GROWTH IN THE SMOOTH NEWT (*TRITURUS VULGARIS*) DURING THE AQUATIC PHASE OF THE ANNUAL CYCLE

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ABSTRACT

Growth during the aquatic phase of the annual cycle (measured as change in snout-vent length) was investigated in a natural population of smooth newts (*Triturus vulgaris*) at a pond in southern England in 1983. Two types of data were collected: growth at the population level (quantified as changes in mean snout-vent length) and growth in individual, recaptured newts. For the population as a whole, significant growth was detected during the aquatic phase. At the level of individual newts, rate of growth during this period was negatively correlated with snout-vent length at entry to the pond; such a relationship is common in the Amphibia. The average growth rate of adult newts observed during the present field study (1.1-1.5mm) agrees closely with an independent estimate (about 1.5mm) obtained during a previous, skeletochronological investigation (Verrell and Francillon, 1986).

INTRODUCTION

Despite the widespread occurrence and distribution of European newts in the genus *Triturus*, little is known about the growth of individual newts. A common assumption in the amphibian literature is that growth is indeterminate in these animals, but in many taxa, growth rate shows considerable individual variation, and body size is a poor predictor of individual age (see review by Halliday and Verrell, in press). The few published data which are available indicate that growth follows a similar pattern in the smooth newt, *Triturus vulgaris* (Hagstrom, 1977, 1980; Harrison, Gittins and Slater, 1984), the crested newt, *T. cristatus* (Hagstrom, 1977, 1980; Glandt, 1981), the alpine newt, *T. alpestris* (Smirina and Rocek, 1976) and the marbled newt, *T. marmoratus* (Caetano, Castanet and Francillon, 1985).

In the natural environment, growth can be measured at either the level of the population (by comparing the average body sizes of the same groups of animals at different times) and/or at the level of individuals (by marking and then recapturing known animals over time). The interval of time between episodes of measurement can be relatively short (within-years) or long (across-years). The best data for *Triturus* published to-date are for growth across, not within, years.

In a previous study (Verrell and Francillon, 1986), preliminary information on average annual growth rate in adult *Triturus vulgaris* was obtained during a skeletochronological investigation of the relationships between individual body size, age and investment in reproduction. In the present paper, field data are presented on growth in body size in a population of *T. vulgaris* visiting pond in southern England. Growth is considered during the aquatic phase of the annual cycle, at both the population and individual levels.

METHODS

The study pond, near Soulbury, Buckinghamshire, has a surface area of approximately 120m^2 and is a deep, permanent pond situated on private farmland. It is a breeding site for smooth newts, crested newts, common frogs (*Rana temporaria*) and common toads (*Bufo bufo*).

From February 1983 to May 1984, the pond was completely encircled by a polythene drift fence, 25cm high and buried in the soil to depth of at least 5cm; plastic pitfall traps were sunk along the outside of the fence at intervals of about 8m. Every two or three days, smooth newts were collected from the pitfall traps and from the ground adjacent to the fence. The sex of each newt was recorded, together with its snout-vent length (SVL) measured to the nearest 0.5mm. Newts are notoriously difficult to measure when held in-the-hand, due to their frantic wriggling. The latter was reduced by suspending each newt up-side down by its pelvic area for a few seconds before SVL was measured. This appears to induce a quiescent state in the animals, resembling a condition known as tonic immobility. Individuals caught on the outside of the drift fence (i.e. entering the water) were marked by removing phalanges to show date of capture; each combination of phalanges removed was unique for a period of four days in duration (this method of marking was devised by Malkmus, 1980, during a study of *T. boscai* populations in Portugal). In addition, any characteristics such as limb deformities were noted, to aid in the identification of individuals at recapture. After measurement and marking, all newts were released onto the opposite side of the drift fence to that on which they were caught.

In addition to this field-work, a laboratory study was conducted in order to determine the precision with which SVL can be measured. Seven adult smooth newts (two males and five females) were brought into the laboratory in 1984 and, over the course of two days, the SVL of each was measured to the nearest 0.5mm (as described above) on eight, randomly-assigned occasions.

RESULTS

Before considering the field data obtained during this study, it is pertinent to consider the precision with which SVL can be measured in adult smooth newts; few authors address the important issue of precision in morphometric studies (but see Bell, 1977; Lee, 1982). The results of the precision study conducted in the laboratory are summarised in Table 1, and indicate that SVL can be measured quite precisely. However, it should be noted that the margin of error of measurement (0.5-1.0mm) corresponds to the change in SVL recorded for the majority of newts recaptured in the field (see below). Two lines of evidence suggest that the changes in SVL of these recaptured newts were due to real growth and not mere error of measurement. First, as discussed below, no recaptured individuals showed a decrease in SVL in the interval between entry to and exit from the pond. Secondly, as shown in Table 1, 42 (75 per cent) of the 56 SVL measurements taken from the captive newts scored as 'same' within individuals. However, it is clear that data on apparent growth should be treated with some caution, especially if the precision of measurement is either low or unknown.

