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Life History Variation and the Growth of Juvenile *Notophthalmus viridescens* from Massachusetts

WILLIAM R. HEALY

Juvenile newts (*Notophthalmus viridescens*) exhibit different growth patterns in aquatic and terrestrial habitats. Aquatic juveniles grow at a faster annual rate and mature earlier than the terrestrial efts. The growth of efts is largely concentrated in the summer; whereas, aquatic juveniles achieve most of their annual increment in the spring. The mean annual growth increment of the efts varied more from year to year than did that of the aquatic juveniles. These differences in growth were attributed to temperature and moisture conditions which influenced the amount of time the newts spent foraging.

EASTERN red-spotted newts from coastal localities in Massachusetts omit the terrestrial stage in their life history and reproduce earlier than individuals from inland populations which possess the usual eft stage (Healy, 1966). The adult and larval stages are aquatic in both life histories and, except for the occasional appearance of neotenes in the coastal populations (Healy, 1970), show little morphological variation between coastal and inland localities. Juveniles, from the two localities, however, differ markedly in their adaptations to the distinct habitats. Coastal juveniles have the same aquatic adaptations as the adults, e.g., smooth skin, flattened tail and olive coloration. Juveniles from inland populations possess rough skin, round tails and orange-red coloration which is more adaptive in the terrestrial habitat. This difference in the habitat occupied by post-metamorphic juveniles constitutes the major difference between the two life history variations in *Notophthalmus v. viridescens*. This paper reports a detailed study of the growth pattern of both aquatic and terrestrial juveniles and compares the two growth patterns from larval metamorphosis to the acquisition of sexual maturity.

MATERIAL AND METHODS

A coastal population containing aquatic juveniles was sampled from 1961 to 1965 in Swampscott (21 km NE of Boston), and

during this period 2,068 specimens were examined. The growth of juveniles was estimated from the difference in the mean snout-vent lengths of age specific size classes between successive samples. The recognition of distinct age specific size classes was made possible by annual fluctuations in larval abundance which produced peak numbers of larvae in alternate years. In each sample the first two age classes were readily distinguishable in size frequency histograms (Fig. 1). More detailed information concerning this population has been presented elsewhere (Healy, 1970) and need not be repeated here.

Terrestrial juveniles were studied in an oak-pine woodland in Charlton (24 km SW of Worcester) and growth was estimated from snout-vent length increments observed in marked individuals between recaptures. From 1968 to 1970, 820 efts were marked and released; all specimens collected in 1971 were preserved. Between 1968 and 1971, 383 efts were recaptured of which 149 were recaptured more than once. Individuals were recognized by their dorsal spot patterns, although different toe clip combinations were used to mark each sample as an aid in identification.

OBSERVATIONS AND RESULTS

Efts varied in growth both seasonally and from year to year (Table 1). Comparison

