufficient to describe the effects of the two predators together on the anuran assemblage. Although the effects of *Siren* and *Notophthalmus* were strictly additive, their individual impacts on the an-

uran assemblage were very different. *Notophthalmus* altered the species composition of the anuran assemblage by preferentially feeding on strong competitors. *Siren* lowered the total density of tadpoles without altering the species composition.

Reproduction and adult growth of *Notophthalmus* were negatively density dependent; more than twice as many offspring were produced at low density as at high density. This result has now been obtained experimentally several times (Morin 1983, Morin et al. 1983, Harris 1987, this study) and reinforces data from field studies that suggest that reproductive success is density dependent (Gill 1978, Harris et al. 1988). Because fecundity is positively correlated with adult size (Verrell 1986), density-dependent growth is a further means of population regulation. Density dependence thus could act both within and between generations to regulate *Notophthalmus* populations.

The effect of *Siren* on the fecundity of *Notophthalmus* also depended on density. At low density *Siren* directly reduced the reproductive output of *Notophthalmus* by preying on larvae. Contrary to our expectations, predation by *Siren* did not reduce the densities of larval *Notophthalmus* in high-density ponds. We

TABLE 6. Summary of anuran responses. Entries in the table give population means ± 1 SD.

Species Response	No. predators*	2 *Notophthalmus*	4 *Notophthalmus*	*Siren* + 2 *Notophthalmus*	*Siren* + 4 *Notophthalmus*
Rana					
Survival	0.17 ± 0.04	0.24 ± 0.14	0.16 ± 0.11	0.13 ± 0.08	0.03 ± 0.02
% metamorphosed†	0.10 ± 0.11	0.20 ± 0.45	0.22 ± 0.43	0.06 ± 0.08	0.70 ± 0.45
No. populations‡	2	5	5	5	5
Mass at metamorphosis (mg)	916.3 ± 116.0	1329.0 ± 376.2	880.3 ± 321.7	801.0 ± 138.0	1647.7 ± 631.5
Larval period (d)	151.2 ± 5.9	136.0 ± 4.8	96.7 ± 21.2	87.8 ± 23.8	76.8 ± 6.4
Growth rate (mg/d)	6.1 ± 0.5	10.9 ± 6.6	9.0 ± 1.4	9.3 ± 1.7	21.5 ± 8.5
Pseudacris					
Survival	0.01 ± 0.01	0.12 ± 0.17	0.21 ± 0.16	0.06 ± 0.09	0.04 ± 0.02
No. populations	1	5	5	3	5
Mass at metamorphosis (mg)	74.4	76.7 ± 23.3	98.2 ± 20.3	123.2 ± 5.2	211.0 ± 75.8
Larval period (d)	51.0	54.5 ± 3.5	52.2 ± 4.4	50.8 ± 4.2	52.5 ± 4.3
Growth rate (mg/d)	1.5	1.4 ± 0.4	1.9 ± 0.4	2.4 ± 0.3	4.0 ± 1.3
Bufo					
Survival	0.16 ± 0.11	0.08 ± 0.11	0.02 ± 0.3	0	0
No. populations	2	2	1	0	0
Mass at metamorphosis (mg)	152.1 ± 24.4	163.3 ± 7.8	164.9	···	···
Larval period (d)	40.6 ± 0.9	39.3 ± 0.5	39.0	···	···
Growth rate (mg/d)	3.7 ± 0.6	4.1 ± 0.2	4.2	···	···
Hyla					
Survival	0.03 ± 0.04	0.03 ± 0.08	0	0	0.001 ± 0.002
No. populations	1	1	0	0	1
Gastrophryne					
Survival	0.24 ± 0.33	0.03 ± 0.08	0	0	0
No. populations	2	1	0	0	0

* Only two replicates in this treatment; all other treatments had five replicates.
† Percentage of survivors (metamorphs + overwintering tadpoles) that metamorphosed.
‡ Number of populations producing metamorphs.

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TABLE 7. Multivariate and univariate analyses of the final number of anurans surviving.†

MANOVA

(Response vectors: no. *Rana, Pseudacris, Bufo, Hyla, Gastrophryne* metamorphs; no. *Rana* tadpoles)

Source of variation	df	Wilks' λ	F	P
Siren presence/absence	6,12	0.397	3.04	.048
Notophthalmus density	12,24	0.331	1.48	.201
Siren × *Notophthalmus* density	6,12	0.797	0.51	.791

Partial correlations and P values

Species	*Rana*	*Bufo*	*Hyla*	*Gastrophryne*	*Rana* tadpoles
Pseudacris	−.001	−.424	−.239	−.042	−.453
	.972	.080	.339	.868	.059
Rana		.009	.108	.222	−.205
		.970	.669	.375	.414
Bufo			.436	.450	.382
			.070	.061	.118
Hyla				.306	.321
				.217	.194
Gastrophryne					−.132
					.601

