

Variation in Metamorphosis in Spotted Salamanders *Ambystoma maculatum* from Eastern Missouri

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ABSTRACT.—I examined timing of metamorphosis in the spotted salamander *Ambystoma maculatum* for five years at a pond in east-central Missouri. Timing of metamorphosis was variable both among and within years. In three years most larvae failed to undergo metamorphosis by November and either died or overwintered and metamorphosed from the pond in the following spring. In two other years most larvae apparently metamorphosed by October and did not overwinter. In 1986, 81 newly transformed animals were captured from June to September. Individuals that metamorphosed later exhibited larger body sizes than those that left the pond early in the season. Variation in time and size at metamorphosis may be important in population regulation by affecting adult traits that contribute to fitness.

INTRODUCTION

In several amphibian species larval traits such as timing of metamorphosis and size at metamorphosis are known to affect adult traits that contribute to fitness (Smith, 1987; Semlitsch *et al.*, 1988). Variation in these larval traits could therefore be important in the regulation of amphibian populations (Wilbur, 1980; Berven, 1990). For populations that experience a seasonally fluctuating climate larval overwintering, or the inability of larvae to metamorphose before the end of the growing season, can be a very important regulating factor. Here, I describe variation in timing of metamorphosis, including larval overwintering, in a population of spotted salamanders *Ambystoma maculatum* studied during five years, and variation in time and size at metamorphosis for one year. Larval overwintering of *A. maculatum* has been reported for populations in Nova Scotia (Bleakney, 1952), Rhode Island (Whitford and Vinegar, 1966) and Massachusetts (Stangel, 1988) but the present study documents variation in timing of metamorphosis for a longer interval and in a warmer climate than the previous studies.

LOCATION AND METHODS

The focus of this study is a shallow fishless pond located on a ridge top in second growth oak-hickory forest in the 800-ha Tyson Research Center of Washington University in western St. Louis County, Missouri (Sexton *et al.*, 1986). The pond, known as Salamander Pond, is crescent shaped, approximately 50 m long and 5 to 8 m wide. At high water, the surface area is approximately 350 m² and the maximum depth is 1 m. It was constructed in 1965 and has never dried completely. Twelve spotted salamander egg masses were introduced from a nearby (2 km) fishless pond in August, 1968 and egg masses of the wood frog, *Rana sylvatica*, were introduced in the spring of 1980. Naturally occurring amphibians include *A. tigrinum*, *Notophthalmus viridescens*, *Rana sphenoccephala*, *R. catesbeiana*, *Hyla versicolor*, *Pseudacris triseriata*, *P. crucifer*, *Acris crepitans* and *Bufo americanus*. Small boards were scattered on the ground along the shore and the pond was completely enclosed by a screen-wire drift fence and 26 pairs of 5-liter drop cans from 1986 to 1989 (Phillips and Sexton, 1989). From May 1986 to February 1987 the drift fence was covered with plastic sheeting to prevent newly metamorphosed salamanders from crawling through the screen-wire mesh. Metamorphs escaped from the pond undetected in other years.

I collected larvae from Salamander Pond approximately once a month (excluding De-

ember and January) from November 1984 to November 1988 with a 2.3-m-long, 5-mm-mesh seine. In 1986, an effort was made to sample through the winter. During each visit, I seined the entire pond, usually in two hauls. Spotted salamander larvae were counted and 5–30 were preserved in 10% formalin. The preserved animals were returned to the laboratory where snout-to-vent length (SVL) and total length (TL) were measured to the nearest mm. I checked the drop cans and boards daily for newly metamorphosed salamanders from February through May in all years, and at least weekly from May to December in 1986 when the plastic sheeting was in place. The drop cans were closed after May in 1984, 1985, 1987 and 1988 but the boards were checked occasionally from May to November during these years. All newly metamorphosed salamanders encountered were measured to the nearest mm for TL and released on the outside of the drift fence. Water temperature was recorded at irregular intervals throughout the five-year period.