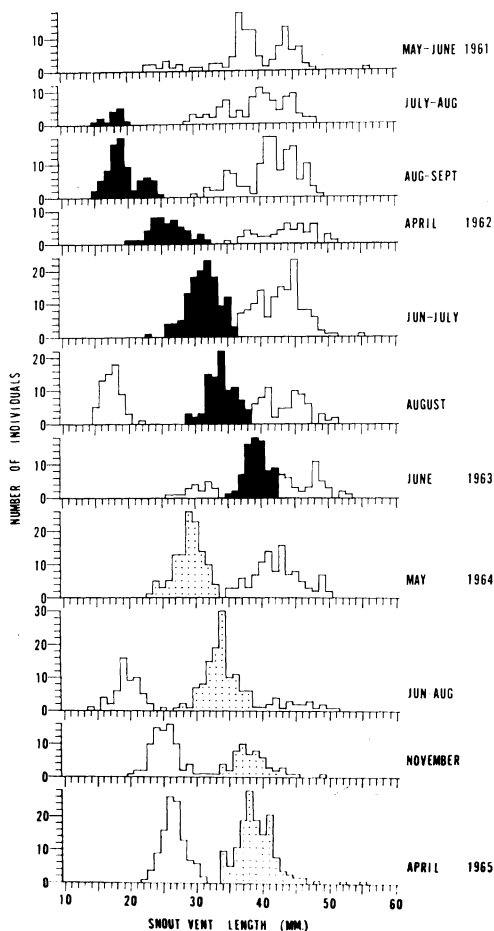


Fig. 1. Size-frequency histograms of *Notophthalmus viridescens* from Swampscott, Mass. depicting growth from the larval stage to sexual maturity (black squares) and from age one year to sexual maturity (stippled). In this population sexual maturity is achieved two years after egg deposition which occurs in the spring. The white squares represent the remainder of each sample which does not reveal the growth sequence.

of growth increments between years was made difficult because collections could not be made on the same dates in different years. Efts could only be collected during or immediately after rainy periods when they emerge from beneath the leaf litter and walk abroad; and these rainy periods did not occur with any regularity.

Due to the small number of specimens recaptured between successive sampling periods all recaptured specimens, regardless of size, were used in calculating the mean

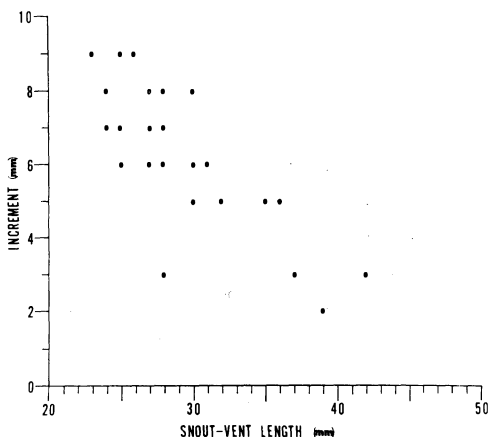


Fig. 2. Growth in body length of terrestrial *Notophthalmus viridescens* marked in Charlton, Mass. in June, 1969 and recaptured in Sept. and Oct., 1970. Each point represents a single individual. The abscissa is the SVL at time of marking.

growth increments. This presented a further difficulty in making comparisons because a strong inverse relationship between size and increment was observed in this population (Fig. 2), and the average size of specimens marked in 1969 was less than that of those marked in 1970. This difference was attributable to the failure of small eft s to reach the study area in 1970 due to the high rate of mortality suffered by post-larval juveniles in 1968 as a result of being marked by limb amputation. As a consequence the larger mean annual growth increment for 1969 was due in part to the smaller average size of the specimens marked in 1969 in comparison to those marked in 1970. That a real difference in growth increment occurred between these two years was demonstrated by a comparison of the annual growth achieved by a subsample of specimens which were similar in size at the time of marking (Table 2).

Some of the marking intervals shown in Table 1 were quite extensive, but no significant growth was observed within these periods as judged from the size of specimens marked at the beginning of the period and recaptured at the end, as well as from a comparison of the growth of specimens marked within the period and recaptured at later dates. Therefore, these pooled collections were treated as single samples.

In contrast to the variation in annual

TABLE 1. MEAN GROWTH INCREMENT (SVL) OF MARKED EFTS RECAPTURED IN CHARLTON, MASS. BETWEEN 1968 AND 1971.