ANOVAs (F statistics)

Source of variation	*Rana*	*Rana* tadpoles	*Pseudacris*	*Bufo*	*Hyla*	*Gastrophryne*
Block	7.79*	2.78	3.23	0.84	1.10	479.40****
Siren presence/absence	3.62	17.32*	11.49*	2.67	0.96	1.00
Notophthalmus density	3.30	5.98	3.21	2.14	0.83	1505.71****
Block × *Siren* presence/absence	1.33	1.68	5.20	0.63	1.03	1.00
Block × *N.* density	2.31	2.29	2.21	0.82	0.97	574.88****
Siren × *N.* density	0.55	0.22	2.72	1.19	1.07	1.00

* = $P < .05$; **** = $P < .0001$.

† Values for the MANOVA are the numbers of metamorphs of each species and the number of overwintering *Rana* tadpoles. Partial correlations from the error sums of squares and cross-products matrix provide an estimate of the intensity of competition among the anurans. ANOVAs evaluate the effects of each predator on each individual anuran species.

expected a reduction in larval densities, with a concomitant increase in size at metamorphosis and reduction in larval period due to competitive release. Instead, *Siren* indirectly enhanced reproductive success by reducing survival of adults, apparently relaxing cannibalism by adults on their larvae (contra Harris 1987). Surviving larvae were smaller and had longer larval periods than those in *Siren*-free tanks, indicating a more intense competitive environment. Predation by *Siren* cannot be expected to regulate *Notophthalmus* populations if this indirect effect remains strong over a wide range of densities, but it can still be expected to have an effect on *Notophthalmus* demography.

Interactions between *Siren* and *Notophthalmus* depend on more than just density; they also change as the salamanders grow. As long as the size of each species exceeds the gape of the other, interactions are limited to competition. A previous experiment (Fauth et al. 1990) demonstrated that larvae of *Siren* and *Notophthalmus* compete in artificial ponds, but are initially competitive equals. A second experiment (J. E. Fauth and W. J. Resetarits, Jr., *unpublished data*) indicated that competition between juvenile *Siren* and adult *Notophthalmus* results in decreased growth rates in each. Diminished growth rates may decrease the fecundity of both species, increase the age at first re-

production of *Siren*, and increase its vulnerability to desiccation (Fauth et al. 1990). The present experiment demonstrated the competitive effects of *Siren* on adult *Notophthalmus* survival and growth rates. Based on comparisons of growth rates, a single adult *Siren* appears to be the competitive equivalent of two adult *Notophthalmus*. We were unable to measure the reciprocal interaction, but we expect that adult *Notophthalmus* compete with adult *Siren*, as well as juvenile *Siren*, because these two life stages are ecologically very similar.

When the gape of one species of predator exceeds the size of another, interactions may shift from competition to non-lethal injury and ultimately to predation (Werner and Gilliam 1984, Wilbur 1984, 1988). *Siren* reduced the number of *Notophthalmus* metamorphs by 59% in low-density treatments. The qualitative responses of these efts (greater mass and shorter larval periods) indicate that adult *Siren* are predators on larval *Notophthalmus*. *Notophthalmus* eggs, which are laid singly on aquatic vegetation or pond debris, are probably also vulnerable to predation by *Siren*. If we were to explore the interactions between these two species further, we would expect adult *Notophthalmus* to prey on small larval *Siren*, because they readily consume prey items of similar size (e.g., Harris 1987).

However, *Siren* eggs may be relatively invulnerable to newt predation because *Siren* females brood (Godley 1983). Interactions between *Siren* and *Notophthalmus* thus vary from competition to predation to an indirect mutualism, depending on their relative sizes, densities, and life stages (Werner and Gilliam 1984, Wilbur 1988).

This experiment suggests that the ability to function as a keystone predator derives from the interaction between consistent behavioral properties of certain predators and asymmetries in the competitive relationships within prey assemblages. Behavioral properties of the predator that may serve in this regard include taxon-specific prey preferences, strong functional or numeric responses, and size-selective or activity-selective predation, provided the prey characters preferred by the predators are correlated with competitive ability. These properties of both predators and prey assemblages are frequently observed in natural communities (e.g., Holling 1959, Brooks and Dodson 1965, Paine 1966, Sprules 1972, Dodson 1974, Kerfoot 1975, Morin 1981, Wilbur 1987, Morin and Johnson 1988; see also reviews by Lawton and Hassell 1981, Connell 1983, Schoener 1983) and provide opportunity for the occurrence of the keystone effect. When both the conditions of the predators and those of the prey assemblage are met, keystone predators can be expected to maintain species diversity in a variety of communities that differ in species composition and densities (Paine 1980).

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