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## FOREST CANOPY AND THE PERFORMANCE OF LARVAL AMPHIBIANS

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**Abstract.** Freshwater ponds inhabited by larval amphibians can become encroached by forest vegetation. Surveys reveal that gradients formed by canopy cover can act as a selective sieve for the distribution of amphibian larvae among ponds. In eastern North America, many species, including spring peepers (*Pseudacris crucifer*), are usually absent from ponds where forest canopies have closed over the pond basin. Relatively fewer species, including wood frogs (*Rana sylvatica*), are commonly present in both closed and open canopy ponds. Long-term observations reveal that canopy development is associated with extinction of spring peeper populations and persistence of wood frog populations. We evaluated performance of spring peeper and wood frog larvae in a set of experiments designed to assess three predictions: (1) that conditions in closed canopy ponds (e.g., lower temperature) are associated with depressed growth rates, (2) that the impact of canopy cover will be more severe on an open canopy specialist vs. a canopy generalist species, and (3) that abiotic differences between closed and open canopy ponds may provide a sufficient explanation for performance patterns. In support of the first prediction, a field transplant experiment showed that both species grew slower in closed vs. open canopy ponds. We found some support for the second prediction during two separate experiments. During the field experiment, the impact of canopy on spring peeper growth was similar to the effect on wood frogs. However, in a common garden experiment (in which physical conditions tended to converge), spring peepers raised on substrates and water from closed canopy ponds grew substantially slower than conspecifics in the presence of water and substrate from open canopy ponds. By contrast, wood frogs grew faster in the closed canopy treatment. Finally, while recognizing that abiotic variation appears to play an important role in performance across the canopy gradient, we rejected the third hypothesis. We found that a biotic manipulation (food addition) partially mitigated depressed growth rates in closed canopy ponds. This result suggests that biotic factors (e.g., variation in abundance and composition of periphyton) also contribute to performance differences across the canopy gradient.

**Key words:** *amphibian; canopy; forest cover; freshwater ponds; growth rate; periphyton; Pseudacris crucifer; Rana sylvatica; tadpoles; temperature; Yale-Myers Forest, Connecticut.*

### INTRODUCTION

Aquatic ecologists have a long-standing interest in the interplay between the environments they focus on and surrounding terrestrial ecosystems. These studies reflect the recognition that terrestrial and aquatic systems are closely linked by the flows of materials and energy, and through their joint use by resident species (e.g., Gill 1978, Bormann and Likens 1979, Power et al. 1995). However, most concepts of community organization in aquatic systems rely exclusively on parameters related to the aquatic habitats themselves. As an example, communities composed of larval amphibians and their predators are believed to be structured by factors including the permanence of ponds and the composition of the predator fauna (reviewed by Wellborn et al. 1996, Skelly 1997). The terrestrial context of the pond has not often been considered (see Bussler

1982, Hill et al. 1995, and Werner and Glennemeier 1999 for exceptions).

In this study we are concerned with impacts of terrestrial vegetation on amphibians within freshwater ponds. In eastern North America, ponds surrounded by early successional habitats can be completely unshaded by terrestrial vegetation while ponds located in mature forests can have forest canopy over the entire basin. The results of a long-term survey show that many amphibian species are absent from closed canopy ponds, and that extinction of populations is associated with canopy overgrowth (Skelly et al. 1999). For most species, canopy overgrowth is linked with a high probability of population extinction. For relatively few species, there is a high likelihood of persistence in closed canopy ponds.

We chose to focus on two species characteristic of canopy generalists and open canopy specialists. Wood frogs (*Rana sylvatica*), and spring peepers (*Pseudacris crucifer*), are widely distributed across eastern North

America (Conant and Collins 1991). At the 3500-ha Yale-Myers Forest in Connecticut, USA, these species are the two most common spring breeding anuran species. Both species begin chorusing as early as mid-March while snow is still on the ground and metamorphosis typically begins in June (D. K. Skelly, L. K. Freidenburg, and J. M. Kiesecker, *personal observations*). Like most local amphibians, spring peepers are restricted to open canopy ponds. The wood frog is the only local anuran that regularly breeds in closed canopy ponds.

The observed relationship between canopy overgrowth and the distribution of wood frogs and spring peepers could be the result of two broad classes of mechanisms (Skelly, *in press*). First, adult amphibians are known to be selective about where they breed (e.g., Resetarits and Wilbur 1989, Hopey and Petranka 1994, Kiesecker and Skelly 2000). The absence of many species from closed canopy environments could result from adult breeding preferences. Alternatively, larval amphibians can be highly sensitive to environmental gradients (Smith 1983, Skelly 1995). Larval amphibians could be eliminated from closed canopy ponds because they are unable to grow and develop to metamorphosis.

Below, we evaluate three hypotheses related to the role of larval performance in limiting distributions across the gradient of forest canopy: (1) relative to open canopy ponds, ambient conditions in closed canopy ponds lead to depressed rates of growth, (2) the impact of canopy on performance is unequal among species such that species known to persist in closed canopy ponds are less affected by closed canopy conditions, and (3) the impact of closed canopy on larval amphibians is solely the result of abiotic conditions (e.g., lower temperature and dissolved oxygen) that limit performance.

We evaluated these hypotheses in field and common garden experiments. In the field experiment we transplanted larvae of canopy generalist and closed canopy specialist species into open and closed canopy ponds. In the common garden experiment, larvae of the same species were brought into a common environment and exposed to water and benthic substrates from the same set of open and closed canopy ponds. The role of abiotic factors was assessed two ways by taking advantage of variation in forest canopy among natural ponds, and by using the common garden to equilibrate physical conditions. In the field experiment we added food to some enclosures to determine whether we could modulate growth rate in the face of prevailing abiotic conditions. As a corollary, by raising larvae in a common environment we were able to assess their response to aspects of open and closed canopy environments in conditions of equal light and temperature, and high concentrations of dissolved oxygen.

TABLE 1. Characteristics of ponds at the Yale-Myers Forest, Connecticut, used in a field transplant experiment.

