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THE ECOLOGY OF THE EGGS AND LARVAE OF THE SMOOTH NEWT (*TRITURUS VULGARIS* (LINN.))

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INTRODUCTION

Triturus is a European genus of the family Salamandridae, and includes those urodele amphibians which are usually called newts rather than salamanders. It is related to the Asian *Sinops* and to the North American *Notophthalmus*. The genus has eight species, of which the smooth newt *Triturus vulgaris* is the most abundant and widespread. The nominate subspecies, *T. vulgaris vulgaris*, is found throughout most of continental Europe, and is the only form in Britain. The appearance and distribution of the various other subspecies are described by Steward (1969).

Like other members of the genus, *T. vulgaris* is a small carnivorous poikilotherm which returns to the water to breed and which has an aquatic larva. It is only rarely found in running water, almost invariably breeding in small ponds. There is no satisfactory account of the ecology of the smooth newt in the literature; summaries of the few observations that have been made are given by Smith (1951) and by Gislen & Kauri (1970), but they amount to little more than an elementary natural history. More recently, work has been done on the breeding behaviour (Halliday 1972) and on food and parasites (Avery 1968, 1971), but no studies comparable to those of certain North American salamanders (e.g. Organ 1961; Tilley 1973) have appeared. The present paper attempts to sketch the principal events in egg and larval life; it includes a detailed account of the survival curves of eggs and larvae, which have not previously been described for any similar vertebrate. It is hoped that a later paper will deal with the ecology of the metamorphosed newt.

THE STUDY LOCALITIES

Populations of the smooth newt were studied in an area of about 35 km² between Oxford and Abingdon, in south-eastern England. This is lowland agricultural country, gently undulating, broken up by small woods and drained by the Thames and its tributaries. There are on average about 1.5 ponds/km². These are usually small bodies of water, of no more than 1000 m² in surface area, which were dug for agricultural purposes between 80 and 150 years ago. The introduction of the pipe-fed water-trough and the extension of land drainage has led to the disappearance of a great proportion of such ponds; those that remain are neglected and often dystrophic. However, 23 of the 27 ponds found in the main survey area supported populations of smooth newts, and of these three were chosen for sampling eggs and larvae.

(i) *The Nuneham Courtenay Arboretum pond*. (Nat. Grid ref. SU 554987.) This was originally a small field pond, but was cleared and made five or six times bigger in 1967,

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shortly after Oxford University acquired the site of the Arboretum. It is unlined, and lies at the foot of a slope of light sandy loam. During the winter it fills up to a depth of about 6 ft, but at the height of most summers it is not more than 6 in deep; in the exceptionally dry summer of 1972, it was completely dry from late August until the beginning of December. Its vegetation is the most diverse of any pond in the neighbourhood, and includes relatively large amounts of *Hottonia*, *Ranunculus*, *Glyceria*, *Elodea* and *Stratiotes*. There is an abundant zooplankton, consisting chiefly of *Daphnia obtusa* Kurz, *Chydorus* spp., copepods and ostracods; amongst larger invertebrates the dominant species are the caddis *Limnephilus vittatus* (Fab.), the shrimp *Crangonyx pseudogracilis* Bousfield and planarians, all of which are present in large numbers. Dytiscid beetles and *Notonecta* are also common. There are no fish, the only resident vertebrate predators being a few grass snakes, *Natrix natrix* (Lac.).

(ii) *The Nuneham Courtenay 'Venison South' pond.* (Nat. Grid ref. SU 545974.) This is a more typical field pond. It stands on arable land, but although eutrophic is not heavily polluted. The only submerged vegetation is a dense growth of *Callitriche*, which occupies almost the whole of the pond. The zooplankton is similar to that of N.C. Arboretum, but generally sparser; *Daphnia obtusa* is replaced by *D. pulex* Müll. *Asellus*, corixids and *Dytiscus* spp. are common, and in 1972 there were resident water shrews (*Neomys fodiens* (Penn.)) several of which proved on dissection to have been eating newt larvae.

(iii) *Stadhampton Shallow Glyceria.* (Nat. Grid ref. SU 609982.) This is an old pasture pond, built about 300 years ago. Apart from one small deep area in the middle, it now consists of shallow water invaded by *Glyceria*; the central area contains a bed of *Callitriche*. *Asellus* and ephemopteran larvae are the dominant invertebrates, and *Dytiscus* and *Notonecta* the most common predators. Like the other two ponds, it is regularly visited by waterfowl which, since they eat water-plants, presumably also eat the eggs and larvae of newts.

None of these three ponds is more than 400 m² in surface area. In 1972 they supported populations of smooth newts estimated to include about 1000, 240 and 180 adults respectively. N.C. Arboretum and Stadhampton also supported small populations of the crested newt, *Triturus cristatus* (Laur.); the third British species, *T. helveticus* (Raz.) does not occur within 20 km of these ponds.

Observations were also made during 1974 at a pond near Moor Monkton, York (Nat. Grid ref. SE 506569). This is a pond of about 700 m² surface area which is no more than 1 m in depth, and, like the Arboretum pond, it is prone to disappear during dry spells. The vegetation comprises a dense marginal growth of *Glyceria*, which encloses a ring of *Juncus*, which in turn encloses a central area of open water in which *Potamogeton* grows. The zooplankton is extremely dense, but the only larger non-predatory invertebrates which are at all common are ephemopteran larvae. There are also very large numbers of the leech *Haemopsis sanguisuga* (L.). The only animals present likely to eat newt larvae are a few ten-spined sticklebacks, *Pungitius pungitius* (L.) the pond being unusual in that dytiscid beetles and *Notonecta* are very rare. There is a small population of crested newts.

THE EGG

The egg is not more than 2 mm in overall diameter. The vitellus is surrounded by a thin jelly envelope which is partitioned by a series of membranes. Like most pond-dwelling

salamandrids (see Noble 1931), the smooth newt lays its eggs singly, wrapping them in the leaves of water-plants; *Hottonia* and *Callitriche* are the preferred plants in the laboratory. If the females are denied suitable oviposition sites, however, they may lay strings of as many as fifteen eggs, in a manner reminiscent of the primitive stream-dwelling genera *Typhlotriton* and *Pleurodeles*.

SURVIVAL

Methods of sampling and estimation

The habitat chosen for sampling eggs in the field was the bed of *Hottonia* in the N.C. Arboretum pond. In 1971, it was found by netting newly-hatched larvae that almost all the eggs laid in the pond were laid on the *Hottonia*. Samples were taken almost every week during the spring and early summer of 1972 with a core-sampler about 2 ft in diameter. This was thrust into a haphazardly chosen area of the weed-bed, shearing the weed and penetrating the bottom to a depth of 4 in or so. All the weed in the core was then removed and taken back to the laboratory, where it was stored for about 20 h at 4° C before being searched for eggs. Since every frond was carefully inspected, it is unlikely that any eggs were overlooked. A large sampler was needed to cut through the weed, but restricted the number of samples that could be taken. Core-sampling damaged the weed-bed noticeably towards the end of the sampling period, and in 1973 an experimental approach was used to obtain an alternative, independent estimate of egg survival. Female newts kept in the laboratory were allowed to lay eggs on fronds of *Hottonia*, thirteen of which, bearing a total of 227 eggs, were then tied to lengths of cotton and placed in the *Hottonia* bed in the pond. These fronds were examined every few days until hatching was seen to be imminent.

Newt eggs can be aged according to their state of development, and an indirect estimate of survival can be obtained from the age-structure of eggs found in the pond during 1972. Survival to any developmental stage x was calculated as the total number of eggs of stage x in all samples, relative to the number in the earliest stage, taking into account the different duration of different stages:

$$l(x) = \frac{N(x)/t(x)}{N(o)/t(o)}$$

where $N(x)$ is the number of eggs of the x th stage taken in all samples, and $t(x)$ is the duration of the x th stage. This method is formally equivalent to the length-frequency method used to estimate larval survival, which is more fully justified below. Six conditions must be met if this analysis is to be acceptable.

(1) All stages should be easily and consistently distinguishable. To this end, the development of the egg was divided into eleven easily recognized stages. These are listed in Table 1, and are described more fully by Bell (1974a). Table 1 also shows the duration of each stage, which was estimated in two ways. First, large numbers of eggs, known to have been laid on the same night, were examined every few days, and the weighted arithmetic mean of the developmental stages present was calculated. Secondly, a few eggs were cultured singly, and their development observed until just after neurulation. The final estimate is a simple average of these two independent estimates, when both are available.

(2) Collections should be made at more or less equal intervals. With two exceptions, samples were taken weekly.

(3) Collections should be made throughout the period during which the eggs are in the pond. This condition is met fully only for main period oviposition (see below), and a small error may have been introduced because sampling began after the earliest oviposition had started.

(4) The sampling effort should be comparable on all occasions; ideally, the same fraction of the egg population should be collected on each sampling occasion. It was impossible to fulfil this condition strictly, because the number of eggs in the pond on any given date could be calculated only when sampling was completed. An attempt was made to satisfy this requirement by taking about the same weight of weed on each occasion; as the pond shrank, however, rather smaller samples were taken towards the end of the sampling period. The mean weight of weed taken in each sample was 256.5 g, with a standard deviation of 92 g.

Table 1. *The duration of developmental stages used in the assessment of egg survival; data from eggs laid in the laboratory by N.C. Arboretum females (cultured in shallow aerated pondwater at a mean temperature of 16.5° C)*

| Stage | Description | Duration in days or fraction of a day | | | |
|----------|-------------------------------------------|---------------------------------------|-----------------|------|------------------|
| | | Mass cultures | Single cultures | Mean | Modal age (days) |
| 1 | Uncleaved egg | 0.1 | 0.1 | 0.1 | } 1.2 |
| 2 | Cleavage | 0.5 | 0.5 | 0.5 | |
| 3 | Blastula | 1.8 | 1.8 | 1.8 | |
| 4 | Gastrula | 2.65 | 1.4 | 2.0 | 3.4 |
| 5 | Neurula | 0.9 | 1.1 | 1.0 | 4.9 |
| 6 | Postneurula | 0.85 | 2.0 | 1.4 | 6.1 |
| 7 | } Further Prelarval Differentiation | 2.1 | — | 2.1 | 7.9 |
| 8 | | 2.25 | — | 2.25 | 10.0 |
| 9 | | 3.2 | — | 3.2 | 12.7 |
| 10 | | 3.05 | — | 3.05 | 15.9 |
| 11 | | 2.1 | — | 2.1 | 18.4 |
| Hatching | | — | — | — | 19.5 |

(5) The time course of oviposition should not be strongly skewed, since, if it were, a bias would be introduced by sampling at equal intervals. It is argued below that this condition is met.

(6) The pond temperature, and thus the rate of development, should remain more or less constant throughout the period of sampling. Since, of course, the temperature of the pond increased between April and June, this condition could not be met. The effect of the increase in temperature would be to exaggerate the importance of earlier samples, because earlier in the year the eggs will take longer to develop. An approximate correction was therefore devised, which was based on the assumption that the number of degree-days (number of days \times mean temperature in °C) needed to complete any given developmental stage is constant over the range 9° C–16° C. Five maximum-and-minimum thermometers were used to measure the temperature of the pond, from which this correction was calculated.

An estimate of the survival of eggs on the marked fronds in 1973 was obtained directly by plotting the number of eggs remaining against time.

Estimates of survival

The age-structure of eggs in the pond on different dates in 1972 is shown in Table 2.