In 1983, I recorded the SVLs of adult *T. vulgaris* entering (N= 321, March to June) and leaving (N= 176, June to December) the study pond. Summary statistics of the SVLs of these two classes of newts are given in Table 2. Sexual dimorphism in mean SVL was not apparent for either class (P>0.1 for both intersexual comparisons, Students's t-test). Within 1983, mean SVL was significantly greater in adult newts leaving the water than in newts entering (for males, t = 2.8, P<0.05; for females, t = 4.15, P<0.01, Student's t-test). These data indicate that, taking the adult newt population as a whole, both males and females increased in SVL by an average of 1-1.5mm during their period of residence in the water.

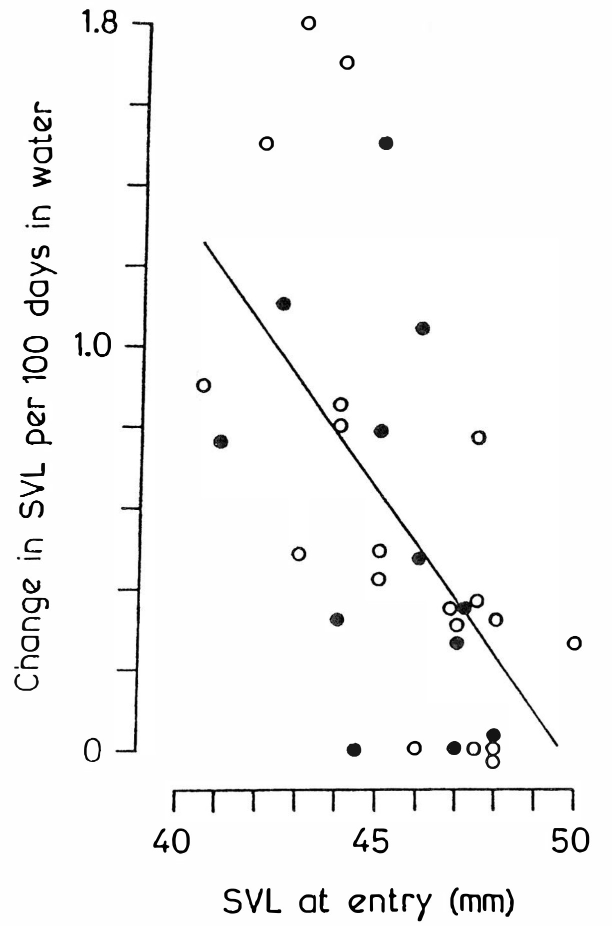

Fig. 1 Growth in 31 adult *Triturus vulgaris*, measured at entry to the study pond and recognised as individuals at exit from the pond; open circles are males (N= 19), closed circles are females (N= 12). Each circle represents change in snout-vent length per 100 days in water as a function of snout-vent length at entry to the pond. The regression equation is: y = ⁻0.139x + 6.88. See text for further details.

Sex	Number of 'same' scores	Variance	Min	Max	Range
Male	6	0.140	40.0	41.0	1.0
Male	6	0.130	41.0	42.0	1.0
Female	6	0.071	41.5	42.5	1.0
Female	5	0.053	44.0	45.0	1.0
Female	7	0.030	46.0	46.5	0.5
Female	6	0.071	46.5	47.5	1.0
Female	6	0.053	50.0	50.5	0.5

TABLE 1: Number of 'same' scores, variances, minima, maxima and ranges for snout-vent length measurements taken on eight, randomly-assigned occasions from each of seven adult *Triturus vulgaris*. See text f r further explanation.

Data on changes in SVL for individual smooth newts are available for 19 males and 12 females. These newts bore easily recognisable marks, and it proved possible to extract their individual SVL records at entry to and exit from the pond from the records for the population as a whole. The total amount of time that these newts spent in the water ranged from between 55 and 205 days (mean = 129 days). Seven newts did not change in SVL during their stay in the water, and no newts showed a decrease in SVL during this period, as mentioned above (such a decrease was observed by Glandt, 1981, who called it 'negative growth'). Twenty-four newts (77 per cent of the total) exhibited an increase in SVL during their stay in the water and of these, 19 (79 per cent) changed in SVL by either 0.5 or 1.0mm (as noted above).