Pond	Percent cover	Surface area (m <sup>2</sup> )	Maximum depth (cm)	pH
Blacksmith	77	360	75	5.3 ± 0.1
Boulder	98	1390	48	5.4 ± 0.1
Dentist	6	5200	54	6.4 ± 0.1
Morse	21	66 800	190	6.8 ± 0.1
Quarry	80	310	117	6.5 ± 0.1

*Notes:* Percent cover of forest canopy was measured using a spherical densiometer at five locations within the pond basin. Surface area was estimated at spring high water level when maximum water depth also was measured. Within each pond, pH was measured on at least four dates during May and June of 1997. The pH measurements are presented as mean ± 1 SE.

## METHODS

### Field experiment

We conducted a field experiment in a set of five ponds that varied in degree of canopy cover (Table 1). All ponds are located at the Yale-Myers Forest (~3500 ha) located in Tolland and Windham Counties in northeastern Connecticut. This experiment was designed to evaluate the performance of wood frog and spring peeper larvae exposed to different canopy conditions in the absence (control) or presence (food added) of an additional food source. In order to estimate overall canopy cover, spherical densiometer (Forestry Suppliers, Jackson, Mississippi) measurements were taken at five locations within a pond basin (N shoreline, E shoreline, S shoreline, W shoreline, and center) and averaged. Three ponds (Blacksmith, Boulder, and Quarry) with high canopy cover (estimates >75%) were classified as closed canopy, while two ponds (Dentist, Morse) with low canopy cover (estimates <25%) were classified as open canopy. All measurements were taken after leaves had leafed out (early May).

The overstory at closed canopy ponds was primarily composed of mature red maples (*Acer rubrum*) at Blacksmith and Boulder Ponds and of red pine (*Pinus resinosa*) at Quarry Pond.

Between 11 and 14 May 1997, we placed six 0.64 × 0.64 × 0.71 m open-bottomed enclosures in each pond. Enclosure locations were chosen to be equivalent in depth (~40–45 cm) within and among ponds and to be representative of the conditions within each pond. Enclosures were constructed of wooden frames, had a lower edge of 20 cm wide aluminum flashing, and were covered with black fiberglass window screening (1.5-mm mesh). Enclosures were placed in a rectangular array with no enclosure <15 cm from its nearest neighbor. In ponds with soft substrates enclosures were pressed directly into the pond bottom. In ponds with rockier substrates, fiberglass screening skirts were added to the lower edge of the enclosures, and the enclosures were sealed by placing rocks around the perimeter

of the enclosure base. Immediately after being placed in the ponds, enclosures were cleared by repeatedly dipnetting the water column. Each cage was dipnetted for three 2-min intervals and all macroinvertebrates (e.g., beetle larvae) and vertebrates (tadpoles and salamander larvae) were removed. Following clearing, a lid of fiberglass screening was placed over the enclosure. In each pond, cages were paired with their neighbor to the east or west and treatment, control, or food added, was allocated by a coin flip. Because of staggered breeding phenologies, wood frogs and spring peepers were evaluated sequentially in the same enclosures. In addition, spring peeper larvae are small enough upon hatching to pass through the mesh of field enclosures. Spring peepers to be stocked into the field experiment were reserved in wading pools until they reached a size that prevented them from being able to escape from enclosures.

Wood frogs were collected as eggs on 16 April 1997 from four ponds (two open canopy ponds and two closed canopy ponds; two clutches from each pond). Larvae were reared in wading pools and given access to a mix of senesced deciduous leaves and pelleted rabbit chow. Larvae from different ponds were mixed together and used haphazardly to stock enclosures. Wood frogs were stocked on 15 May (day 0) when 10 larvae ( $20 \pm 1$  mg [mean mass  $\pm 1$  SE], median Gosner Stage 25,  $n = 15$ ) were placed into each of the 30 enclosures. This density was used because it is within the range of naturally observed densities, because it would ensure that enough larvae would be recovered at the conclusion of the experiment to calculate responses, and so that it would be low enough to mitigate the impacts of conspecifics on resources. At 0, 3, 6, 9, and 12 d after stocking, 2 g of pelleted rabbit chow was placed in each food added enclosure. Wood frog tadpoles were collected from all cages 14 d after stocking by dipnetting the water column and removing and sorting through the upper strata of the benthic substrate. Recovered tadpoles were returned to the laboratory, weighed to the nearest milligram, and preserved in 70% EtOH for later determination of Gosner developmental stage (Gosner 1960).

Spring peepers (which lay their eggs singly) were collected as eggs and recent hatchlings from two different open canopy ponds. Larvae were reared in wading pools and given access to a mix of senesced deciduous leaves and pelleted rabbit chow. Larvae from the two ponds were mixed together and selected haphazardly to stock enclosures. On 2 June, each enclosure was restocked with 8 L of benthic substrate from outside of the enclosures (volume added matched to the volume removed). Each enclosure was dipnetted for three, 2-min intervals and lids were replaced on cages. On 4 June, 10 spring peeper larvae ( $89 \pm 10$  mg, median Gosner Stage 33,  $n = 15$ ) were stocked into each enclosure. Methods of food addition and takedown were identical to the the wood frog portion of the ex-

periment with one exception. Because of imminent drying, tadpoles were collected from Boulder Pond (closed canopy) 9 d after stocking. Per day growth rates were calculated and compared with rates from 14-d periods for the rest of the ponds.

#### *Common garden experiment*

We performed an experiment in which we raised tadpoles on benthic substrate and water from different ponds brought into a common environment. Tadpoles were from the same stocks as those used in the field experiment. Substrate and water were collected from the same ponds as those used in the field experiment and the experiment was run over the same time period (May and June of 1997). The goal of the common garden experiment was to evaluate the performance of wood frog and spring peeper tadpoles given access to resources from ponds that differed in canopy under otherwise similar conditions.