From these data, an estimate of survival was obtained by the method described in the previous section. The estimates of survival at different stages seem to be satisfactory, in the sense of descending at successively later stages (see Fig 1(a)) except in stages two and three, which are too low. The reason for this is probably that the earliest stages are the shortest, and are, therefore, the most liable to errors of two sorts, (1) an increased tendency to random error and (2) an increased probability that the eggs will have passed these stages between collection and examination. To minimize these errors, the scores for stages 1, 2 and 3 were pooled, and survival values for the remaining stages recalculated relative to this pooled score. There remained the problem of scores which were pooled during examination: these refer to stages which were not clearly distinguished in the early collections before the scoring system was fully worked out. These were allocated to the stages to which they referred in the ratio indicated by the modified

Table 2. *The age-structure of egg from the Hottonia bed at N.C. Arboretum in 1972*

| Date | Stage | | | | | | | | | | | Dead | Total |
|----------|-------|----|----|-----|----|----|----|----|----|----|----|------|-------|
| | 1 | 2 | 3 | 4 | 5 | 6 | 7 | 8 | 9 | 10 | 11 | | |
| 7 April | 11 | | | | | 8 | 10 | 11 | 3 | 5 | | — | (48) |
| 14 April | 1 | | | | | | | | | | | — | (1) |
| 21 April | 14 | 2 | 6 | | | 3 | 10 | 3 | 1 | 2 | | 31 | 72 |
| 28 April | 1 | | | | | | | 2 | 4 | 2 | 4 | — | (13) |
| 5 May | 3 | 9 | | | 2 | | 2 | 2 | 2 | | | 10 | 30 |
| 12 May | 1 | 8 | 6 | 37 | 4 | 13 | 9 | 2 | 6 | 4 | | 42 | 133 |
| 19 May | | 4 | 24 | 57 | 37 | 25 | 31 | 10 | 9 | 9 | 4 | 107 | 317 |
| 30 May | 3 | 1 | 20 | 19 | 10 | 16 | 13 | 12 | 26 | 11 | 2 | 163 | 296 |
| 9 June | | 2 | | 1 | 1 | 4 | 5 | 5 | 4 | 6 | 1 | 61 | 90 |
| 16 June | 2 | | 2 | 12 | 4 | 1 | | | | | | 22 | 54 |
| 23 June | 1 | 1 | 4 | 3 | 2 | 2 | 5 | 1 | 5 | | | 50 | 74 |
| 30 June | 1 | | 3 | 10 | 7 | 3 | 2 | 1 | | | | 37 | 64 |
| 7 July | | | | | | | | | | | | 0 | 0 |
| 14 July | | | | | | | | | | | | 0 | 0 |
| Totals | 26 | 19 | 59 | 139 | 67 | 77 | 91 | 47 | 58 | 41 | 7 | 549 | 1218 |

Figures in parentheses are total numbers of eggs in samples where dead eggs were not counted; they are thus the total number of live eggs only.

survival values, and added to them. The recalculated estimates of survival were then used to construct a survival curve (Fig. 1(a)). The final point, for stage 11, still does not lie near the mean regression line. The reason for this is probably that the embryo at this stage is very close to hatching, is moving vigorously within its envelope, and the envelope itself has become so fragile that handling is liable to rupture it. The regression of Fig. 1(a) therefore excludes data for stage 11.

The survival curve shown in Fig. (1a) is a straight line under a double logarithmic transformation, the so-called Type IV of Slobodkin (1961); the rate of survival increases with age.

The number of eggs recruited into the larval cohort can now be calculated. The proportion of eggs which hatch on a given date after laying is known from the mass cultures. The fraction of eggs unhatched at the beginning of a given day, and the fraction surviving to this point, are known, and can be used to calculate the number of larvae

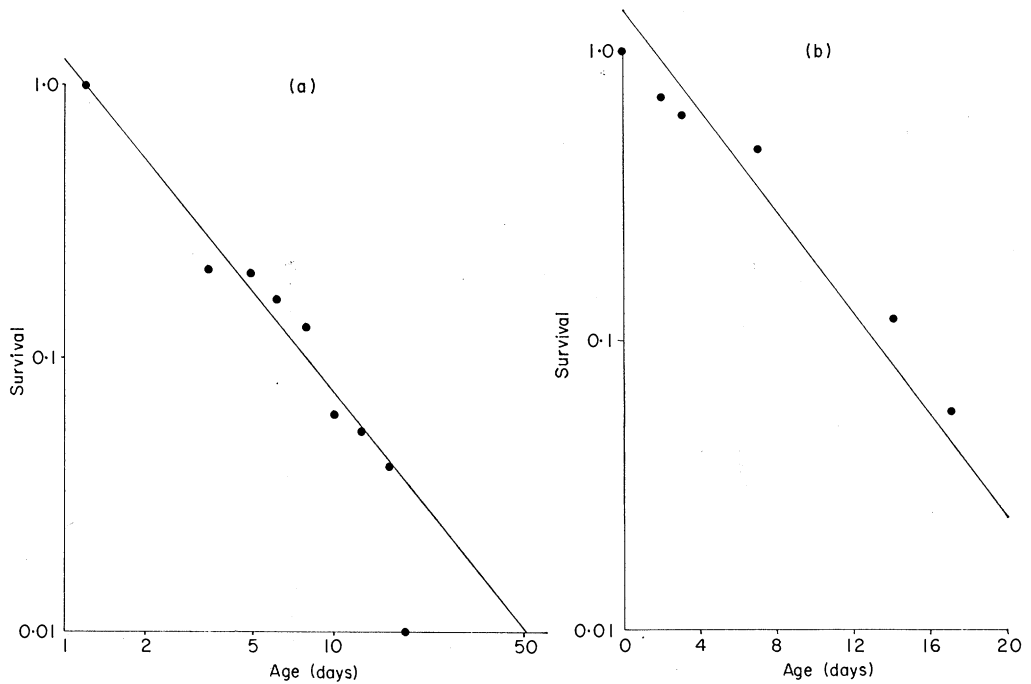


FIG. 1. The survival of eggs in a bed of *Hottonia* at N.C. Arboretum. (a) 1972, estimated from age-structure (see Table 2). The equation of the regression is $\log Y = -1.21 \log X + 3.09$. (b) 1973, estimated by experiment (see Table 3). The equation of the regression is $\log(1000 Y) = -0.0874 X + 3.143$.

Table 3. Calculation of the number of larvae recruited per egg laid for two years at N.C. Arboretum

| | Age in days | $l(x)$ | Percent of eggs hatched | Number of eggs remaining | Number of larvae recruited per egg laid |
|------------------------------------------------|-------------|--------|-------------------------|--------------------------|-----------------------------------------|
| (a) 1972, by observation | 18 | 0.029 | 0 | 0.029 | 0 |
| | 19 | 0.0275 | 38 | 0.01705 | 0.01045 |
| | 20 | 0.026 | 58 | 0.00677 | 0.00935 |
| | 21 | 0.0245 | 73 | 0.00172 | 0.00494 |
| | 22 | 0.023 | 83.5 | 0.00027 | 0.00135 |
| | 23 | 0.022 | 91 | 0.00002 | 0.00023 |
| | 24 | 0.021 | 98 | 0 | 0.00002 |
| | 25 | 0.020 | 100 | 0 | 0 |
| Total number of larvae recruited per egg laid: | | | | | 0.02634 |
| (b) 1973, by experiment | 18 | 0.0372 | 0 | 0.372 | 0 |
| | 19 | 0.0304 | 38 | 0.0154 | 0.01155 |
| | 20 | 0.0249 | 58 | 0.00527 | 0.00893 |
| | 21 | 0.0203 | 73 | 0.00116 | 0.00385 |
| | 22 | 0.0166 | 83.5 | 0.00016 | 0.00097 |
| | 23 | 0.0136 | 91 | 0.00001 | 0.00015 |
| | 24 | 0.0111 | 98 | 0 | 0.00001 |
| | 25 | 0.0091 | 100 | 0 | 0 |
| Total number of larvae recruited per egg laid: | | | | | 0.02546 |

hatching on that day. The result of these calculations is set out in Table 3. The overall survival of eggs to hatching at N.C. Arboretum in 1972 is estimated to have been 0.0263.

The fate of eggs on marked fronds of *Hottonia* in the N.C. Arboretum pond during May 1973 is detailed in Table 4. The fraction of eggs which survived until hatching was estimated to be 0.0255, which is very similar to the estimate obtained in 1972. However, this may be coincidental, since the shape of the survival curve in 1973 was quite different, being a straight line under a semi-logarithmic regression. This approximates to the so-called Type III of Slobodkin (1961), the rate of survival remaining constant with age. Evidence is presented below that not only the overall survival but also the form of the survival curve in larval populations are subject to variation both between localities and

Table 4. Summary of data concerning the estimation of egg survival by experiment at N.C. Arboretum in 1973

| Weed frond | Number of eggs remaining | | | | | |
|-----------------------------|--------------------------|--------|-------|--------|--------|--------|
| | 1 May | 3 May | 4 May | 8 May | 15 May | 18 May |
| 1 | 4 | 3 | 2 | 0 | — | — |
| 2 | 11* | 9 | 4 | (lost) | — | — |
| 3 | 29 | 18 | 17 | 14 | 2 | (lost) |
| 4 | 5 | 5 | 5 | (lost) | — | — |
| 5 | 45 | 36 | 32 | 29 | 9 | 5 |
| 6 | 19 | 14 | 13 | 11 | 4 | 2 |
| 7 | 45 | 37 | 30 | 22 | 4* | 1 |
| 8 | 12 | 7* | 5 | 4 | 2 | (lost) |
| 9 | 7+2 | 4+1 | 3+1 | 1+1 | 0+0 | — |
| 10 | 13+11+3 | 11+8+2 | 11+7" | 7" | 2 | 1 |
| Total eggs at inspection | 227 | 157 | 135 | 93 | 23 | 9 |
| Total eggs after inspection | 227 | 155 | 123 | 89 | 19 | — |
| Overall survival | | 0.692 | 0.871 | 0.756 | 0.258 | 0.474 |
| Survival per 24 h | | 0.832 | 0.871 | 0.933 | 0.824 | 0.779 |

* One egg accidentally removed.

" One frond accidentally removed. Numbers 9 and 10 comprised bunches of two and three fronds respectively.

between years. In this animal, at least, any given function is adequate to describe only the survival of a given life-stage in a given population in a given year. Attempts to characterize the survival curve of a species, or even of a population, as being of a certain 'type' may be highly misleading. This point has been made before by Caughley (1966).

In view of the disasters which overtook the larvae in 1972 and in 1973 (see below), the estimates of egg survival obtained in these years may be lower than is usual in smooth newt populations.

In 1973, 277 eggs were cultured in the laboratory in glass petri dishes in 4 cm of aerated water. All the eggs were fertile, and commenced development; 241 completed development to hatching. The physiological survival of eggs is thus at least $241/277 = 0.87$. Most deaths in the laboratory were caused by developmental failure before gastrulation; most deaths in the field are presumably caused by predation. Larvae of the caddis *Limnophilus vittatus* were extremely abundant in the *Hottonia* bed at N.C. Arboretum, and on many occasions they were seen eating newt eggs; on several such occasions it was possible to verify that the egg was alive before being eaten. In other ponds with large newt populations this caddis is rare or absent, and presumably the eggs have other predators. Large snails (e.g. *Planorbis corneus* (Linn.)) and frog tadpoles will eat newt

eggs in the laboratory, and birds such as moorhen *Gallinula chloropus* (L.) and mallard (*Anas platyrhynchos* L.) which eat pondweed presumably also eat the eggs attached to it. Newts will eat their own eggs in the laboratory.