Date Marked	Date Recaptured	N	Increment (mm)	
			Mean \pm S.E.M.	Annual
27 June-18 July 1968	2-25 August 1968	29	0.38 \pm 0.10	
2-25 August 1968	16 April-3 June 1969	18	0.17 \pm 0.14	
16 April-3 June 1969	16-19 June 1969	42	1.02 \pm 0.10	1.57
16-19 June 1969	13-28 July 1969	31	1.26 \pm 0.17	
13-28 July 1969	3-4 September 1969	25	2.00 \pm 0.20	
3-4 September 1969	3 May-6 June 1970	31	0.55 \pm 0.10	
3 May-6 June 1970	22-27 June 1970	32	0.69 \pm 0.10	4.50
22-27 June 1970	11 Aug.-10 Sept. 1970	21	1.24 \pm 0.14	
11 Aug.-10 Sept. 1970	3 May-9 June 1971	32	0.59 \pm 0.10	
3 May-9 June 1971	June, 1971	—	— —	> 1.83

growth observed in terrestrial juveniles, the growth of aquatic juveniles from Swampscott was remarkably stable from 1961 to 1965 (Fig. 1). The data presented in Fig. 1 was not complete enough to depict the growth of juveniles from larval stage to adulthood for each month in which samples were taken. As a result the sequence of aquatic juvenile growth, which is compared with the growth of eft s in Fig. 3, was obtained by pooling samples taken in different years. This method was considered valid because the pattern of juvenile growth in the Swampscott population was stable over the five year study period and samples of the same age class taken on comparable dates but in different years did not differ significantly in mean snout-vent length (Table 3). The data for age specific growth of eft s was obtained from the size of marked individuals in the youngest age class of eft s in the spring of 1969 (known to be two years old) as they were recaptured periodically through 1971. Because eft s in their first year do not reach the study area until the fall after metamorphosis, little information regarding the growth of this age class was obtained except

for a small sample of five specimens collected near the pond in April of 1969.

Fig. 3 reveals that not only do the aquatic juveniles grow at a faster rate than their terrestrial counterparts, but also that seasonal differences exist in the growth patterns of the populations. These differences are clearly evident in a comparison of the growth of one year old aquatic juveniles with two year old eft s from one spring to the next (Fig. 4). Eft s show little growth during spring or winter, and much more in the summer. The bulk of their spring growth is concentrated in June for no growth was observed from April to early June. The aquatic juveniles, on the other hand, achieve most of their growth in the spring, and their growth rate declines thereafter. Unlike the eft s, most of the growth of the aquatic juveniles occurs in the cooler months and their growth from fall to spring is about the same as the summer.

An explanation of the terrestrial growth pattern of this species is suggested by the diurnal activity of eft s when the woodland floor is wet. Eft s have been observed feeding in the study area when the substrate is

TABLE 2. MEAN ANNUAL SVL INCREMENT (MM) OBSERVED FOR EFT S IN THE SIZE RANGE 29-34 MM (SVL) WHEN MARKED.

Date Marked	Date Recaptured	N	Mean SVL \pm S.E.M. at Time of Marking	Mean Increment upon Recapture
27 June-3 July 1968	3-19 June 1969	8	32.38 \pm 0.49	1.75
3-19 June 1969	5-27 June 1970	14	31.57 \pm 0.44	5.79
5-27 June 1970	3-9 June 1971	8	31.63 \pm 0.49	2.00

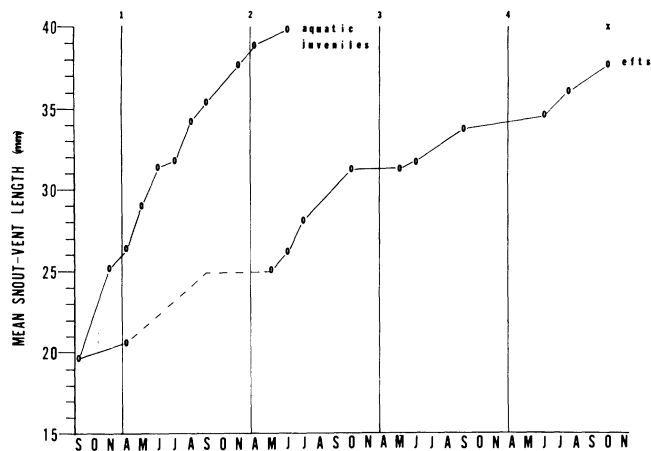


Fig. 3. Growth of aquatic and terrestrial *Notophthalmus viridescens* from late larval stage to sexual maturity. The broken line represents a hypothetical pattern of growth for efts in their first year on land. The average size of sexually mature efts migrating to the pond to breed for the first time is designated by the letter x.