Wood frogs were stocked into containers on 19 May. Each container had already received equal amounts of benthic substrate and water from one of five ponds. We collected the upper strata of the benthic substrate near the shore of each pond. In closed canopy ponds, benthic substrates were dominated by senesced deciduous leaves (chiefly *Acer rubrum* and *Quercus rubra*), while in open canopy ponds substrates were composed of senesced grass and sedge stems and leaves (e.g., *Typha latifolia*, *Carex stricta*, *Sparganium eurycarpum*). Additionally, we collected water from the open region of each pond. Each of 15 plastic containers (three replicates per pond treatment) was assigned to a pond treatment and given 8 L of water from the appropriate pond and 60 g of damp substrate (prior to being weighed substrate was gently compressed in a systematic fashion). Once placed in a container, substrate was spread throughout, and was sufficient to cover the entire container bottom with a benthic zone composed of multiple layers of vegetation. Containers ( $39 \times 25 \times 14$  cm) were placed outdoors at the Yale-Myers field research facility on a platform 1.5 m below a layer of shade cloth that reduced incident solar radiation by  $\sim 50\%$ . Container location was randomized within three spatial blocks on the platform. After placing substrate and water into containers, each was searched carefully and all macroinvertebrates and amphibian larvae were removed.

Into each container we placed three wood frog tadpoles ( $33 \pm 2$  mg, median Gosner Stage 26,  $n = 9$ ). Water and substrate were replaced with fresh material 3, 6, 9, and 12 d after initial stocking. Wood frog tadpoles were collected 14 d after stocking and immediately weighed to the nearest milligram. Subsequently, tadpoles were preserved in 70% ethanol for later assessment of Gosner developmental stages.

Because of staggered phenologies, spring peeper larvae ( $45 \pm 4$  mg, median Gosner Stage 28,  $n = 9$ ) were stocked into a separate set of 15 containers later than

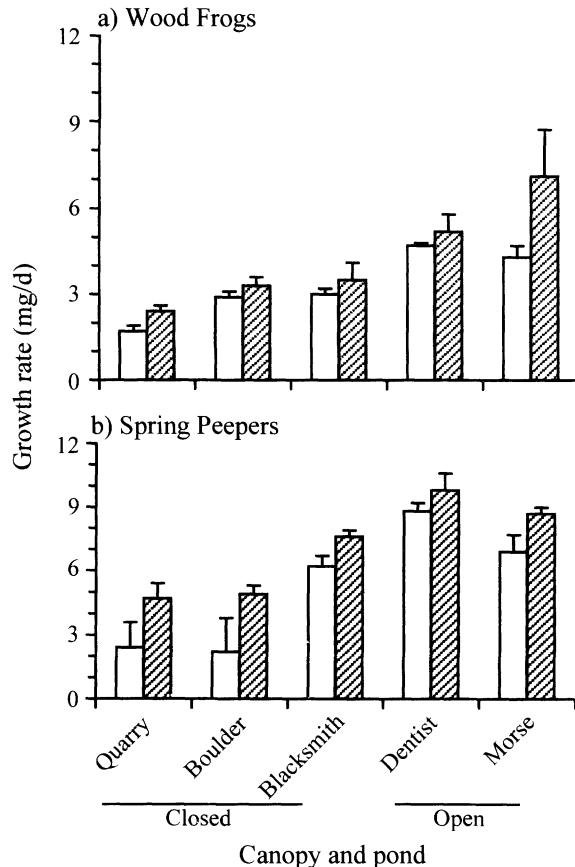


FIG. 1. Growth rate responses of (a) wood frog and (b) spring peeper larvae reared in enclosures in three closed canopy and two open canopy ponds for a 2-wk period. This canopy treatment was crossed with a food addition treatment. Enclosures were given no food (open bars), and food added enclosures (hatched bars) received regular additions of rabbit chow). Bars indicate means + 1 SE.

wood frogs (25 May vs. 19 May). As with wood frogs, water and substrate were replaced 3, 6, 9, and 12 d after stocking. Tadpoles were collected and preserved 14 d after stocking.

#### Measurement of temperature and dissolved oxygen

During the period of the field and common garden experiments, we regularly visited each pond and recorded dissolved oxygen concentration using a YSI Model 55 meter (YSI Incorporated, Yellow Springs, Ohio). Measurements were taken at a fixed location near the field enclosures in each pond. During each measurement, the probe tip was located 10 cm below the water surface and gently moved back and forth until the reading stabilized. From 15 May until 19 June of 1997 each pond was visited on 17 separate days between 0800 and 1900.

In addition, we measured temperature using Hobo temperature loggers (Onset Computer Corporation, Pocasset, Massachusetts) placed in submersible cases 10

cm below the water surface and programmed to record temperature once per hour. Loggers were placed in four of the five ponds used in the experiment (Boulder, Dentist, Morse, and Quarry).

#### Periphyton assays

During 1998, we assayed the productivity and composition of periphyton (a food source for tadpoles) in three open (Dentist, Kozey Road, Pussywillow) and three closed (Blacksmith, Quarry, Woodpile) canopy ponds at Yale-Myers Forest. In each pond, racks holding six standard, glass microscope slides were placed in each pond. The racks, constructed of wooden slats and steel bolts, held slides lengthwise and oriented vertically. Racks were attached to a square, foam float (inside opening  $20 \times 20$  cm) by wires such that the top edge of the slides was  $\sim 0.5$  cm below the water surface. Suspended beneath the float, a bag of fiberglass window screening prevented access by macrograzers.

Initially, racks were placed in ponds on 29 April. One rack was tethered to a stake roughly 2 m from the north shore of each pond and a second rack was similarly oriented near the south shore. In situ incubation was concluded on 13 May by retrieving the rack and carefully placing slides in screw top histological vials that held slides upright and separated from one another. Slides were immediately returned to the laboratory where three slides were used to determine periphyton biomass. Periphyton was scraped from these slides and vacuum filtered onto a pre-weighed Whatman GF filter paper that had been dried to constant mass at  $80^\circ\text{C}$ . Subsequently, filter papers were again dried to constant mass at  $80^\circ\text{C}$  and reweighed. Productivity was ex-

TABLE 2. Results from an ANOVA examining the growth rate responses of larval (a) wood frogs and (b) spring peepers to different forest canopy environments and the presence or absence of an additional food source (regular allocations of pelleted rabbit chow).