OVIPOSITION

The time-course of oviposition

The time-course of oviposition in 1972 can be discovered from the core-sample data (Table 2). The date on which eggs of any given developmental stage, collected on any given date, were laid can be estimated from the data in Table 1, with the assumption that the number of degree-days needed to complete development is constant over the range of temperature observed in the pond. The number of eggs laid on that date giving

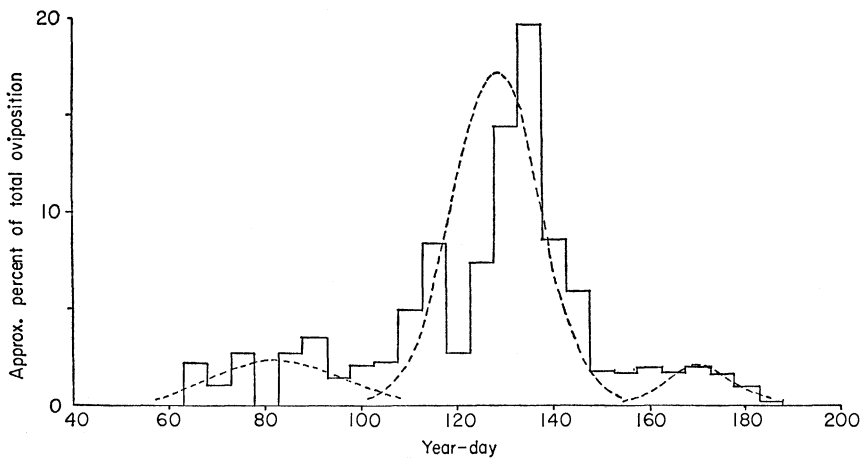


FIG. 2. The time-course of oviposition at N.C. Arboretum in 1972. Symmetrical normal curves have been fitted to the data by the method of Harding (1949).

rise to the eggs in the sample is then estimated as $N(x)/l(x)$, where $N(x)$ is the number of eggs of a given stage in the sample and $l(x)$ is the rate of survival to the midpoint of that stage. The results for all samples and all stages are summed to give an estimate of the total number of eggs laid on different dates. These are set out, at 10-day intervals, in Fig. 2. When the data on Fig. 2 are plotted on probability paper (see Harding 1949), it can be interpreted either as a single normal curve with extensive 'tails', or, more credibly, as a trimodal curve with one major peak and two minor peaks. There is a certain amount of indirect evidence to support the latter interpretation. In particular, data on the length-structure of larval populations (presented below) indicates that in some ponds and in some years two large distinct larval cohorts can be recognized. Further, it will be shown that the timing of the sampling programme and the events in the pond in 1972 would both tend to minimize the importance of the first and third modes. Fig. 2 will, therefore, be interpreted as illustrating the presence of three separate periods of oviposition, which will be called the early, main and late periods.

The early period contains about 15% of the estimated total oviposition, and is centred about day 83 (23 March). Because core-sampling did not start until 7 April, the importance of this early breeding activity is almost certainly underestimated, and its peak may well be reached about the middle of March, or even earlier.

The main period of oviposition, which seems to be the only period described by previous authors (e.g. Smith 1951), has its peak about day 128 (7 May), and extends (95% limits of fitted curve) from day 108 (17 April) to day 151 (30 May); its duration is thus about 43 days. This may be compared with an independent estimate of the duration of an oviposition period, presented below.

The late period included only about 7.5% of the total oviposition in 1972. The evidence for the identify of the presumptive late oviposition period with the late larval cohort observed at N.C. Arboretum in 1971 and at N.C. Venison South in 1972 (see below) is that when the growth-curves for these two larval cohorts are extrapolated back to the size at hatching, they indicate that the hatching of the late larval cohort began on about day 176 (24 June) on both occasions. The pond temperature at the time was about 17° C and the development period of the egg can be taken to be 20 days. The eggs from which these late cohort larvae hatched began to be laid, then, about day $(176 - 20) = 156$ (4 June). The data on Fig. 2 indicate that the relevant 95% limit of the late period oviposition curve occurs at day 154 (2 June). The late oviposition period did not give rise to a large late larval cohort at N.C. Arboretum in 1972. During June the level of the pond fell, until by the end of the month only 2–3 cm of water remained. Under these circumstances it is scarcely surprising that few late period eggs were laid; the observed late period oviposition of 1972 is thus only the rudiment of what could be potentially a much more important component of total oviposition.

At the peak of the early oviposition period, the spring breeding migration has scarcely begun; moreover, the female newts require some time to mature their ovarian oocytes once they reach the water (Bell 1974a). The early period must, therefore, involve principally, or only, those animals which migrated to the pond in the previous autumn; the significance of this behaviour will be discussed in a later paper. The late oviposition period, on the other hand, seems to involve all surviving females. The evidence for this will be presented in a later publication, but may be summarized briefly as follows. First, the distribution of the length-weight ratio (which is a measure of reproductive condition in females) remains unimodal throughout the breeding season; secondly, there is no indication from pitfall data of movement to or from the pond at the end of the main oviposition period; and thirdly, when three females which laid eggs in the laboratory during April and early May 1973 were remated and fed to excess, two of them later laid another complement of eggs.

Adaptive aspects of the timing of oviposition

Dead eggs were often found in the core-samples; they were usually mere wisps of rotten vitellus, with the fragments of the jelly envelope still holding the *Hottonia* leaves together. Dead eggs having this appearance were found on the fronds of *Hottonia* used in the direct estimation of survival in 1973, confirming that these are not merely eggs which have hatched. When the percentage of dead eggs found in the sample taken on a particular date is plotted against the percentage of total oviposition estimated to have taken place on that date, there is a highly significant negative regression (Fig. 3(a)). That is, the average rate of mortality becomes less towards the middle of the main oviposition period. Changes in mortality will automatically accompany changes in the age-structure of the egg population, since the instantaneous rate of mortality is greatest for the youngest eggs (see Fig. 1(a)); but, if this were the only factor acting, one would expect the average rate of mortality to be *greatest* near the middle of the main oviposition period, since the birth-rate is greatest at this time. To the extent that the timing of ovi-

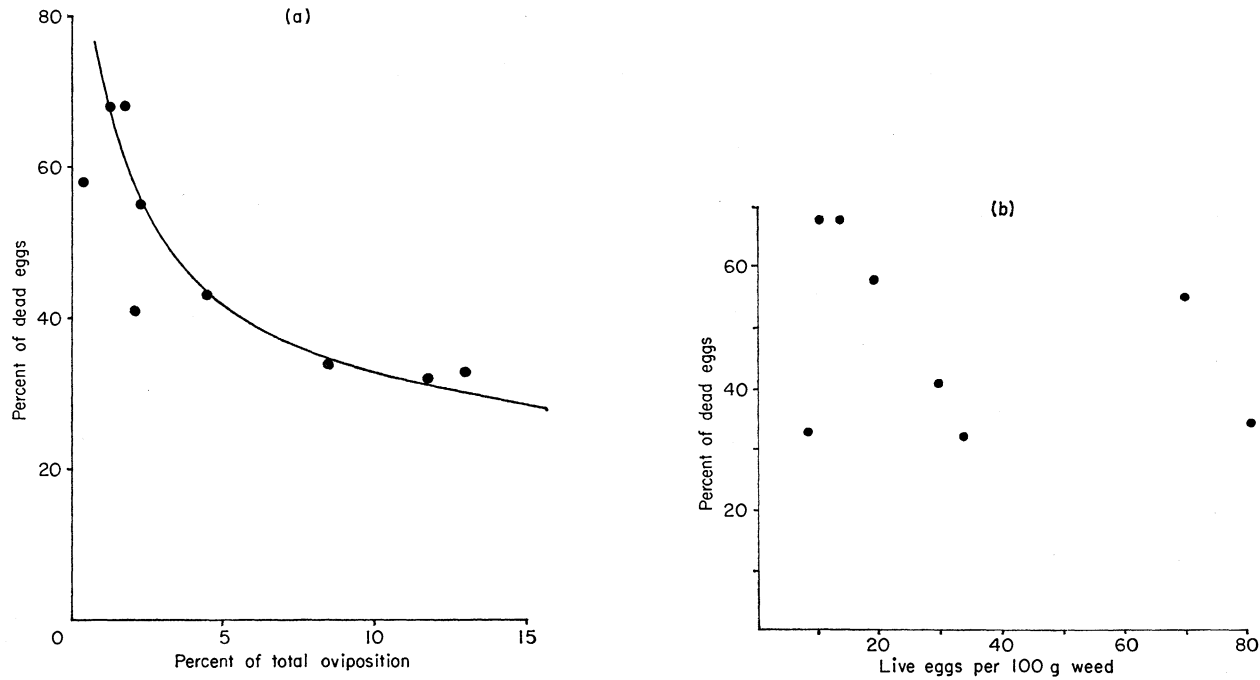


FIG. 3. The change in the proportion of dead eggs found in samples taken from the bed of *Hottonia* at N.C. Arboretum during the main oviposition period of 1972. (a) The decline in egg mortality towards the middle of the main oviposition period. The equation of the regression is $\log Y = -0.28 \log X + 1.80$. The 99% limits of the regression coefficient are -0.03 , -0.53 . (b) The relationship between egg mortality and egg density. The regression is not significantly different from zero at the 5% level.

position is inherited, there will be selection for a mean date of oviposition (within each oviposition period) at which the mortality of the eggs is least. Because mortality is observed to be least around the modal date of the main oviposition period, we suggest that such selection has taken place.

It might also be argued that the decrease in mortality towards the middle of the oviposition period is a function, not of any inherent quality of that time of year, but simply of the number of eggs in the pond at this time. If, for example, predators become satiated at high egg densities, there might be selection for females which laid most of their eggs at the same time as most other females; but the time of the year at which they do this might, in itself, be selectively irrelevant. This hypothesis can be tested by plotting the percentage of dead eggs in a given sample against the observed egg density on that date. Although the percentage of total oviposition occurring on a given date and the egg density on that date are to some extent autocorrelated, this second regression (Fig. 3(b)) is non-significant. We conclude that unidentified events in the pond conspire to make conditions especially suitable for egg survival in the first half of May.

If this argument is accepted, it might be suggested that a further advantage would be gained by females which increased the rate at which they laid eggs towards the middle of the oviposition period. To test this idea, the rate of oviposition was measured for two populations in two different ways. During the latter part of the main oviposition period at N.C. Arboretum in 1972, female newts were taken into the laboratory and kept for a short time in small glass bowls. During this time they laid large numbers of eggs, from which the mean rate of oviposition per female could be calculated for different dates. Another method was used for the Stadhampton population. Females collected early in the year were killed and dissected, and a rate of oviposition calculated as the rate of disappearance of large yolked oocytes from the ovaries of females of known length (see Bell 1974a). These estimates of the rate of oviposition lead incidentally to a second estimate of the length of an oviposition period. If the length-specific fecundities and the length-structure of the females of a population are known, then the mean fecundity of these females can easily be calculated; these data are available for N.C. Arboretum and for Stadhampton, and will be presented in a later paper. The predicted length of an oviposition period is then simply the mean fecundity divided by the mean rate of oviposition. The values obtained in this way are 38.6 days for N.C. Arboretum and 33.6 days for Stadhampton, which compare reasonably well with the 43 days estimated from the data of Fig. 2. However, the rate of oviposition is not constant; it is found to decline from the middle to the end of the oviposition period. This is shown in Fig. 4 for the mean rate of oviposition at N.C. Arboretum and for three length-classes taken separately at Stadhampton. If it is true that the timing of oviposition has undergone selection, then an increase in the rate of oviposition near the peak of the oviposition period will, clearly, reinforce the advantage gained by distributing oviposition around this peak.

In conclusion, we suggest that both the mean date of oviposition and the change in the rate of laying eggs during the oviposition period, are characters which have undergone, and which are presumably still undergoing, natural selection and that, in this sense, they can be said to be adaptive characters.