These data for the 31 recaptured newts were then analysed in order to examine the relationship between growth rate and body size. As shown in Fig. 1, change in SVL per 100 days in the water was negatively correlated with SVL at entry to the pond ($r = {}^{-}0.61$, $P<0.001$). Mathematically, this relationship can be defined thus: Change in $SVL_{(mm)}$ per 100 days in water = 6.88 - 0.139 . $SVL_{(mm)}$ at entry. Growth rate was thus a decreasing function of body size, as predicted by the general growth model of von Bertalanffy (see Bertalanffy, 1957; Andrews, 1982). However, note that SVL at entry accounts for only 37.2 per cent of variance in growth rate.

		Males	Females
Entry to pond		44.5±2.7	44.2±2.7
		37.5 - 51.0	37.0 - 52.5
		(*N* = 105)	(*N* = 216)
Exit from pond		45.6±2.7	45.7±2.9
		38.0 - 50.0	37.0 - 52.0
		(*N* = 81)	(*N* = 95)

TABLE 2: Summary statistics (mean ± standard deviation, range and sample size) of snout-vent measurements (mm) taken from male and female *Triturus vulgaris* caught entering and leaving the study pond in 1983. Statistical analyses of these data are presented in the text.

DISCUSSION

It is clear from Table 2 that adult *T. vulgaris* increased in SVL by an average of 1.1mm in males and 1.5mm in females during that part of the annual cycle spent in water; previous work has revealed that, during this time, the newts both breed and feed (Verrell, 1985; Verrell and Halliday, 1985; Griffiths, 1986). These data, obtained for the population as a whole, mask considerable variability in the growth rates of individual newts. As shown in Fig. 1, growth rate was negatively correlated with SVL at the beginning of the aquatic phase of the annual cycle. Such a relationship seems to be common in the Amphibia (for anuran studies see Ryan, 1953; Jameson, 1956; Bellis, 1961; for urodele studies see Stebbins, 1954; Hendrickson, 1954; Taber, Wilkinson and Topping, 1975). It must be stressed that this relationship between growth rate and size cannot be taken as evidence for a similar relationship between growth rate and age. Despite the common assumption that growth is indeterminate in the Amphibia, there is now mounting evidence that body size is a poor predictor of individual age in these animals (see review by Halliday and Verrell, in press).

To my knowledge, the data presented in this paper are the first to document growth in SVL in a natural smooth newt population within a single year; studies of growth in the genus *Triturus* are few in number, and all are connected with growth across, not within, years. Many of the studies available have combined mark-release-recapture and skeletochronological methods to determine patterns of growth. In skeletochronology, histological sections of long bones (either humerus or femur) are examined for 'lines of arrested growth'; these lines record periods when no bone growth occurs, such as winters in species living in temperate areas (see Smirina, 1972; Francillon, 1979, 1980; Gibbons and McCarthy, 1983; Francillon and Castanet, 1985). The number of lines of arrested growth in a bone should therefore record the age of the individual in years. Hagstrom (1977, 1980) has studied growth in populations of *T. vulgaris* and *T. cristatus* in Sweden. He found that, after the attainment of sexual maturity, growth rate slows and body size and age become poorly correlated; presumably, this reflects the diversion of resources from somatic growth to reproduction. In addition, rate of growth across years appears to decrease with body size. Similar data have been obtained by Glandt (1981) and A. Bielinski (unpublished data) for populations of *T. cristatus* in Germany and southern England, respectively.

I have no data on growth across years for the population described in this paper, largely as a consequence of phalangeal regeneration preventing the recognition in 1984 of newts marked in 1983. However, independent evidence obtained during a skeletochronological study of smooth newts revealed that, between the ages of two and six years, the mean annual change in SVL was approximately $^{+}1.5$mm (Verrell and Francillon, 1986). This value is comparable with the average change in SVL observed between entry to and exit from the pond in the present study (Table 2). I tentatively interpret this similarity as indicating that most, if not all, growth in any one year occurs during the aquatic phase of the annual cycle (although physiological processes, such as the yolking of oocytes, continue during the winter: see Verrell, Halliday and Griffiths, 1986).

In summary, growth in SVL in *T. vulgaris* occurs during the time that the population spends breeding and feeding in the water; on average, males grow by 1.1mm and females by 1.5mm. These estimates mask considerable variation in the growth rates of individual newts; rate of growth is negatively correlated with body size. These field data were derived from a single population studied over a relatively short period of time. There is considerable evidence that growth patterns in amphibians and reptiles vary over both space and time (e.g. Schoener and Schoener, 1978; Van Devender, 1978); thus, further research is needed in order to confirm that the growth pattern of *T. vulgaris* conforms to the pattern outlined above. A study in which a cohort of individuals of known age (such as newly-metamorphosed young-of-the-year) are marked and then frequently recaptured over long intervals of time would undoubtedly yield valuable information on growth in these animals.

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