RESULTS

The only years in which larvae were not caught in large numbers in the fall were 1985 and 1986 (Table 1). In fact, in 1986, no larvae were captured in Salamander Pond on 9 September even though the number of seine hauls was three times that of the normal sampling effort. Larvae sampled in 1985 and 1986 were large and showed morphological signs of metamorphosis (Table 1). These observations suggest that most larvae metamorphosed before winter in these two years. In contrast, in 1984, 1987 and 1988, large numbers of small larvae, showing no signs of metamorphosis, were seined from Salamander Pond in late autumn (Table 1), suggesting that most larvae overwintered in these three years. To substantiate this claim, larvae were collected through the winter of 1987–1988. Eleven larvae were taken from a hole chopped in the ice on the seventeenth of December ($n = 11$; \bar{x} SVL = 30 mm \pm 3.9 SD; \bar{x} TL = 57 mm \pm 2.9 SD), 50 to 100 overwintered larvae were seined from the pond on 26 March 1988, and approximately 30 on 9 May 1988. Newly hatched larvae were also present on the latter date. Measurements were taken on a small sample of the overwintered larvae (26 March: SVL: $n = 3$, $\bar{x} = 34$ mm \pm 1.0 SD; TL: $n = 3$, $\bar{x} = 62$ mm \pm 2.5 SD; 9 May: SVL: $n = 5$, $\bar{x} = 37$ mm \pm 1.3 SD; TL: $n = 3$, $\bar{x} = 69$ mm \pm 1.2 SD).

The data for newly metamorphosed juveniles document variation in timing of metamorphosis among and within years at Salamander Pond. The largest number of newly metamorphosed individuals was encountered in 1986 when the drift fence was covered with plastic and the drop cans were kept open until December. On 23 April 1986, an overwintered, newly transformed salamander was captured in a drop can (SVL: 42 mm; TL: 77 mm) and another on 1 May 1986 (no measurements). From 9 June to 8 September 1986, a total

TABLE 1.—Sample size and larval measurements for the last sampling effort in each of the five study years

Date	Number seined	Number measured	SVL		TL	
			\bar{x} (mm)	SD	\bar{x} (mm)	SD
26 Nov 1984	>100	6	23	0.9	39	2.1
8 Oct 1985*	5	4	34	2.2	64	4.4
21 Aug 1986*	2	2	31	1.4	65	0.7
18 Nov 1987	>100	7	32	2.1	57	3.0
7 Nov 1988	>100	10	18	3.8	31	7.1

* = larvae taken in these years showed signs of metamorphosis

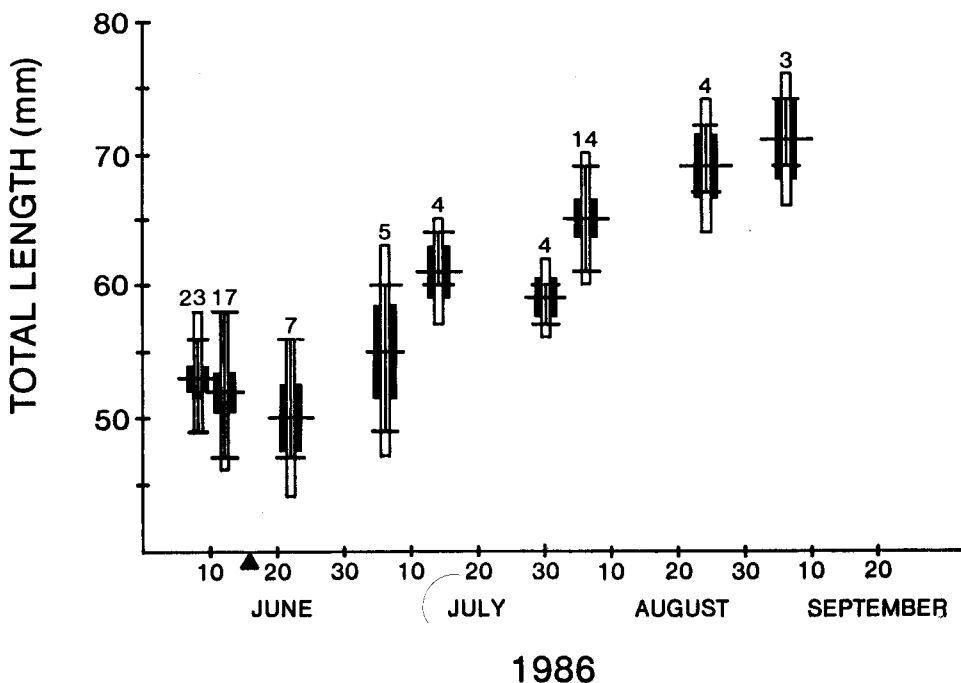


FIG. 1.—Total length plotted against date of capture for newly transformed spotted salamanders encountered at the Salamander Pond drift fence in 1986. Central horizontal line represents the mean; the narrow horizontal lines, range; the open box, \pm two SD; the solid boxes, \pm two SE. The triangle on the x-axis represents the date of capture for the 18 unmeasured individuals

of 99 newly transformed, nonoverwintered salamanders were encountered at the drift fence, either in drop cans or under boards (TL: $n = 81$, $\bar{x} = 57$ mm \pm 6.7 SD). There is a significant positive correlation between TL and date of capture ($n = 81$, $r = 0.885$, $P < 0.001$, Fig. 1).