THE LARVA

The larvae hatch by violent flexion of the body, perhaps aided by enzymic digestion of the jelly envelope. They are fragile animals about 7 mm long, and cling to the leaves of

water-plants by means of an oral sucker. If disturbed they may swim downwards with an irregular 'flickering' motion, although they will often remain quite motionless. They are coloured with a disruptive pattern of longitudinal black and yellow stripes resembling the coloration of the early instars of *Aeshna* and *Anax* (Odonata) larvae, where it is thought to lessen predation by visual predators (Corbet 1957). They do not feed, presumably subsisting on the remains of their yolk; similar behaviour is shown by the external gill stage tadpoles of the common frog *Rana temporaria* Linn. (Savage 1961). At a length of about 9.5 mm a number of important changes occur. Teeth are already present on the dentary, coronoid, premaxilla, palatine and vomer. The stripes fade, and are replaced by the cryptic 'agouti' colouration which persists for the rest of larval life. The balancer disappears, the external gills greatly increase in size, and the caudal and

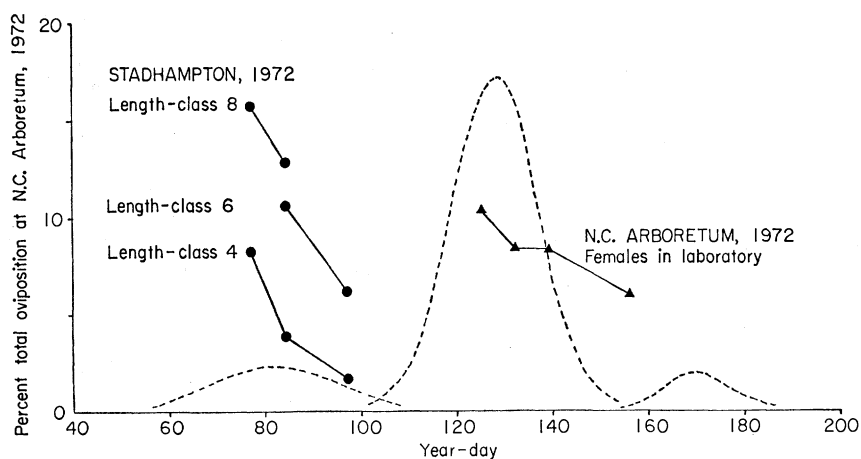


FIG. 4. The relationship between the rate of oviposition and the time-course of oviposition. The solid lines represent the mean number of eggs laid per female per day (see text for details). The broken lines represent the time-course of oviposition in the field (from Fig. 2).

dorsal crests develop. The forelimbs push through, and the digits differentiate. These changes mark the beginning of fully autonomous larval life. The larva spends most of its time immobile, preying on passing cladocerans, although it may move short distances through the weed. At a total length of about 14–18 mm the hind limbs appear, and the larvae are more often seen moving through the weed or searching actively for prey on the bottom of the pond. For the first time, animals such as chironomid larvae and small gammarids, which are usually captured by stalking, appear in the diet. A little later, teeth appear on the maxilla. At a length of about 30–34 mm, premetamorphic changes occur. The external gills and the caudal and dorsal crests regress. The smooth larval skin develops a matt texture. The cloaca, until now a slit in the ventral caudal crest, becomes a relatively bulky rounded eminence. The coronoid teeth regress from their bases upwards, leaving a litter of tooth points in the flesh inside the lower jaw of newly metamorphosed animals; at the same time the palatine and prevomer fuse to form a single vomerine element. It seems likely that these changes in dentition are adapted to the change in diet associated with the adoption of a terrestrial existence. Animals which have recently metamorphosed can be recognized by the faint remnants of the external gills ('gill scars').

THE COURSE OF LARVAL LIFE

Distinct larval cohorts are generated by the distinct periods of oviposition described above. The early oviposition period gives rise to an early larval cohort, the main period to a main cohort and the late period to a late cohort. The early cohort, which is apparently the least important, will be considered last.

The simplest larval history is one in which a single main cohort hatches, passes through larval life, and metamorphoses in the same year. This happened at the Stadhampton pond in 1972. Most of the adults were removed from the pond for dissection during March and April, but a single larval cohort was produced. The level of the pond dropped sharply during the drought of July, preventing a late oviposition attempt by the remaining adults, but larval growth continued to be good until metamorphosis in the middle of the month. The few large larvae which could be caught after this date metamorphosed or died before the pond finally dried up in early August. These events are illustrated by means of length frequency diagrams in Fig. 5(a). A similar situation was observed at the Moor Monkton pond in 1974 (Fig. 5(b)), where newly-hatched larvae were first seen in early May. By the middle of May the hatch was well under way, and growth continued to be good until the end of June, despite the dropping water level. In early July and water almost entirely disappeared, and no more samples could be taken. The samples from this locality were so large that if any late cohort had been produced it would have been detected in the later June samples.

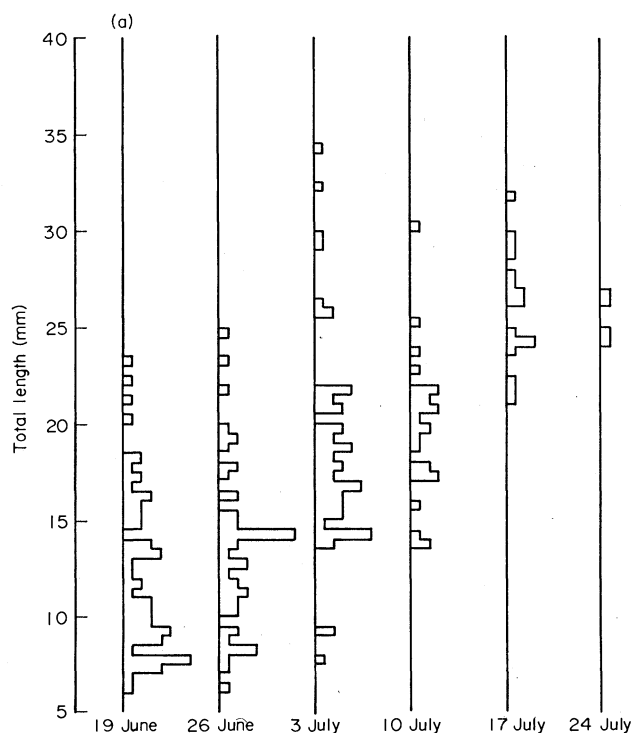


FIG. 5. Length-distributions of larvae in four populations. (a) Stadhampton, 1972 ($N = 220$); (b) Moor Monkton, 1974 ($N = 1665$); (c) N.C. Venison South, 1972 ($N = 339$). □, main cohort; ■, late cohort. (d) N.C. Arboretum, 1971-2 ($N = 837$). ▨, early cohort; ■, main cohort; □, late cohort; □, overwintering group of late cohort animals.

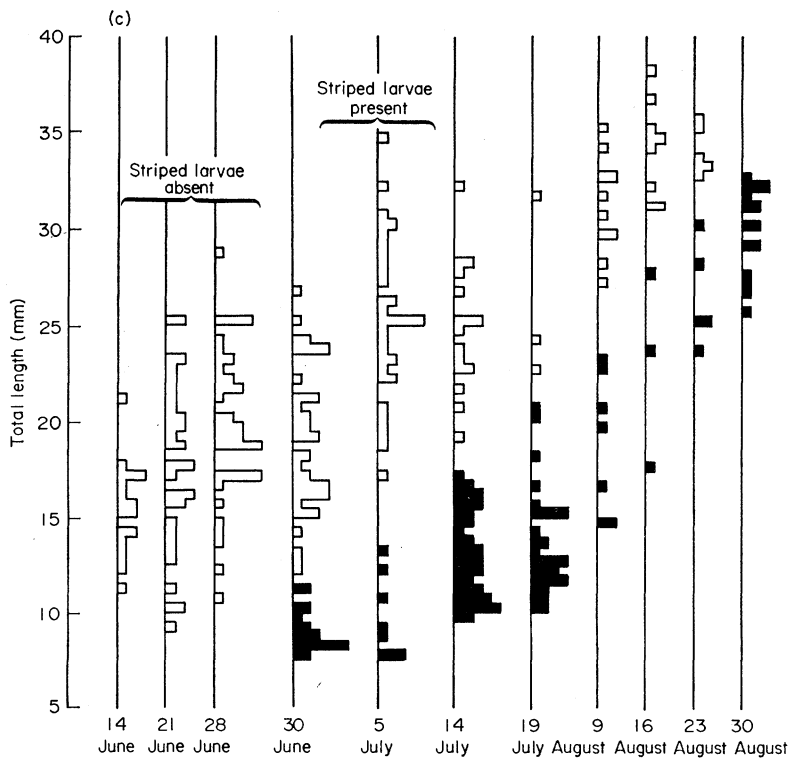
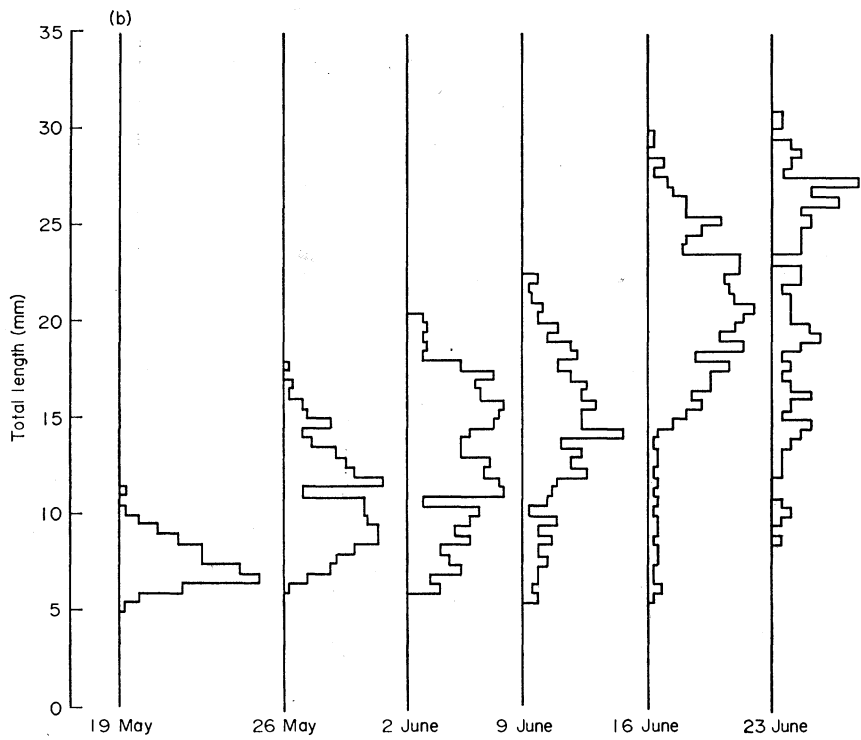


FIG. 5 cont.

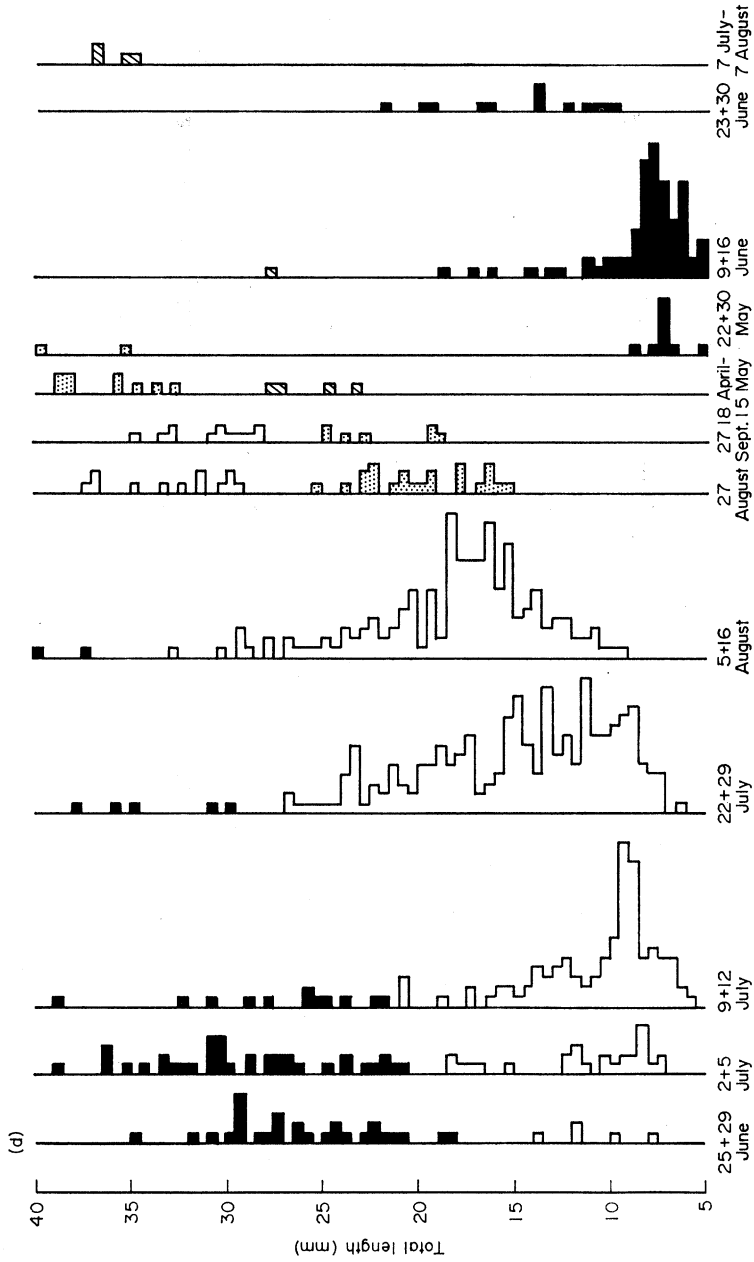


FIG. 5 cont.