moist, but when the surface of the woods is dry they remain in moist enclaves under the leaf litter. A comparison of the contents of the small intestine of efts collected during the first and second days of a 48 hr rainy period in July revealed that specimens collected on the second day had approximately twice as much material in their small intestines as those collected on the first day of rain. This difference was statistically significant and suggests that more food is consumed during rainy periods than when the weather is dry. At the time of both collections the efts were feeding since their stomachs were full.

Efts are most active on the forest floor when the substrate is moist and the temperature is above 13 C. At temperatures below 10 C they rarely appear even during very

moist conditions. Thus, their activity is dependent on both temperature and rainfall. If efts consume more food during rainy periods, it is reasonable to assume that their growth should be related to periods of warm, wet weather. Fig. 5 shows that the number of rainy days when the temperature is suitable for active foraging is greatest between June and September—the observed period of maximum seasonal growth (Fig. 4).

Yearly growth differences may also be explained by temperature and rainfall conditions. A marked difference in mean annual growth was observed between 1968 and 1970 (Table 2). When the number of rainy days with a mean daily temperature above 13 C was counted from the beginning of the marking periods shown in Table 2 to the end of the following August, the years with

TABLE 3. COMPARISON OF AGE-SPECIFIC SIZE GROUPS OF *Notophthalmus v. viridescens* SAMPLED IN SWAMPSCOTT, MASS. IN DIFFERENT YEARS.

Age (mo.)	N	Snout-vent Length (mm)		Date of Sample	p (t-test)
		Range	Mean \pm S.E.M.		
12	50	20-32	26.06 \pm 0.35	April, 1962	0.4 > p > 0.2
	109	22-31	26.51 \pm 0.17	April, 1965	
14	56	26-36	30.95 \pm 0.32	June, 1962	0.5 > p > 0.4
	20	26-33	30.45 \pm 0.45	June, 1963	
15-16	25	29-36	33.20 \pm 0.41	July-Aug, 1961	0.5 > p > 0.4
	116	27-38	33.56 \pm 0.20	July-Aug, 1964	

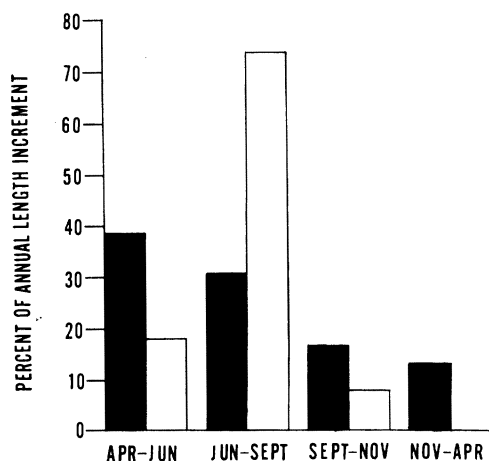


Fig. 4. Seasonal growth pattern of aquatic (black bars) and terrestrial (white bars) *Notoththalmus viridescens*. The mean total annual SVL increment for aquatic juveniles is 12.9 mm and 6.6 mm for eft.

the highest annual increment were found to have the greatest number of rainy days, i.e., 1968 (16 days), 1969 (33 days), and 1970 (19 days).