Source	df	Sum of squares	F	P
a) Wood frogs				
Canopy	1	44.60	59.99	<0.001
Food addition	1	6.78	9.12	0.006
Pond(Canopy)	3	6.48	2.90	0.057
Canopy $\times$ Food addition	1	3.72	5.00	0.035
Error	23	17.10		
Total	29	77.02		
b) Spring peepers				
Canopy	1	109.23	63.87	<0.001
Food addition	1	22.98	13.44	0.001
Pond(Canopy)	3	50.46	9.84	<0.001
Canopy $\times$ Food addition	1	0.73	0.43	0.518
Error	23	98.86		
Total	29	225.44		

Notes: A nested factor, pond, describes the significance of variation in growth rate responses among ponds within each canopy treatment. Larvae were raised in field enclosures for a 2-wk period.

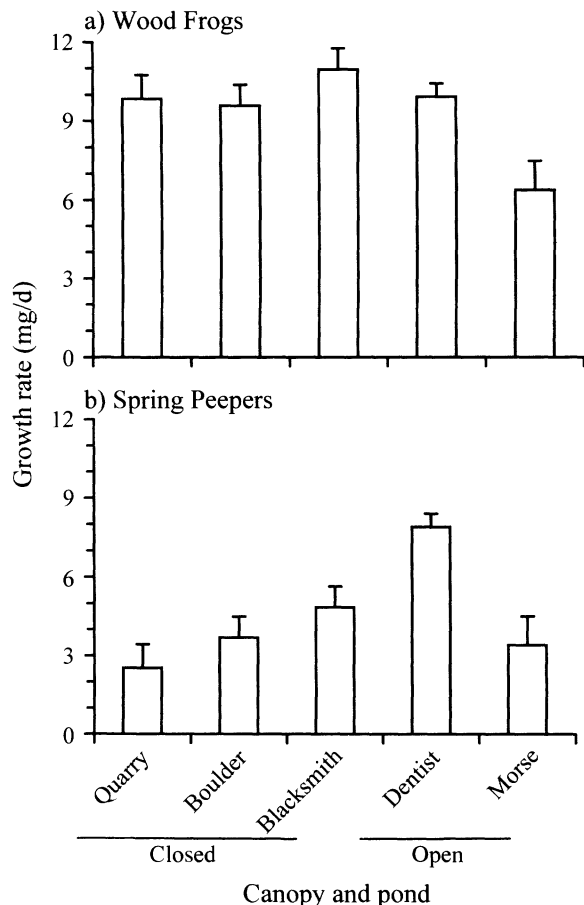


FIG. 2. Growth rate responses of (a) wood frog and (b) spring peeper larvae reared in containers holding water and benthic substrates from three closed canopy and two open canopy ponds. During the 2-wk experiment, water and benthic substrates were replaced with fresh material every 3 d. Bars indicate means + 1 SE.

pressed as the milligrams dry mass of periphyton accumulated per square centimeter per day.

Productivity of periphyton was measured during two subsequent assays. Racks and floats were washed, and new slides were placed in racks and deployed as before. The second incubation began on 17 May and slides were retrieved on 2 June. The final incubation began on 29 June and concluded on 14 July. Productivity was measured as before except periphyton from four slides was scraped onto each filter paper. Hereafter, the three incubation periods are referred to as early May, late May, and early July.

Composition of periphyton was assayed on two separate slides collected from each rack in the early May assay. At the time of collection, periphyton on these slides was scraped into Lugol's solution and stored in glass vials. Following the method of Marks and Lowe (1989), periphyton samples were examined at 400 $\times$ , up to 300 cells were counted, and the major taxa within three groups (green algae, diatoms, cyanobacteria)

were identified to genus. Major taxa were defined as those representing at least 10% of the cells counted on a slide.

#### Statistical analyses

Experiments were analyzed using analysis of variance (ANOVA). For all analyses of tadpole responses, per day growth rate (calculated as the enclosure or container mean) was the focal response variable and separate analyses were conducted on each tadpole species. The field experiment was analyzed using canopy and food addition as main factors, and pond as a factor nested within canopy. This last factor allowed us to determine the significance of variation among ponds within canopy categories. Additional analyses of environmental variables (e.g., survival, temperature, periphyton productivity) used a comparable ANOVA structure.

Growth rate responses from the common garden experiment also were analyzed using ANOVA. Canopy was the main factor analyzed and pond was included as a factor nested within canopy.

## RESULTS

### Field experiment

The average wood frog tadpole more than tripled in body mass during the experiment (Fig. 1, Table 2). Both canopy and food addition factors had significant effects on wood frog growth. Wood frogs reared in open canopy ponds grew 90% faster than their counterparts in closed canopy ponds. Food addition was associated with an increase in growth rate; however this effect was larger in open (38% increase) vs. closed (15% increase) canopy ponds. Variation among ponds within canopy treatments was marginally nonsignificant ( $P = 0.057$ ).

Overall, 68% of wood frog larvae survived to the

TABLE 3. Results from an ANOVA examining the growth rate responses of larval (a) wood frogs and (b) spring peepers to benthic substrates and water collected from ponds in different forest canopy environments.

Source	df	Sum of squares	F	P
a) Wood frogs				
Canopy	1	14.13	9.88	0.010
Pond(Canopy)	3	21.93	5.11	0.021
Error	10	14.30		
Total	14	50.36		
b) Spring peepers				
Canopy	1	13.77	6.41	0.030
Pond(Canopy)	3	38.24	5.93	0.014
Error	10	21.48		
Total	14	73.49		

Notes: A nested factor, pond, describes the significance of variation in growth rate responses among ponds within each canopy treatment. Larvae were raised in plastic containers in a common environment for a 2-wk period during which benthic substrates and water were regularly replaced.

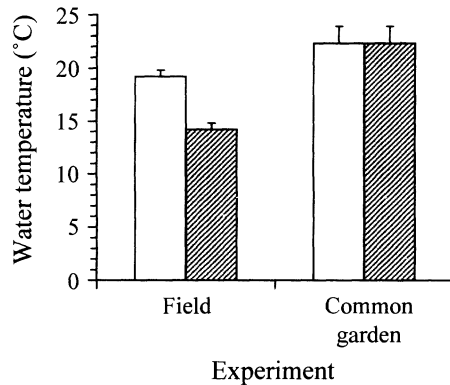


FIG. 3. Water temperature during field and common garden experiments. During field experiments water temperature was measured on 19 dates. During common garden experiments, water temperature was measured on 7 dates. Bar shading indicates pond canopy: open for open canopy and hatched for closed canopy. Bars indicate means + 1 SE.

conclusion of the 2-wk period. Wood frogs stocked into closed canopy ponds survived somewhat better than their counterparts stocked into open canopy ponds (77% vs. 55%,  $P < 0.005$ ). There were no effects of either food or pond on wood frog survival.