At N.C. Venison South in 1972, the length-frequency diagram reveals the presence of two large larval cohorts (Fig. 5(c)). The growth of the main cohort is already well advanced by the middle of June, when sampling began, and towards the end of June the late cohort enters the population. Although animals from the two cohorts overlap considerably in length they can be separated by plotting length frequencies on probability paper, which reveals the presence of two separate distributions in all samples taken between 30 June and 23 August. The late cohort does not always appear, however, even in large populations. The reasons for this are sometimes obvious. In 1971 the N.C. Arboretum pond held at least 40 cm of water until the middle of September, and the late cohort was large and successful. In 1972, however, a prolonged drought caused the pond to dry up completely by the end of July, jeopardizing the main cohort larvae and entirely preventing the appearance of a late cohort. The drought of 1972 did not affect the N.C. Venison South pond so disastrously, and the late cohort was reasonably successful. But in 1971, despite a higher water level and apparently suitable conditions, only the main cohort appeared. The reason for this is unknown.

It is possible to obtain a crude estimate of the relative strengths of the two cohorts. A sample of 59 larvae was taken from N.C. Venison South on 14 July 1972, when recruitment of the late cohort had just ceased but before metamorphosis of the main cohort had begun. Knowing the number of animals in each cohort, and their rate of survival (see below), it is possible to estimate the relative number of animals in each cohort as though both were censused at an age of about ten days. The result is that the main cohort is estimated to include about 73% of the total number of larvae. This observation might be explained in two ways: more eggs may be laid during the main oviposition period, or the survival of main cohort larvae might be better. The only relevant evidence concerns the estimation of female fecundity (Bell 1974a and unpublished). Yolked ovarian oocytes can be divided into two groups: large, heavily yolked oocytes which are thought to be just about ovulated, and smaller, less heavily yolked oocytes which are thought to be matured in time for the next oviposition period. If the number of eggs laid in the two major oviposition periods is equal, then the ratio of these two categories of oocytes should be 50%; the value obtained from dissection of 90 Stadhampton females was 52%. We have tentatively concluded, therefore, that the main oviposition period, and thus the main larval cohort, may contribute more animals to later age-classes than does the late period; that this difference may be due to differences in larval survival; and that in some ponds and in some years no late cohort is produced.

This picture of larval life is further exemplified and extended by the fate of larvae in the N.C. Arboretum pond during 1971 and 1972, which is illustrated in Fig. 5(d). Towards the end of June 1971, when sampling began, the main cohort was in the middle of its development. These animals gradually disappeared from the pond during July. About the middle of July a large late cohort appeared, and grew well in favourable conditions during July and August. Towards the end of August, the late cohort larvae separated into two major components, as the result of an increase in the growth-rate of the larger larvae, which were about to metamorphose. There was then no observable growth between late August and late September. However, the length frequency distribution of recently metamorphosed animals which were caught on the banks of the pond in pitfall traps at this time was very similar to that of the group of larger larvae, and it seems certain that it was these larger larvae that metamorphosed during September and early October. The smaller larvae did not metamorphose in 1971, but passed the winter in the pond; they were subsequently found in every sample taken between 18

April and 9 June 1972. The overwintering of smooth newt larvae in Britain has previously been reported by Smith (1951) and by Bell (1970). Between early March and late June 1972, recently metamorphosed animals were trapped in small numbers around the pond, and these were taken to be the survivors of the overwintered populations.

In the first half of May 1972, two larvae were captured at N.C. Arboretum which seem to be too small to be overwintering larvae, and may have been survivors of a small early cohort. The large larvae found in July and August may also be early cohort animals, since their size seems to exclude any other interpretation. However, the early oviposition period seems only rarely to produce a large larval cohort. Hatching of the 1972 main cohort occurred during the end of May and the first week of June. Shortly afterwards the water-level began to drop rapidly, and by the middle of July half the bed of the pond had been exposed, and only the few presumptive early cohort larvae could be found.

Neoteny, the retention of the larval phenotype into adult life, is known to occur occasionally in British populations of the smooth newt (Smith 1951; A. S. Cooke, personal communication). A larva 56.1 mm in total length which was captured at N.C. Venison South on 19 July 1972 seems too large to be an overwintered second-year animal, and may have been a potential neotenic in its third year; unfortunately, the specimen was lost without having been dissected. Of approximately 4000 breeding adults examined from the Nuneham Courtenay area, none was neotenic; one neotenic animal was found in a collection of about 1500 adults from ponds near York.

Having completed their development, the larvae emerge from the pond and disperse on land. Main cohort larvae metamorphose about the middle of July; late cohort larvae either metamorphose about the middle of September or overwinter and emerge in the spring and early summer of the following year.

LARVAL GROWTH

Growth in linear measurements

Three linear measurements were recorded: total length (the distance between the tip of the snout and the tip of the tail), standard length (the distance from the tip of the snout to the hinder margin of the cloaca) and head width. These different measurements were found to lead to similar conclusions, and the discussion below is restricted to total length. Two methods of measurement were used. In 1971, larvae from N.C. Arboretum were sucked up into glass tubes just wide enough to contain them, and then measured with vernier callipers. In 1972, all larvae were first anaesthetized in a 1:15 000 solution of the anaesthetic MS222, and then measured under water by means of a micrometer eye piece fitted to a binocular dissecting microscope. When anaesthetized the larvae are quite limp, and can be measured to an accuracy of 0.1 mm.

In most cases, growth was estimated as the change in mean total length of samples of larvae between sampling dates. This apparent growth-rate may not coincide with the real individual growth-rate: cases in which the apparent growth-rate is influenced by mortality which does not act randomly with respect to size are discussed below. With this in mind, Fig. 6 shows the apparent growth in total length of larvae in the three natural populations and in the laboratory. In all cases the growth-curves are rectilinear. The growth of laboratory animals both in total length and in head width appears superficially to follow a negatively-accelerated curve (Fig. 6(f)) but this effect is due entirely to the last two sampling occasions, by which time a number of larvae had already metamorphosed. Since these were the fastest-growing animals in the population, their omission

from the samples biases the growth-curve downward, and when they are excluded from the regression it is found to be rectilinear. The differences between the rates of growth of the seven populations of Fig. 6 is shown in Table 5. There are two important effects. First, there is no significant difference between the growth of populations in the laboratory (two replicates), at N.C. Arboretum (1971 late cohort), and at N.C. Venison South (1972 main and late cohorts). Secondly, apparent growth at N.C. Arboretum (1972 main cohort) and at Stadhampton (1972 main cohort) was exceptionally rapid. The survival curves for these two populations (see below) show that they suffered exceptionally heavy mortality, and that small larvae survived even less well than large larvae. The differential removal of small larvae will bias the growth-curve upwards; and the greater the differential, the greater will be the difference between the apparent rate of growth estimated from population data and the real rate of growth of individuals. This interpretation is supported by the fact that the rank of apparent growth-rate coincides

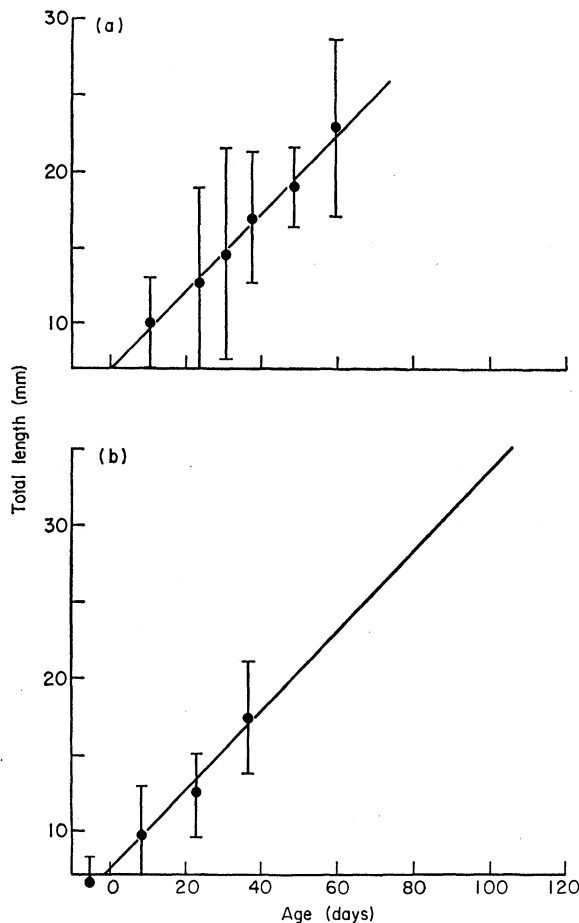


FIG. 6. The apparent rate of growth in total length of larvae in three natural populations and in the laboratory. (a) N.C. Arboretum, 1971 late cohort: time to metamorphosis $T_m = 109$ days. (b) N.C. Arboretum, 1972 main cohort; $T_m = 53.9$ days. (c) N.C. Venison South, 1972 main cohort: $T_m = 103$ days. (d) N.C. Venison South, 1972 late cohort: $T_m = 87.4$ days. (e) Stadhampton, 1972: $T_m = 55.7$ days. (f) Laboratory (two replicates): $T_m = 107$ days.