DISCUSSION

In the more common life history expression of *Notoththalmus viridescens* post-metamorphic individuals from the same population occupy distinct habitats, i.e., juveniles are terrestrial and adults aquatic. This mode of life history offers the opportunity for comparing terrestrial and aquatic adaptations in the same species. Previous studies have demonstrated differences between terrestrial and aquatic individuals in the toxicity of skin glands (Brodie, 1968), in visual pigments (Wald, 1958), and in relative immunity from predation (Hurlbert, 1970a). Since, however, the terrestrial and aquatic habitats are normally occupied by two distinct and temporally separated phases in this species' life history, these comparisons do not involve specimens of the same age or degree of maturity. The discovery of a life history variation in which post-larval juveniles forsake the terrestrial sojourn and remain in the water has permitted a more exact comparison of the effects of aquatic and terrestrial environments.

In this study three basic differences were found in the growth pattern of aquatic and terrestrial juveniles: aquatic juveniles grow

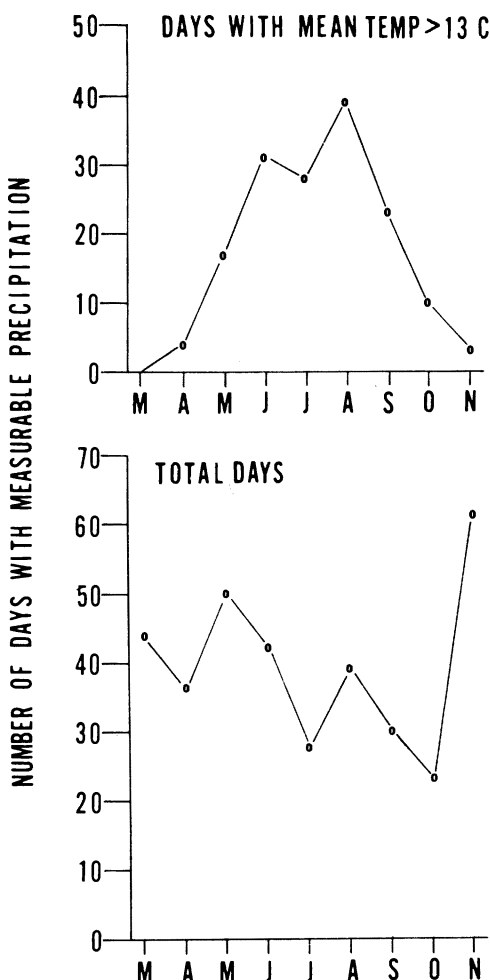


Fig. 5. Monthly precipitation during a four year period (1968-1971) near Charlton, Mass. including all days regardless of mean daily temperature (bottom) and including only those days with a mean daily temperature above 13 C (top). (Data supplied by the U. S. Weather Bureau in Worcester, Mass.)

at a faster annual rate than their terrestrial counterparts; growth on land is largely restricted to the summer months, while aquatic juveniles grow throughout the year and achieve most of their annual growth in the spring; and annual increments are far more variable from year to year on land than they are in the aquatic environment.

The differences in growth observed in the two habitats is a reflection of the intensity and duration of individual activity. Springer (1909) found that the rate of growth in this species is directly proportional to the

amount of food consumed. Morgan and Grierson (1932) demonstrated that aquatic newts continue to feed and molt during the winter and, therefore, are active throughout the year. Low temperatures restrict the activity of efts to a relatively short period in the year and the amount of moisture is even more restrictive within this period. Efts respond to rain by emerging from under leaf litter and actively moving over the forest floor. Although they often forage during this time, their response to moisture does not appear to be directly related to foraging, i.e., because of an attraction to a greater abundance of prey on the surface when the weather is moist. Migrations to and from the pond occur mainly when the substrate is moist (Hurlbert, 1969, 1970b), and on wet nights efts emerge and remain motionless on small plants above the surface and make no attempt to feed (Healy, unpublished). Food may be more plentiful during rainy periods, but the surface activity of efts appears to be largely a response to moisture. If, as is suggested by the analysis of intestinal contents, feeding is greatest during wet weather, efts have far fewer opportunities to feed than do aquatic juveniles. As a result aquatic juveniles grow at a faster annual rate than do efts.