Spring peeper tadpoles roughly doubled in body mass, on average, over the course of the field experiment (Fig. 1, Table 2). Spring peeper larvae stocked into open canopy ponds grew 83% faster than conspecifics stocked into closed canopy ponds. Tadpoles in enclosures where food was added grew 34% faster, on average. There was no evidence that the impact of food addition differed between canopy treatments. There was strong variation in growth among ponds within canopy treatments ( $P < 0.001$ ).

Sixty-eight percent of spring peeper larvae survived to the conclusion of the field experiment. There were no effects of canopy, food addition, or pond on spring peeper survival.

#### Common garden experiment

In the common garden experiment, tadpoles were raised for 2 wk in containers in a common environment, each holding water and substrate from one of five different ponds. For each species, there was a significant impact of canopy treatment on growth rate (Fig. 2, Table 3). However, trends were in opposite directions for the two species. Wood frogs grew 25% faster in closed vs. open canopy containers while spring peepers grew 35% slower in closed vs. open canopy containers. For each species, growth varied among ponds within canopy treatments. All larvae survived to the conclusion of the common garden experiment.

#### Temperature, dissolved oxygen, and periphyton

Measurements made during May and June of 1997 suggested that environmental conditions sharply differed between open and closed canopy ponds. Notably, mea-

surements made during regular visits revealed that open canopy ponds averaged 5°C warmer and dissolved oxygen concentrations were more than twice as high (Figs. 3 and 4, Table 4). Data from temperature loggers confirmed that open and closed canopy ponds consistently showed differences in water temperature (Fig. 5).

By contrast, measurements of conditions within the common garden experiment revealed alteration of conditions in experimental containers relative to natural ponds (Figs. 3 and 4, Table 4). In the common garden setting, temperature was equivalent between canopy treatments. While still differing between canopy treatments, dissolved oxygen concentrations were, overall, substantially higher during the common garden experiments.

Periphyton assays showed that open canopy ponds tended to be more productive than closed canopy ponds (Fig. 6). This tendency was weakest in early May samples and strongest in early July samples. Composition of periphyton differed greatly between canopy types (Table 5). Across the pool of samples, periphyton was composed of a variety of taxa including diatoms, green algae, and blue green algae (cyanobacteria). Among the six ponds, the number of dominant genera (sensu Marks and Lowe 1989) ranged from one to six. Each of the three closed canopy ponds were dominated by a single taxon, the unicellular diatom, *Eunotia*. Composition of periphyton in open canopy ponds varied, but in each case periphyton was composed of multiple codominant taxa including a number of filamentous green algal species.

#### DISCUSSION

In eastern North America, patterns of forest cover have changed continually during both historical (Foster 1995), and prehistorical (Foster and Zebryk 1993, Spear et al. 1994) times. In recent decades, forest cover has been increasing steadily in many areas including

TABLE 4. Analyses of variance of abiotic variables measured during field and common garden experiments conducted during May and June of 1997.

Source	df	Sum of squares	F	P
a) Water temperature				
Experiment	1	351.36	33.67	<0.001
Canopy	1	158.59	15.20	<0.001
Experiment × Canopy	1	68.63	6.58	0.013
Error	49	511.39		
Total	52	1095.90		
b) Dissolved oxygen				
Experiment	1	150.05	56.06	<0.001
Canopy	1	113.32	42.34	<0.001
Experiment × Canopy	1	2.81	1.05	0.311
Error	49	131.16		
Total	52	400.62		

Notes: Water temperature and dissolved oxygen were measured on several dates in each pond. On each date, the average was taken across all ponds of a particular canopy type.

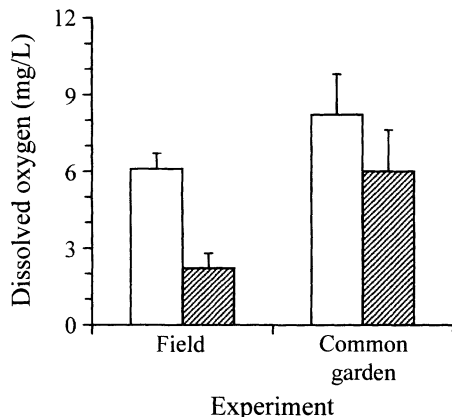


FIG. 4. Dissolved oxygen concentrations during field and common garden experiments. During field experiments dissolved oxygen was measured on 19 dates. During common garden experiments, dissolved oxygen was measured on 7 dates. Bar shading indicates pond canopy: open for open canopy and hatched for closed canopy. Bars indicate means + 1 SE.

New England. Distributional surveys (e.g., Skelly et al. 1999) and our experimental results suggest that changes in forest cover near aquatic environments may be of great importance to resident amphibians. In fact, in eastern North America most amphibian species are absent from closed canopy ponds. Results from a long-term survey suggest that canopy closure is associated with selective extinction of local amphibian populations (Skelly et al. 1999). With a few exceptions (e.g., Bussler 1982, Werner and Glennmeier 1999) ecologists have not considered impacts of the canopy gradient on resident aquatic stages of amphibians. In this study, we hypothesized that amphibian performance would be depressed in closed vs. open canopy ponds, that these effects would fall more severely on an open canopy specialist species, and that the effects of closed canopy may be mediated through abiotic variation alone.

In support of our first hypothesis, we found that conditions in enclosures in closed canopy ponds were associated with reduced performance of two local amphibian species. Compared with open canopy ponds, growth rates were nearly halved in closed canopy ponds. Because these species often live in temporary ponds, decline in growth rate can be associated with mortality when ponds dry (e.g., Skelly 1995). Thus, our preliminary evidence suggests significant challenges could be posed by closed canopy environments. The design of our field experiment was directed at uncovering associations between canopy and performance rather than evaluating the role of a specific causal factor. Nevertheless, simultaneous measurement of abiotic and biotic variables among ponds reveals potential mechanisms for the patterns we observed.