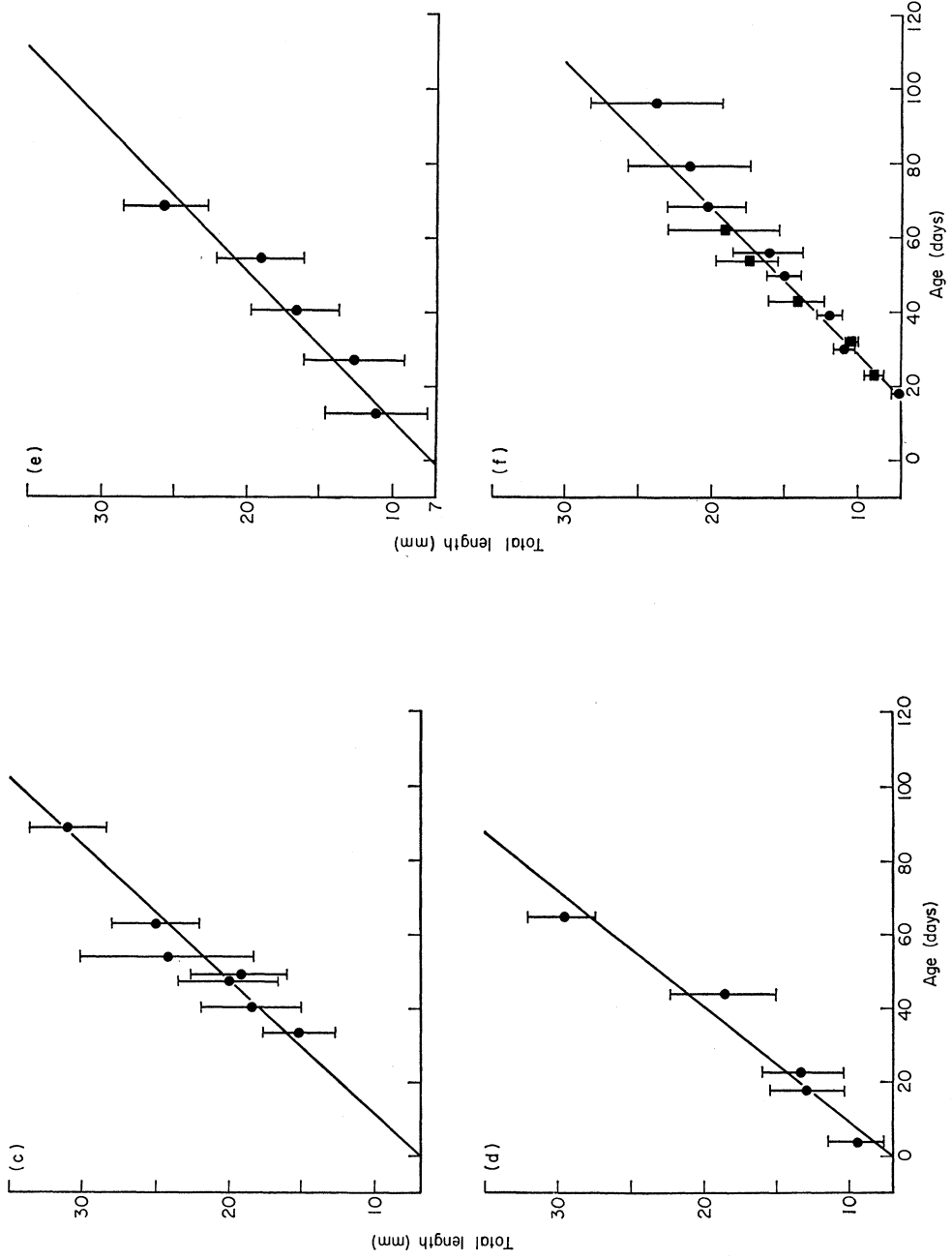


Fig. 6 cont.

Table 5. Significance of differences between the linear regression coefficients for apparent growth in total length in seven larval populations

| Population | Population | | | | | | |
|------------------------------------------|------------|-------|-------|-------|-------|-------|-------|
| | 1 | 2 | 3 | 4 | 5 | 6 | 7 |
| (1) Laboratory, replicate 1 | - | >0.70 | >0.70 | <0.05 | >0.50 | >0.10 | <0.01 |
| (2) Laboratory, replicate 2 | | - | >0.50 | <0.05 | >0.10 | >0.10 | <0.01 |
| (3) N.C. Arboretum, 1971 late cohort | | | - | <0.01 | >0.30 | <0.10 | <0.01 |
| (4) N.C. Arboretum, 1972 main cohort | | | | - | <0.05 | <0.05 | ~0.10 |
| (5) N.C. Venison South, 1972 main cohort | | | | | - | >0.20 | <0.01 |
| (6) N.C. Venison South, 1972 late cohort | | | | | | - | <0.05 |
| (7) Stadhampton, 1972 | | | | | | | - |

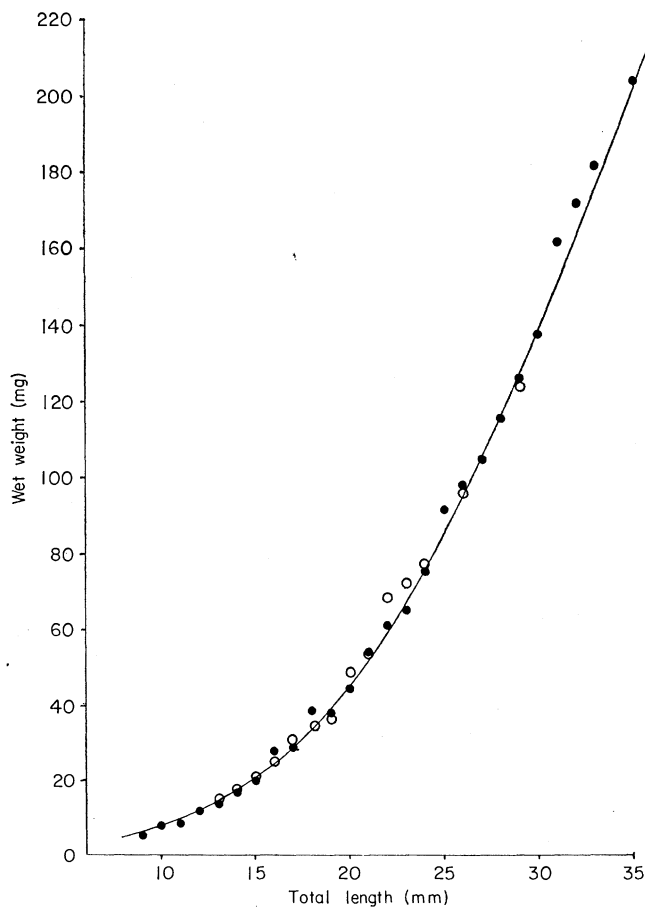


FIG. 7. The relationship of total length to wet weight in two populations of larvae. ●, N.C. Venison South, 1972, $W = 0.69 L^{2.69}$; ○, Stadhampton, 1972, $W = 0.91 L^{2.79}$.

with the rank of rate of survival in the series: laboratory; N.C. Arboretum (1971 late cohort); N.C. Venison South (1972 main and late cohorts); Stadhampton (1972 main cohort); N.C. Arboretum (1972 main cohort).

The mean total length of seventeen larvae from N.C. Venison South which were thought to be about to metamorphose was 35.0 mm. After metamorphosis the animals are slightly shorter. The time between hatching and metamorphosis (T_m) was therefore estimated for each population from the regression equation describing the apparent growth-rate. It is on average 90–100 days. Because this estimate does not take into account the spurt of growth immediately before metamorphosis observed in 1971 at N.C. Arboretum, it may be a slight overestimate.

Biomass and condition

As soon as possible after capture, larvae from N.C. Venison South and Stadhampton were weighed live on a torsion balance to the nearest milligramme. Fig. 7 shows the relationship of weight to length, which is of the usual logarithmic form. Visual inspection suggests that there is no significant difference between the two localities. From these data the curve of $l(x)\bar{w}(x)$ against total length can be drawn, where $l(x)$ is the rate of survival and $\bar{w}(x)$ the geometric mean weight at length x . Since $l(x)$ is given the value of unity at a length of 10 mm, this curve represents the weight of larvae produced for each larva which survives to 10 mm in length; smaller larvae are thought not to feed (see above). The $l(x)$ curve is discussed below; its form is complex, and hence the $l(x)\bar{w}(x)$ curve is also complex, tending to rise whenever the rate of survival is high, and vice versa. This curve could be used to estimate the biomass of larvae in a pond if only a single cohort hatching synchronously and growing at a constant rate were present. Because more than one cohort may be present, and because not all animals of the same cohort are of the same size, the $l(x)\bar{w}(x)$ curve must be weighted by the frequency of animals in different size-classes. Then:

$$\text{biomass} = \sum_x 100 l(x)\bar{w}(x) \cdot c(x)$$

where $c(x)$ is the proportion of the population estimated by sampling to be in length-class X , and the units of biomass are mg per 100 larvae reaching 10 mm in length. This relative estimate can be converted into an estimate of the total biomass by multiplying by $N/100$, where N is the total number of 10 mm larvae. Fig. 8 shows the estimated larval biomass at N.C. Venison South during the summer of 1972. It can be seen that the overwhelming effect of large larvae causes the curve to peak at the beginning of July (main cohort survivors) and towards the end of August (late cohort survivors).

All things being equal, the impact of the larval population on its food resources might be expected to be greatest when the larval biomass is the greatest. We have further supposed that the availability of food will be reflected by the condition of the larvae. 'Condition' is defined as:

$$k = w(x)/\bar{w}(x)$$

where $w(x)$ is the weight of any particular larva in length-class x . Since the summation for $\bar{w}(x)$ is taken over all samples, the mean condition of larvae captured on a given date can be estimated by the average of individual k s on that date. These data can then be used to test the hypothesis that there is a negative correlation between mean condition and biomass, which would imply the presence of food limitation. Fig. 9 shows that there

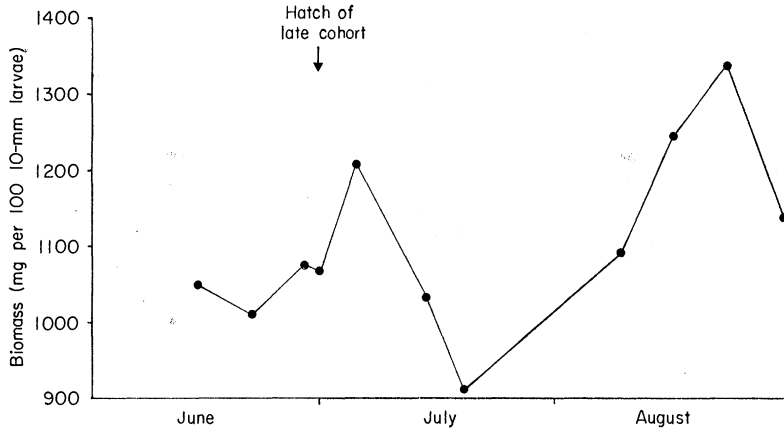


FIG. 8. Larval biomass at N.C. Venison South in the summer of 1972.

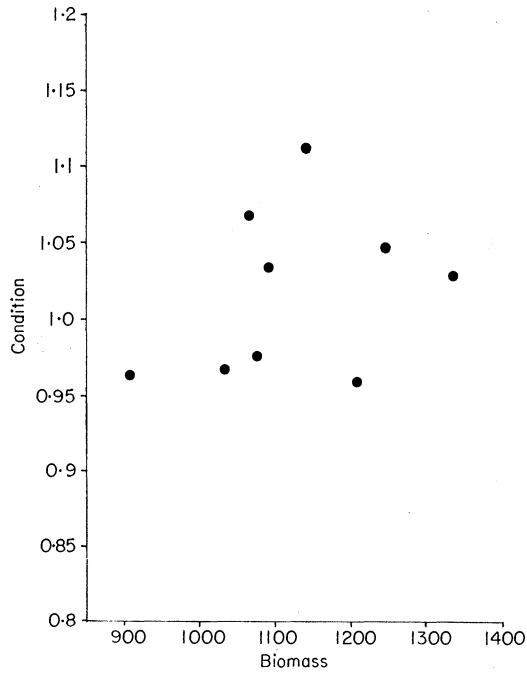


FIG. 9. The relationship between larval condition and larval biomass at N.C. Arboretum in 1972. The regression coefficient is not significantly different from zero at the 5% level.

is no significant regression of condition on biomass for the N.C. Venison South population in 1972. Two rather different tests were also applied to the data. The first was to eliminate the possibility that certain length-classes were more sensitive to food shortage than others by dividing the samples into 5-mm classes and repeating the original test for each of these. The second was partially to eliminate the possible effect of the different length-class composition of the total biomass on different dates by regressing change in condition ($k(t)/k(t-1)$) on change in biomass ($B(t)/B(t-1)$). Neither test gave a significant result. The analysis was repeated on the smaller amount of data available for Stadhampton, with the same negative result. The failure of this analysis provides evidence that larval populations are not normally limited by their food supply. This result was to some extent anticipated by the observation that larvae collected in the field always had their guts packed tight with food; animals which were starved in the laboratory developed visible bubbles of gas in their guts, but this was never observed in wild animals. The similarity of the larval growth-curves for laboratory animals with an abundant food supply and field collections of larvae (see above) also supports the hypothesis that the larvae are not normally limited by their food supply.