Because the growth of terrestrial juveniles appears to be influenced by periods of warm, wet weather, their annual growth is largely concentrated in the summer. Aquatic juveniles achieve their maximum rate of growth in the spring and show a decline in growth in the summer. During this study of the Swampscott population an extensive drought lowered the level of the pond and raised the water temperature during the summers from 1962 to 1965. Springer (1909) observed that the rate of growth of adult newts decreased with increased temperature and increased size. The increase in water temperature during the summer could explain this decreased growth rate, and the continued decline in the fall and winter may be due to the larger size of the juveniles as a result of prior growth. These differences in the period of maximal growth reflect seasonal differences in the physical characteristics of the respective habitats.

The temperatures in the aquatic environment may be less variable from year to year than the temperature and moisture conditions on land. This smaller range of vari-

ability in aquatic vs terrestrial systems seems to be the most likely reason for the greater stability in growth pattern observed in the aquatic juveniles. The above comparisons indicate that the environmental factors operating in the aquatic environment are far more favorable for growth of juveniles in this species than those existing in the terrestrial environment. Organ (1961) in his comparison of the population dynamics of five species of *Desmognathus* noted that the larger of the five species were also the most aquatic, although he did not study growth. In general, the salamander species which attain the largest individual size spend most of their existence in the water, and so the aquatic environment appears to favor large size and more rapid growth in salamanders.

Individuals metamorphose as larvae and acquire sexual maturity at approximately the same size in both life history variations (Fig. 3); hence, the difference in growth rate results in a reduction in the age at first reproduction in the coastal populations which omit the eft stage. Reduction in the age of first reproduction increases the intrinsic rate of natural increase and thus has important population consequences (Cole, 1954). Earlier reproduction is achieved in coastal populations as a result of an alteration of post-metamorphic juvenile behavior whereby the juveniles remain in the water and forsake the eft stage. The result of these two patterns of post-metamorphic behavior is the development of juveniles in two very different habitats. This difference in habitat affects morphology, growth pattern and population dynamics and, therefore, constitutes the most fundamental difference in the two expressions of the life history of *Notophthalmus viridescens*. The basic question still to be answered is the cause of this behavioral difference.

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Weather Bureau in Worcester for supplying me with weather data. This study was supported in part with funds from the Horace H. Rackham School of Graduate Studies of the University of Michigan and from a Research Corporation grant to the College of the Holy Cross.

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Response of *Rana temporaria* Tadpoles to Chronic Doses of pp'-DDT

A. S. COOKE

Tadpoles (*Rana temporaria* L.) were maintained in concentrations of 0.0001 or 0.001 ppm pp'-DDT from the end of the external gill stage until the appearance of the front legs. Slight hyperactivity was noted amongst tadpoles in 0.001 ppm DDT. During the final few days of treatment, tadpoles exposed to the lower level of DDT developed more quickly than the controls. In addition, during tail resorption after treatment had finished there was a significant positive relationship between development rate and the severity of prior exposure to DDT. DDT residues accumulated during chronic dosing caused neither mortality nor obvious effects on behaviour at body levels of 2-5 ppm. After acute exposure, tissue levels of 2 ppm or less can cause hyperactivity in tadpoles and death in small frogs. Differences in response to acute and chronic dosing are probably related to the extent of storage of residues in fatty tissue. Several treated tadpoles had lateral kinks at the base of the spine and two also had permanently extended left legs.

A recent enquiry indicated that the two most abundant British anurans, the frog *Rana temporaria* L. and the toad *Bufo bufo* L. suffered widespread declines in the British Isles during the 1960s (Cooke, 1972a). Destruction or modification of suitable freshwater habitat was considered to be the main reason for the declines. Pesticides

have probably only had harmful effects on amphibian populations in Britain when breeding sites or adult feeding areas have been accidentally polluted or deliberately treated to control invertebrate pests. In order to be able to recognize and evaluate such effects in breeding sites, spawn or tadpoles have been subjected to acute exposure