Of the several mechanisms by which canopy cover may mediate changes in amphibian growth rates, the most fundamental may be temperature. During our field

experiment, we found that water temperatures averaged 5°C warmer in open vs. closed canopy ponds (Fig. 5). Like most ectotherms, temperature governs an entire array of physiological processes in amphibians (Dodd and Dodd 1976, Ultsch et al. 1999). In particular, ambient temperature is known to have strong effects on tadpole growth and developmental rates (Marian and Pandian 1985, Newman 1998). Controlled laboratory experiments using species such as *Rana pipiens* (Smith-Gill and Berven 1979) and *Pseudacris ornata* (Harkey and Semlitsch 1988) have demonstrated that an increase in water temperature of 5°C can lead to a doubling of larval growth rate. Thus, it is possible that effects on growth of the magnitude we observed could be produced by temperature differences alone.

Dissolved oxygen was a second abiotic factor associated with canopy cover; closed canopy ponds had concentrations about half of those found in open canopy ponds (see also Werner and Glennmeier 1999). Unfortunately, the impacts of chronic hypoxia on growth and development of larval anurans are not well understood. Hypoxic conditions have been associated with tadpole mortality, and tadpoles are known to alter behavior in the presence of low concentrations of dissolved oxygen (Noland and Ultsch 1981). In particular, several species are known to increase their frequency of bobbing (Wassersug and Seibert 1975, Crowder et al. 1998). Bobbing is often characterized as rapid dashes to the water surface. By either gulping air from the atmosphere, or by spending time in relatively oxygen rich microenvironments, tadpoles may be able to mitigate some negative consequences of low concentrations of dissolved oxygen. Given wide variation in ambient dissolved oxygen concentrations among ponds and strong tendencies of some species to choose oxygen rich microsites (Noland and Ultsch 1981), the

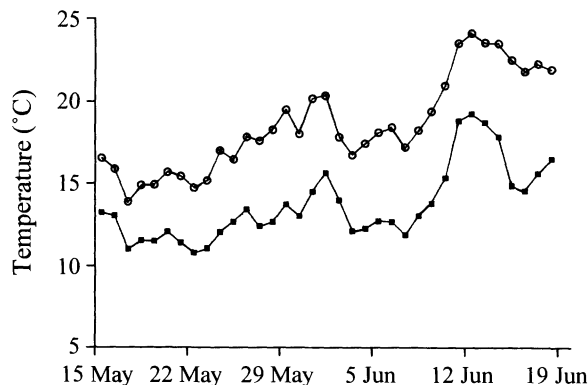


FIG. 5. Water temperature in open (open circles) and closed (filled squares) canopy ponds at Yale-Myers Forest during May and June of 1997. Each point represents the average daily temperature in two ponds. Temperature was recorded once per hour by a logger located at a depth of 10 cm to generate the daily average within that pond. The interval shown here spans the time period when field experiments were conducted in the same ponds.



TABLE 5. Major periphyton taxa found on glass slides incubated in three closed and three open canopy ponds at Yale-Myers Forest during May of 1998.

Taxon	Canopy and pond					
	Closed			Open		
	O	B	W	P	D	K
<b>Green</b>						
<i>Bulbochaete</i>					X	
<i>Coleochaete</i>					X	X
<i>Microspora</i>				X	X	
<i>Oedogonium</i>				X	X	X
<i>Ulothrix</i>						X
<b>Blue-green</b>						
<i>Hapalosiphon</i>					X	
<i>Stigonema</i>					X	
<b>Diatom</b>						
<i>Aulocoseira</i>				X		
<i>Eunotia</i>	X	X	X			X
<i>Gomphonema</i>						X
<i>Meridion</i>						X
<i>Tabellaria</i>						X

Note: Pond codes are as follows: Q, Quarry; B, Blacksmith; W, Woodpile; P, Pussywillow; D, Dentist; and K, Kozey Road. An X indicates that the taxon is present.

relationship between dissolved oxygen and amphibian performance is likely to reward further study.

In addition to abiotic factors, we quantified the abundance and composition of periphyton. The impacts of light and temperature on composition and productivity of periphyton are well documented (Robinson and Minshall 1986, Sheath et al. 1986, Hill et al. 1995, De-Nicola 1996). Compared with closed canopy ponds, our assays suggest that periphyton in open canopy ponds tended to be more abundant and more diverse (Table 4, Fig. 5). These patterns are consistent with results found in shaded vs. unshaded streams (Hill et al. 1995). Results from a number of studies suggest that periphyton is a common food source for pond dwelling tadpoles (Jenssen 1967, Dickman 1968, Diaz-Paniagua 1985, Holomuzki and Hemphill 1996, Holomuzki 1998). In addition, Kupferburg et al. (1994) showed that direct manipulation of periphyton composition was associated with large effects on tadpole growth rates. More numerous studies of macroinvertebrate grazers in stream systems have shown the critical role of periphyton abundance and composition for grazer performance (reviewed by Feminella and Hawkins 1995). Taken together, these results suggest that variation in food resources may be important for understanding tadpole distributions among ponds.

Our second prediction focused on the relative impacts of canopy on our focal species. We expected that, compared with a canopy generalist (wood frog), performance of an open canopy obligate (spring peeper) would be more negatively impacted by closed canopy conditions. The results of our experiments provided mixed support for this prediction. In the field experiment, both species suffered similar reductions of

growth rate in closed vs. open canopy ponds. The common garden experiment furnished clearer evidence that canopy effects differed between species. In that experiment, wood frogs tended to grow faster in the presence of closed canopy water and benthic substrates. Following the pattern in the field experiment, spring peepers grew substantially slower in common garden containers holding closed canopy substrates and water.

The absence of spring peeper larvae in closed canopy ponds led us to speculate that spring peeper larvae might be entirely unable to grow, develop, and survive under closed canopy conditions. Our results indicate that such a straightforward intolerance to closed canopy conditions is not the mechanism underlying the distributional pattern of this species. While we have some evidence of relatively severe impacts of canopy on spring peepers, the two species survived about equally well during two weeks of exposure to field conditions. It is possible that differences in life history between species (e.g., longer larval period of spring peepers) may result in a relative inability of spring peepers to complete metamorphosis prior to drying in temporary, closed canopy ponds. We are currently assessing this hypothesis using larval period length transplant experiments. Alternatively, larvae of the two species may suffer relatively equally from closed canopy conditions. In that case, exploration of the mechanisms underlying adult breeding site choice by the two species may improve our understanding of larval distributions (e.g., Hopey and Petranka 1994, Kiesecker and Skelly 2000).