SURVIVAL

Methods of estimation

The most straightforward way of estimating the survival of larval animals is to count the numbers present in successive periods of time. The rate of decline in numbers can then be directly related to the rate of survival. This method has serious drawbacks, however: real mortality is liable to be obscured both by input (hatching) and by other forms of output (metamorphosis); because of the high cost of sampling, only a few estimates of population size are usually available and the rate of mortality must be assumed to be constant. In the present study a method based on the analysis of length frequency distributions was employed, and seems to reduce these difficulties. In essence, it consists of dividing the samples into a number of length-classes, and then counting the number of larvae in each length-class, summing for all sample dates. The total number of larvae in each length-class is then expressed as a fraction of the number in the most abundant class; the curve that such estimates describe is then supposed to represent the survival curve. This method is formally identical to that used to estimate the survival of eggs, and is subject to the same conditions (see above). To test the validity of this method, two simulation experiments were performed, using an artificial population similar in many respects to a population of larval newts; the first experiment used a constant value of survival, whilst in the second the rate of survival changed suddenly at some point during larval life. A detailed account of these experiments is given by Bell (1974a). The conclusions that were drawn from them are twofold. When survival per unit length is constant, the length-frequency and population-size methods (as might be expected) give identical results. However, when survival per unit length is *not* constant, the population-size method fails to describe accurately either the mean rate of survival or the shape of the survival curve, whilst the length-frequency method gives a completely accurate estimate of both. Subject to the sampling conditions laid down above in the discussion of egg survival, therefore, the length-frequency method gives a better estimate of the rate of survival than could be obtained by making either relative or absolute estimates of population size. In the case of larval populations the most onerous of these conditions is probably that the population should be sampled with equal efficiency on each occasion.

Larvae were captured with a fine-mesh pond-net, but the complexity of the pond vegetation, the change in the size of the pond from week to week and the different behaviour of larvae of different sizes made it impossible to standardize this procedure. Attempts to develop a completely consistent sampling method (e.g. core-sampling and trapping) were not successful.

A third estimate of survival was developed; this again relies on the analysis of the length-frequency distribution, but the assumptions that it makes about sampling are quite different from those required by the method discussed above, and do not include the assumption that sampling is of equal efficiency on each occasion. The effect on the apparent growth-rate of the differential mortality of smaller larvae has been mentioned above; conversely, the differential mortality of larger larvae will have the opposite effect on the apparent rate of growth. Fishery biologists have often noticed that 'back-calculations of length frequently exhibit a tendency for computed lengths at a given age to be smaller, the older the fish from which they are computed' (Ricker 1968). The effect of this will be for population data to underestimate real growth-rates. Several possible causes are mentioned by Ricker, all of which depend on some special, although perhaps common, set of circumstances. If, however, length is absolutely correlated with age (that is, if the correlation coefficient r between length and age is unity), then 'Rosa Lee's phenomenon', as it has come to be called, will occur in any large cohort exposed to mortality. This is because animals which have been recruited to the population relatively early in a particular season will at any subsequent time have suffered more mortality than animals which were recruited later. Consider a cohort of animals being recruited from some previous stage in their life-history, for example a cohort of newt larvae hatching from eggs. Recruitment is not instantaneous, but proceeds over a finite period of time, during which recruited animals are growing and dying. Imagine that the time-course of recruitment is normally distributed, and that growth-rate is constant, so that with zero mortality when recruitment is completed the larvae will be normally distributed with respect to some character, say length, which is absolutely correlated with age. Let us divide the larvae arbitrarily into a number of length-classes separated by equal length increments, x . The time at which the first larvae are recruited is (t), and the time corresponding to an increment of x later is ($t+a$). $P(i)$ is the proportion of the recruited population in the i th length-class, and s is the rate of survival between i and $(i+1)$. To obtain the proportion of the i th class at some time ($t+a$) when recruitment has just ceased, the frequency of this class (amongst recruits and potential recruits) at the time of its recruitment must be multiplied by the rate of survival s , raised to the power of the number of time intervals between its recruitment and the recruitment of the first larvae, which is, of course, i . If the rate of survival is not constant, this can easily be taken into account. The sum of $P(i)s$ at time ($t+a$) is then equated with their sum at time (t), so that:

$$P(i, t+a) = \frac{P(i,t) \cdot s^i}{\sum P(i,t) \cdot s^i}$$

This can be used to predict the mean length of the cohort after hatching, given the rate of survival, but it can also be treated as an implicit equation for s if both $P(i, t+a)$ and $P(i,t)$ are known. In practice, one guesses a series of values of $s(i)$ until a series is found that will transform an observed length-frequency distribution into a symmetrical normal curve with the same limits. Newt populations are not often suitable subjects for this analysis, since the length-frequency distribution usually has a great deal of variance,

probably due to differences in individual growth-rates, and may even be polymodal (see Bell 1974a). However, it was possible to apply this method to data from Stadhampton to confirm the results obtained from the more straightforward length-frequency analysis described previously.

The form of the survival curve

Fig. 10 shows the numbers of larvae caught at N.C. Arboretum between June and October 1971. The number of late cohort larvae captured rises during early July as hatching proceeds, and then falls because of mortality. From the middle of September onwards, both mortality and metamorphosis will contribute to the loss of larvae from the population. These data suggest two things. First, the fact that the curve is not markedly

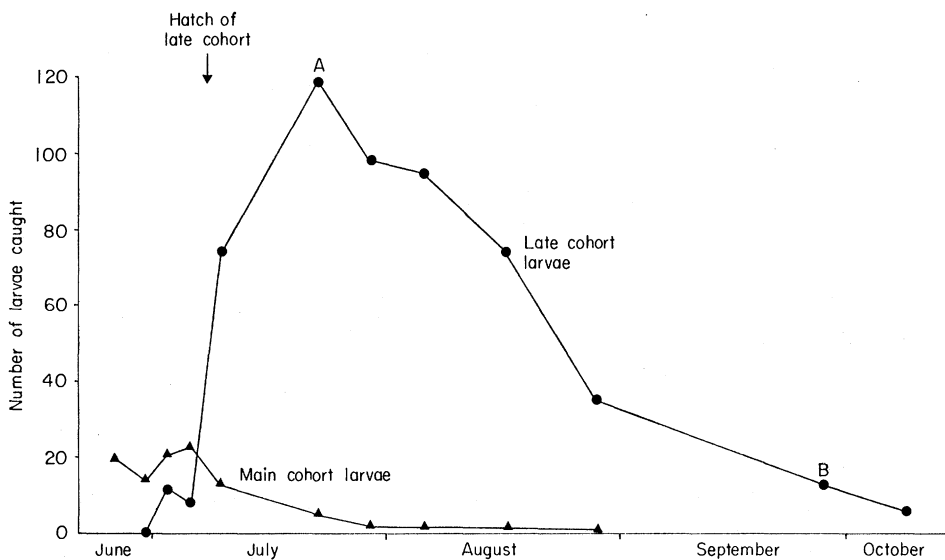


FIG. 10. Numbers of larvae caught at N.C. Arboretum in 1971. The points A and B are referred to in the text. ▲, main cohort; ●, late cohort.

concave in early August suggests that a change in the rate of survival may occur at about the modal length of the animals in these samples, which is 14–18 mm. Secondly, the ratio of maximum to minimum numbers (B/A) suggests that overall survival to metamorphosis may be of the order of 0.10. These tentative conclusions may be verified and extended by length-frequency analysis.

Survival curves for the three Oxford populations obtained by length-frequency analysis are shown in Fig. 11. At Moor Monkton, survival was initially so good that the survival curve estimated by the length-frequency method showed almost no tendency to decline. However, the pond dried up, and the larval population became extinct before metamorphosis. At N.C. Arboretum the survival of the 1971 late cohort larvae was good until a length of about 15 mm, after which it declined sharply. This inflection coincides with the transition from passive to active hunting behaviour described above, and the two phenomena may be related. It may be that active hunting exposes the larvae to a new group of predators, which they are less able to evade. In the N.C. Venison South and

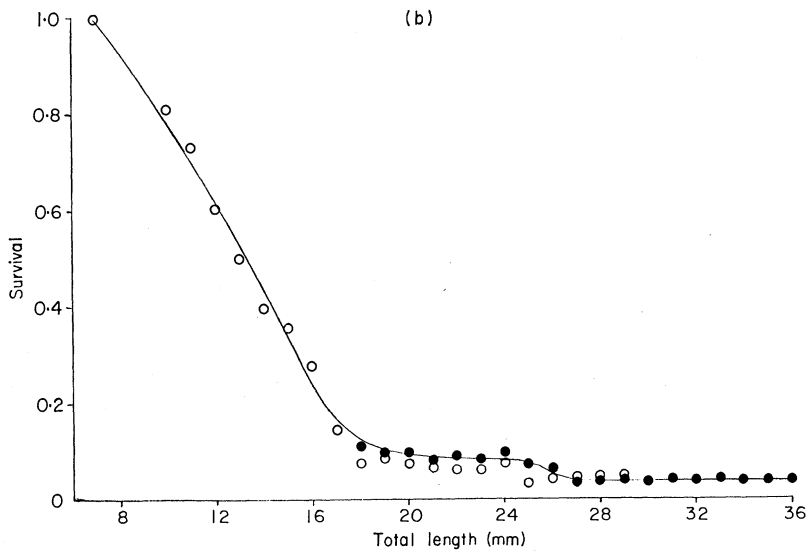
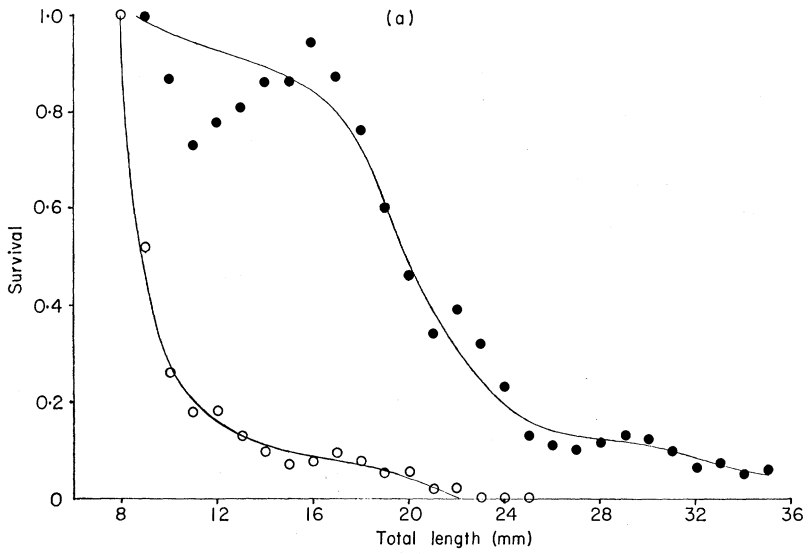


FIG. 11. Survival curves for larvae in three populations, estimated by the length-frequency method. (a) N.C. Arboretum: ●, 1971 late cohort; ○, main cohort. (b) N.C. Venison South: ●, 1972 main cohort; ○, 1972 late cohort. (c) Stadhampton, 1972: ○, estimated by length-frequency; ●, estimated by Rosa Lee equation.

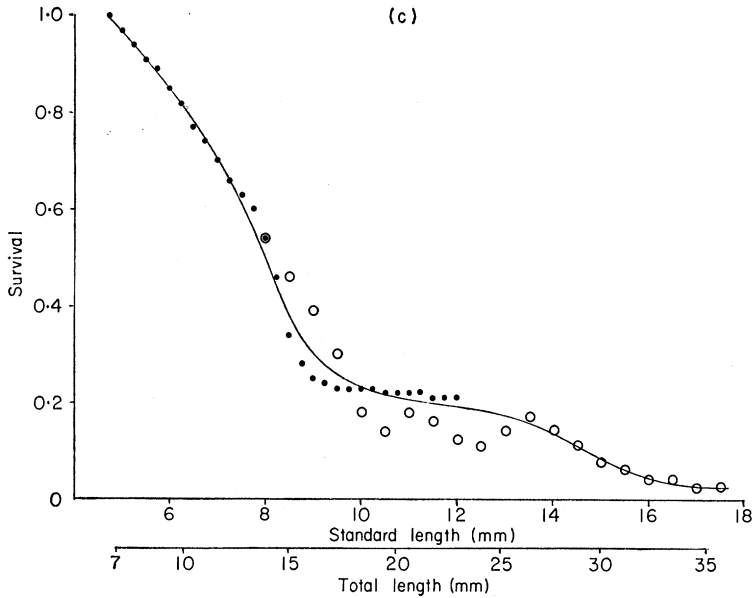


FIG. 11 cont.