On 9 May 1988, four overwintered, newly transformed salamanders were captured in drop cans or under boards at the drift fence (SVL: $n = 4$, $\bar{x} = 41$ mm \pm 1.4 SD; TL: $n = 2$, $\bar{x} = 68$ mm \pm 3.5 SD). The majority of the newly transformed salamanders were encountered during or immediately following rainfall. Water temperatures at Salamander Pond regularly exceeded 15 C in April and May and 25 C in the summer.

DISCUSSION

The presence of only a few large larvae in Salamander Pond in the fall of 1985 and 1986 suggests that these were years in which most individuals metamorphosed in the summer. The alternative explanation, that most larvae died prior to metamorphosis in these years, is unlikely because the decline in the number of larvae taken in the seine hauls over time was accompanied by signs of metamorphosis (reduction of gills and dorsal fin) and, in 1986, 99 newly transformed salamanders were intercepted at the drift fence. These salamanders hatched in 1986 and were not overwintered from 1985 because their development was followed from hatching to first signs of metamorphosis and only five larvae were taken in the last seining effort in the fall of 1985.

In contrast, the large numbers of small larvae taken from Salamander Pond in the fall

ember and January) from November 1984 to November 1988 with a 2.3-m-long, 5-mm-mesh seine. In 1986, an effort was made to sample through the winter. During each visit, I seined the entire pond, usually in two hauls. Spotted salamander larvae were counted and 5–30 were preserved in 10% formalin. The preserved animals were returned to the laboratory where snout-to-vent length (SVL) and total length (TL) were measured to the nearest mm. I checked the drop cans and boards daily for newly metamorphosed salamanders from February through May in all years, and at least weekly from May to December in 1986 when the plastic sheeting was in place. The drop cans were closed after May in 1984, 1985, 1987 and 1988 but the boards were checked occasionally from May to November during these years. All newly metamorphosed salamanders encountered were measured to the nearest mm for TL and released on the outside of the drift fence. Water temperature was recorded at irregular intervals throughout the five-year period.

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of 1984, 1987 and 1988 argues strongly that these were years in which most of the larvae were unable to metamorphose before the onset of winter. The fate of the larvae seined in the fall of 1984 and 1988 is not known for certain because the pond was not sampled through the winter in these years and no attempt was made to census newly transformed salamanders in 1985 and 1989. It is known, however, that at least 30 of the larvae hatched in 1987 were still alive on 9 May 1988 and at least four from this cohort metamorphosed on this date.

While it is certain that the majority of the larvae that hatched in 1985 transformed in late summer and fall, at least two larvae overwintered and transformed the following spring. In 1986, I also observed substantial variation in timing of metamorphosis. Observations from 1985 and 1986 illustrate that timing of metamorphosis varies within as well as among years at Salamander Pond. It is likely that larvae hatched in 1984, 1987 and 1988 also exhibited a broad range in time of metamorphosis. However, since I made no attempt to census newly transformed salamanders in these years, no conclusions can be drawn.

Environmental factors that may affect timing of metamorphosis include water temperature (Bleakney, 1952; Whitford and Vinegar, 1966), larval density (Wilbur, 1972, 1976; Stangel, 1988), prey and predator population levels and time of pond drying. Water temperature and time of pond drying are not potent factors in the present study. Water temperatures were higher than those reported by Whitford and Vinegar (1966) and were uniform among years and, as stated earlier, the pond did not dry during the study period. Density effects could be important at Salamander Pond where as many as 665 female captures have been recorded in a single breeding season (Phillips, 1989). In some years high larval density could prevent most larvae from reaching a minimum size for metamorphosis (Wilbur and Collins, 1973). Finally, there seems to be a within-year size advantage associated with late metamorphosis (Fig. 1). This observation, also recorded for *A. maculatum* by Shoop (1974), could be important in explanations of the genetic component of variation in timing of metamorphosis, especially if size at metamorphosis is positively correlated with adult traits that contribute to fitness (Semlitsch *et al.*, 1988). Under this assumption it would be beneficial for larvae to remain in a permanent pond until they reach a theoretical maximum size (Wilbur and Collins, 1973) even if this means overwintering. These benefits would be balanced by the costs of increased mortality associated with overwintering which would be expected to increase with the severity of the winter season.

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