Finally, we predicted that the impacts of closed canopy ponds might be mediated through abiotic variation. We reasoned that the immediate effects of shading on the abiotic environment in the form of reduced water temperature could provide a sufficient mechanism to explain canopy related effects on larval performance. We used our experiments to conduct two indirect tests of this prediction. The field experiment included a food

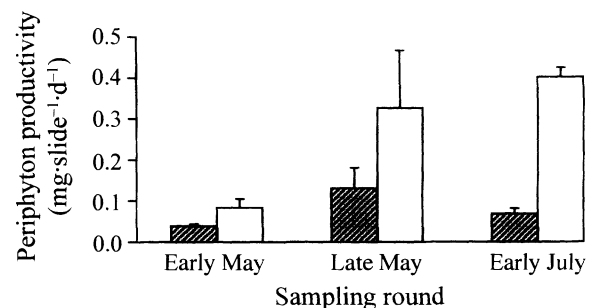


FIG. 6. Productivity of periphyton measured as the dry mass accumulated per day per slide over a 2-wk period. Periphyton was assayed from glass microscope slides incubated in three open (open bars) and three closed (hatched bars) canopy ponds during three sampling rounds during the spring of 1998. A microscope slide has a sampled area of 6 cm<sup>2</sup>. Bars indicate means + 1 SE.

treatment. Addition of food resulted in increased growth rate for both tadpole species. While the effect of food addition did not entirely erase the decline in growth rate associated with the canopy factor, it showed that a biotic factor could be related to reduced performance in closed canopy ponds. Note however, that while added food substantially improved spring peeper growth in closed canopy ponds, wood frogs were less affected by food addition in this context.

The potential importance of biotic variation was further supported by the results of the common garden experiment. Under conditions that reduced or eliminated important abiotic differences between canopy treatments, the effect of canopy remained strong. In particular, reduced growth rate of spring peepers in closed canopy treatments was maintained even when there was no difference in water temperature (correlation between growth rates in the two experiments was strongly positive:  $n = 5$  ponds,  $r = 0.77$ ). By contrast, for wood frogs the reversal in relative growth rates between open and closed canopy treatments suggests that some variable altered between field and common garden experiments is a strong determinant of growth rate (correlation between growth rates in the two experiments was negative:  $n = 5$  ponds,  $r = -0.41$ ). While further work will be necessary to uncover the interactive roles of abiotic and biotic variation there is mounting evidence that factors related to food resource variation may be important (Riha and Berven 1991, Kupferburg et al. 1994).

### Conclusions

Aquatic ecologists have frequently considered the effects of the terrestrial environment on the systems they study. However, these studies have been dominated by a few themes (e.g., the flow of materials into aquatic environments, the role of terrestrial environments as a matrix for organisms living on aquatic islands). In this study we have evaluated the role of the vegetation surrounding a pond much the same way forest ecologists have studied the role of canopy in driving the regeneration of resident plant species (e.g., Pacala et al. 1996). The results of our experiments suggest that the vegetation fringing freshwater ponds may have an overriding impact on the distribution and abundance of resident species.

The role of shoreline vegetation may be particularly salient for understanding present-day amphibian dynamics because forest cover has changed dramatically over the last several decades across much of eastern North America (Hart 1968, Foster 1995) and elsewhere (World Resources Institute 1991). In North America, the pattern of regrowth and the underlying reasons for changes in land use and land cover have been intensively studied. There has, however, been relatively little attention paid to the ramifications of afforestation for freshwater environments and their inhabitants. It is becoming clear that we can expect broadscale changes in

the distribution of organisms in small freshwater habitats as forest cover changes. Projecting the potential impacts of forest succession and forest loss will require an adequate understanding of underlying mechanisms by which forest cover impacts freshwater habitats and species.

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### LITERATURE CITED

- Bormann, F. H., and G. E. Likens. 1979. Pattern and process in a forested ecosystem. Springer-Verlag, New York, New York, USA.
- Bussler, H. 1982. Waldgewasser als lebensraum. *Natur und Landschaft* **57**:128–132.
- Conant, R., and J. T. Collins. 1991. A field guide to reptiles and amphibians of eastern and central North America. Houghton-Mifflin, Boston, Massachusetts, USA.
- Crowder, W. C., M. H. Nie, and G. R. Ultsch. 1998. Oxygen uptake in bullfrog tadpoles (*Rana catesbeiana*). *Journal of Experimental Zoology* **280**:121–134.
- DeNicola, D. M. 1996. Periphyton responses to temperature at different ecological levels. Pages 150–183 in R. J. Stevenson, M. L. Bothwell, and R. L. Lowe, editors. *Algal ecology: freshwater benthic ecosystems*. Academic Press, San Diego, California, USA.
- Diaz-Paniagua, C. 1985. Larval diets related to morphological characteristics of five Anuran species in the biological reserve of Donan (Huelva, Spain). *Amphibia-Reptilia* **6**: 307–322.
- Dickman, M. 1968. The effect of grazing by tadpoles on the structure of a periphyton community. *Ecology* **49**:1188–1193.
- Dodd, M. H. I., and J. M. Dodd. 1976. The biology of metamorphosis. Pages 467–599 in B. Lofts, editor. *Physiology of Amphibia*, volume 3. Academic Press, New York, New York, USA.
- Feminella, J. W., and C. P. Hawkins. 1995. Interactions between stream herbivores and periphyton: a quantitative analysis of past experiments. *Journal of the North American Benthological Society* **14**:465–509.
- Foster, D. 1995. Land use history and forest transformations in central New England. Pages 91–110 in M. J. McDonnell and S. T. A. Pickett, editors. *Humans as components of ecosystems*. Springer-Verlag, New York, New York, USA.
- Foster, D. R., and T. M. Zebryk. 1993. Long-term vegetation dynamics and disturbance history of a *Tsuga*-dominated forest in New England. *Ecology* **74**:982–998.
- Gill, D. E. 1978. The metapopulation ecology of the red-spotted newt, *Notophthalmus viridescens* (Rafinesque). *Ecological Monographs* **48**:145–166.
- Harkey, G. A., and R. D. Semlitsch. 1988. Effects of temperature on growth, development, and color polymorphism in the ornate chorus frog, *Pseudacris ornata*. *Copeia* **1988**: 1001–1007.