Stadhampton populations survival to 15 mm is poorer, and the inflexion is correspondingly less obvious; for the 1972 main cohort larvae at N.C. Arboretum, whose survival was extremely poor, there is no trace of an inflexion in this region.

In all three populations, there appears to be a second inflexion between 24 and 30 mm total length. This seems unimportant only because of the arithmetic scaling of the graphs. At N.C. Arboretum, it seems clear from a consideration of larval growth and length-structure (see above) that this second inflexion is caused by the appearance of two separate groups of larvae, one of which will metamorphose whilst the other overwinters in the pond. The apparently high rate of survival before the inflexion is caused by the reduced growth of the overwintering group, and thus the endpoint of the survival curve represents the survival of the metamorphosing group alone.

The survival curve for Stadhampton is constructed from two types of estimate, one based on straightforward length-frequency analysis and one on the 'Rosa Lee' equation. The latter has been solved for data of 17 July 1972; since most of the larvae taken on this occasion had torn tails, the analysis was performed for the standard length frequency distribution, and the survival values then related to total length using the known relationship between standard and total length (see Bell 1974b). In the region 14–23 mm the estimates given by the two methods overlap and can be compared. Both show an initial period of high mortality (corresponding to the first inflexion discussed above), followed by a period of very low mortality. Because the two methods rely on quite different assumptions, their agreement is taken to be further evidence of the validity of the length-frequency method of estimating survival.

To sum up, the estimation of larval survival by relative population size, by length-frequency analysis or by the 'Rosa Lee' equation leads to the conclusion that the survival curve is complex. The curve probably had two inflexions, the first coinciding with the change from passive to active hunting and the second caused by the relatively slow growth of overwintering larvae.

Overall survival to metamorphosis

From the survival curves, the fraction of the larval population reaching 35 mm in length can be obtained; this is taken to be the fraction of the original larval cohort which survives to metamorphose in the same year. The results are given in Table 6. But although a fraction (0.055) of late cohort larvae metamorphosed in the autumn of 1971 at N.C. Arboretum, another fraction did not metamorphose until the following year. The relative size of the metamorphosing and overwintering groups at hatching can be estimated from the data of 29 July and 16 August 1971 (see Fig. 6(c)) if we know their relative size in the sample and their rate of survival, using the same method used above to calculate the time-course of oviposition. The result is that the overwintering group is estimated to be 60.5% as big as the metamorphosing group at hatching. The fraction of the late cohort which survives as overwintering larvae to the time when the metamorphosing larvae emerge is thus $(0.605 \times 0.055) = 0.033$. The total fraction of the larval population surviving to this point is simply $(0.055 + 0.033) = 0.088$.

Table 6. *Estimates of the fraction of larvae surviving to metamorphosis in three populations*

| Population | Fraction metamorphosing |
|-----------------------------------------|-------------------------|
| N.C. Arboretum, 1971 late cohort | 0.055 (see text) |
| N.C. Arboretum, 1972 main cohort | 0.00+ |
| N.C. Venison South, two cohorts of 1972 | 0.033 |
| Stadhampton, 1972 main cohort | 0.025 |

The most useful way of expressing overall larval survival is as the number recruited into the second-year terrestrial cohort, since this cohort will be the basis for calculating adult life-table parameters. In 1971 and 1972 emerging larvae were captured in a line of small pitfall traps set at approximately 2-mm intervals around the edge of the N.C. Arboretum pond. In autumn 1971 these covered 1/30 of the pond's circumference and trapped 115 emerging larvae; the total number of larvae emerging from the metamorphosing group was thus about $(30 \times 115) = 3450$. By the spring and early summer of 1972 a few traps had been lost, and only 1/35 of the circumference was trapped. 30 emerging larvae were caught at this time, and the total number of larvae emerging from the overwintering group was thus about $(35 \times 30) = 1050$. But the overwintering group was estimated to be 60.5% as big as the metamorphosing group at hatching, so that when the metamorphosing group emerged there would have been about $(0.605 \times 3450) = 2087$ overwintering larvae in the pond. The survival of the overwintering group from the time that the metamorphosing groups emerged to the time that they themselves emerged was thus about $(1050/2087) = 0.5$. The fraction of the total late cohort represented by metamorphosing overwintered animals is then $(0.033 \times 0.5) = 0.017$. Now, by the time that this group has emerged from the pond the metamorphosing group of 1971 had already spent about six months on land, and must have suffered some mortality. The extent of this mortality is not precisely known, but the annual mortality of immature terrestrial animals is thought to be about 20% (Bell 1974a and unpublished). Let us assume that the mortality of the metamorphosing group in their first six months on land was about 10%, so that the fraction of the total late cohort represented by metamorphosing larvae survival until the overwintered larvae had emerged was about $(0.055 - 0.005) = 0.050$. Then the total fraction of the late larval cohort recruited into the second-year terrestrial cohort was about $(0.050 + 0.017) = 0.067$.

It has been shown above that the survivors of the main larval cohort contribute on average 63% of the total number of animals in later year-classes, and that this difference between the two major cohorts is probably due to differences in larval survival. If this is true, the fraction of main cohort larvae recruited to the second-year terrestrial cohort must be $(0.067 \times 1.703) = 0.114$. The probability that any given newly hatched larva will be recruited into the second-year terrestrial cohort can now be estimated, since it is the average of the overall survival of main and second-cohort larvae, i.e. $(0.067 + 0.114)/2 = 0.0905$. It will be noted that this is quite close to the guess made from the relative numbers of animals taken in the samples. It cannot quite be taken at its face value, since many of the procedures involved in its calculation are obviously approximations, but it can be stated rather confidently that the average overall rate of larval survival indicated by the 1971 data from Nuneham Courtenay is about 10%.

Disastrous mortality seems to be rather common in the life of the smooth newt. In 1972 the main larval cohort at N.C. Arboretum was destroyed almost as soon as it hatched (see Fig. 11(a)), whilst the late cohort failed to appear at all because of a prolonged drought, as had already been described. Even after metamorphosis, such catastrophes may occur. Of the emerging 1971 late cohort animals at N.C. Arboretum, only 58% as many were trapped 5 mm from the pond as were trapped on its edge. A careful search of the intervening strip of ground revealed no animals, so it is unlikely that they simply settled around the banks of the pond. At the same time, however, seven shrews (*Sorex araneus* L. and *S. minutus* L.) were caught in the pitfalls over a period of six weeks, although only two were caught in the next two years. Four of these were dissected, and two had the remains of newts in their stomachs. It has been assumed that such heavy post-metamorphosis mortality is exceptional, but this may not be true.

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SUMMARY

(1) This paper describes aspects of the ecology of the eggs and larvae of the smooth newt (*Triturus vulgaris* (Linn.)), concentrating on the survival curve, which has not previously been accurately measured for the young stages of any lower vertebrate.

(2) The survival of eggs was measured by two methods in different years. These agreed in estimating the rate of survival to hatching to be about 0.025, but differed in estimating the form of the survival curve, which appeared to be the Type IV of Slobodkin (1961) in 1972 and the Type III in 1973.

(3) During the breeding season there are three distinct periods of oviposition: the early period, which comprises eggs laid by newts which migrated to the water in the previous autumn, and the main and late periods, to which all surviving animals, most which migrated during the spring, contribute.

(4) The timing of oviposition during the main period may be adaptive, because the rate of egg mortality was found to be least near the middle of the period; moreover, this

was not simply a function of the density of eggs in the pond, but rather of some unknown quality of the time of year. This effect is reinforced by an increase in the rate of oviposition towards the middle of the main period, which is perhaps also adaptive.

(5) Three distinct larval cohorts are generated by the three distinct periods of oviposition. The early cohort is usually small and unsuccessful; the great majority of metamorphosing larvae come from the two later cohorts, the main cohort contributing most.

(6) The success of the larvae differs greatly from pond to pond and from year to year: examples are given in which one, two or all three cohorts were detected. Late cohort larvae may pass the winter in the pond, having had insufficient time to metamorphose, and emerge in the following year.

(7) Neoteny was not observed in Oxfordshire, and is rare near York.

(8) The growth of larvae in several populations was measured, and the effects of mortality on the apparent growth-rate described. The hypothesis that the growth of larvae is normally limited by their food supply was rejected.

(9) Two new methods of measuring the rate of survival, especially in larval populations, are described: both are based on the analysis of the length-frequency distribution, although they use different assumptions, and are specially suitable when the rate of survival is not constant with age. The average survival of smooth newt larvae from hatching to metamorphosis was estimated at about 0.09.

(10) The survival curve is complex, and appears to have two inflections. The second of these is an artefact of the method used to estimate survival, being caused by the relatively slow growth of the late cohort larvae about to overwinter in the pond; but the first seems to be a real change in the rate of survival, and is associated with the transition from passive to active hunting behaviour in the larvae.

(11) Catastrophic mortality seems to happen quite often, and has been observed both before and just after metamorphosis.

REFERENCES

- Avery, R. A. (1968). Food and feeding relations of three species of *Triturus* (Amphibia Urodela) during the aquatic phases. *Oikos*, **19**, 408–12.
- Avery, R. A. (1971). The ecology of newt tadpoles: food consumption, assimilation efficiency and growth. *Freshwat. Biol.* **1**, 129–34.
- Bell, G. A. C. (1970). The distribution of amphibians in Leicestershire with notes on their ecology and behaviour. *Trans. Lit. Phil. Soc. Leicester*, **64**, 122–43.
- Bell, G. A. C. (1974a). *The life of the smooth newt* (*Triturus vulgaris* (Linn.)). D.Phil. thesis, University of Oxford.
- Bell, G. A. C. (1974b). The reduction of morphological variation in natural populations of smooth newt larvae. *J. Anim. Ecol.* **43**, 115–28.
- Caughley, G. (1966). Mortality patterns in mammals. *Ecology*, **47**, 906–18.
- Corbet, P. S. (1957). The life-history of the emperor dragonfly *Anax imperator* Leach (Odonata: Aeshnidae). *J. Anim. Ecol.* **26**, 1–69.
- Gislen, T. & Kauri, H. (1970). Zoogeography of the Swedish amphibians and reptiles with notes on their growth and ecology. *Acta vertebratica*, **1**, 191–397.
- Halliday, T. (1972). *A study of the behaviour of newts*. D.Phil. thesis, University of Oxford.
- Harding, J. P. (1949). The use of probability paper for the graphical analysis of polymodal frequency distributions. *J. Mar. Biol. Ass. U.K.* **28**, 141–53.
- Noble, G. K. (1931). *The Biology of Amphibia*. McGraw-Hill, New York.
- Organ, J. A. (1961). Studies of the local distribution, life history and population dynamics of the salamander genus *Desmognathus* in Virginia. *Ecol. Monogr.* **31**, 189–220.
- Ricker, W. E. (Ed.) (1968). *Methods for Assessment of Fish Production in Fresh Waters*. I.B.P. Handbook No. 3, Blackwell Scientific Publications, Oxford.
- Savage, R. M. (1961). *The Ecology and Life-History of the Common Frog* (*Rana temporaria temporaria*). Pitman, London.

- Slobodkin, L. B. (1961). *Growth and Regulation of Animal Populations*. Holt, Rinehart & Winston, New York.
- Smith, M. (1951). *The British Amphibians and Reptiles*. Collins, London.
- Steward, J. W. (1969). *The Tailed Amphibians of Europe*. David & Charles, Newton Abbott.
- Tilley, S. G. (1973). Life histories and natural selection in populations of the salamander *Desmognathus ochrophaeus*. *Ecology*, **54**, 3-17.

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