- Hart, J. F. 1968. Loss and abandonment of cleared farm land in the eastern United States. *Annals of the Association of American Geographers* **58**:417–440.
- Hill, W. R., M. G. Ryon, and E. M. Schilling. 1995. Light limitation in a stream ecosystem: responses by primary producers and consumers. *Ecology* **76**:1297–1309.
- Holomuzki, J. R. 1998. Grazing effects by green frog tadpoles (*Rana clamitans*) in a woodland pond. *Journal of Freshwater Ecology* **13**:1–8.
- Holomuzki, J. R., and N. Hemphill. 1996. Snail–tadpole interactions in streamside pools. *American Midland Naturalist* **136**:315–327.
- Hopey, M. E., and J. W. Petranka. 1994. Restriction of wood frogs to fish free habitats—how important is adult choice? *Copeia* **1994**:1023–1025.
- Jenssen, T. A. 1967. Food habits of the green frog, *Rana clamitans* before and during metamorphosis. *Copeia* **1967**:214–218.
- Kiesecker, J. M., and D. K. Skelly. 2000. Choice of oviposition site by gray treefrogs, *Hyla versicolor*: the role of potential parasitic infection. *Ecology* **81**:2939–2943.
- Kupferburg, S. J., J. C. Marks, and M. E. Power. 1994. Effects of variation in natural algal and detrital diets on larval anuran (*Hyla regilla*) life history traits. *Copeia* **1994**:446–457.
- Marian, M. P., and T. J. Pandian. 1985. Effect of temperature on development, growth and bioenergetics of the bullfrog tadpole, *Rana tigrina*. *Journal of Thermal Biology* **10**:157–161.
- Marks, J. C., and R. L. Lowe. 1989. The independent and interactive effects of snail grazing and nutrient enrichment on structuring periphyton communities. *Hydrobiologia* **185**:9–17.
- Newman, R. A. 1998. Ecological constraints on amphibian metamorphosis: interactions of temperature and larval density with responses to changing food level. *Oecologia* **115**:9–16.
- Noland, R., and G. R. Ultsch. 1981. The roles of temperature and dissolved oxygen in microhabitat selection by the tadpoles of a frog (*Rana pipiens*) and a toad (*Bufo terrestris*). *Copeia* **1981**:645–652.
- Pacala, S. W., C. D. Canham, J. Saponara, J. A. Silander, Jr., R. K. Kobe, and E. Ribbens. 1996. Forest models defined by field measurements: estimation, error analysis and dynamics. *Ecological Monographs* **66**:1–43.
- Power, M. E., G. Parker, W. E. Dietrich, and A. Sun. 1995. How does floodplain width affect river ecology: a preliminary exploration using simulations. *Geomorphology* **13**:301–317.
- Resetarits, W. J., and H. M. Wilbur. 1989. Choice of oviposition site by *Hyla chrysoscelis*: role of predators and competitors. *Ecology* **70**:220–228.
- Riha, V. F., and K. A. Berven. 1991. An analysis of latitudinal variation in the larval development of the wood frog (*Rana sylvatica*). *Copeia* **1991**:209–221.
- Robinson, C. W., and G. W. Minshall. 1986. Effects of disturbance frequency on stream benthic community structure in relation to canopy cover and season. *Journal of the North American Benthological Society* **5**:237–248.
- Sheath, R. G., J. M. Burkholder, M. O. Morison, A. D. Steinman, and K. L. VanAlstyne. 1986. Effect of tree canopy removal by gypsy moth larvae on the macroalgae of a Rhode Island headwater stream. *Journal of Phycology* **22**:567–570.
- Skelly, D. K. 1995. A behavioral tradeoff and its consequences for the distribution of *Pseudacris* treefrog larvae. *Ecology* **76**:150–164.
- Skelly, D. K. 1997. Tadpole communities. *American Scientist* **85**:36–45.
- Skelly, D. K. *In press*. Distributions of pond-breeding anurans: an overview of mechanisms. *Israel Journal of Zoology*.
- Skelly, D. K., E. E. Werner, and S. A. Cortwright. 1999. Long-term distributional dynamics of a Michigan amphibian assemblage. *Ecology* **80**:2326–2337.
- Smith, D. C. 1983. Factors controlling tadpole populations of the chorus frog (*Pseudacris triseriata*) on Isle Royale, Michigan. *Ecology* **64**:501–510.
- Smith-Gill, S. J., and K. A. Berven. 1979. Predicting amphibian metamorphosis. *American Naturalist* **113**:563–585.
- Spear, R. W., M. B. Davis, and L. C. K. Shane. 1994. Late quaternary history of low-elevation and mid-elevation vegetation in the White Mountains of New Hampshire. *Ecological Monographs* **64**:85–109.
- Ultsch, G. R., D. F. Bradford, and J. Freda. 1999. Physiology: coping with the environment. Pages 189–214 in R. W. McDiarmid and R. Altig, editors. *Tadpoles: the biology of anuran larvae*. University of Chicago Press, Chicago, Illinois, USA.
- Wassersug, R. J., and E. A. Seibert. 1975. Behavioral responses of amphibian larvae to variation in dissolved oxygen. *Copeia* **1975**:86–103.
- Wellborn, G. A., D. K. Skelly, and E. E. Werner. 1996. Mechanisms creating community structure across a freshwater habitat gradient. *Annual Review of Ecology and Systematics* **27**:337–363.
- Werner, E. E., and K. S. Glennemeier. 1999. Influence of forest canopy cover on breeding pond distributions of several amphibian species. *Copeia* **1999**:1–12.
- World Resources Institute. 1991. *World resources report 1991–1992: a guide to the global environment*. Oxford University Press, Oxford, UK.