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Ecological Monographs, Vol. 47, No. 3. (Summer, 1977), pp. 279-299.

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THE LIFE OF THE SMOOTH NEWT (*TRITURUS VULGARIS*) AFTER METAMORPHOSIS¹

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Abstract. After metamorphosis, smooth or common newts (*Triturus vulgaris vulgaris* [Linn]) disperse on land, where they live as juveniles before returning to the water as breeding adults. The population age-structure was obtained by dissecting the standard length frequency distribution, a procedure which is justified in the text. Juveniles have an uncomplicated age-structure, the number of individuals in successively later age-classes being reduced by mortality and by recruitment to the adult population. Among adult newts, the most frequent age-class is nearly central, indicating the existence of extensive variation in the age at maturity. Growth continues throughout life, the rate of growth decreasing with age. The annual survival rate of adult newts as estimated by a census method, and from the age-structure, was found to be $\approx 50\%$, being rather greater in ♀♀ than in ♂♂. Less reliable data indicate the annual survival rate of juveniles was $\approx 80\%$. Maturity is attained between the ages of 3 and 7 yr, most individuals reproducing for the first time at 6 or 7 yr of age. The number of eggs laid increases with age from ≈ 100 at age 3 to ≈ 400 at age 12; there is also an effect of ♀ age on oocyte size, which may influence subsequent larval survival. Smooth newts breed annually. Reproduction diverts surplus energy from somatic growth, and thereby decreases potential future fecundity in animals whose fecundity is proportional to body size. Individuals maturing at different ages, therefore, have different schedules of fecundity, which were estimated through the use of microbomb calorimetry.

Population size was found to be lognormally distributed, with a mean of ≈ 70 . The sex ratio of juvenile newts was near equality, but a majority of ♀♀ comprised most adult populations. This imbalance is due to greater mortality of adult ♂♂, which results in an age-specific trend in the sex ratio. There are 2 breeding migrations: 1 in autumn and 1 in spring. It is likely that newts migrate during autumn when about to reproduce for the first time, and thereafter migrate during spring. Terrestrial newts appear to move little; there is some evidence that colonization of newly dug ponds is achieved by the infrequent emigration of juveniles.

During its life, a smooth newt occupies a succession of ecological niches. Moreover, different individuals may occupy different niches, or may occupy the same niches for different periods of time. It is speculated that in large newt populations the complex life history is able to trap genetic variation and to dampen fluctuations in population size. However, it is suggested that these group attributes have arisen largely as the result of selection between individuals. Breeding only once (rather than repeatedly) will reduce fitness because the additional fecundity necessary to balance the loss of later reproduction cannot be attained. Early maturity appears to be favored in ♂♂, and late maturity in ♀♀; these opposed selection pressures may contribute to the observed age variation at maturity. Finally, the sex ratio does not vary with population density, and is therefore thought to be controlled by natural selection.

Key words: Age structure; Amphibia; demography; England; life history; population dynamics; reproductive strategies; Salamander; sex ratio; Urodela.

INTRODUCTION

The smooth newt (*Triturus vulgaris* [Linn]) is a small carnivorous amphibian which is found throughout Britain and continental Europe. The ecology of its egg and larval stages has been described in a previous paper (Bell and Lawton 1975). The intention of the present paper is to complete this account by describing the survival, fecundity and population structure of the juvenile and adult newts, after metamorphosis from the larva.

The smooth newt breeds in ponds during spring and early summer, returning to land afterwards. The population biology of the nominate subspecies, *Triturus*

vulgaris vulgaris, was studied by sampling 35 ponds in a 27 km² area between Oxford and Abingdon, in southeastern England. Figure 1 shows the position of ponds on the main study area (MSA).

A brief description of all ponds on the main survey area is given by Bell (1973). With few exceptions, they are small field ponds, almost certainly built between 80 and 150 years ago; all appear on the map of 1911. NC Arboretum (Pond 1), NC Venison South (Pond 2) and Stadhampton Shallow Glyceria (Pond 31) are described more fully by Bell and Lawton (1975).

Great variation was observed both between ponds and within the same pond from year to year. Even neighboring ponds may be very different; for example, the two Venison ponds (Ponds 2 and 3) are actually connected by a water-filled channel, but while the South pond is a healthy small field pond with a dense growth of *Callitriche* and a rich invertebrate fauna, the

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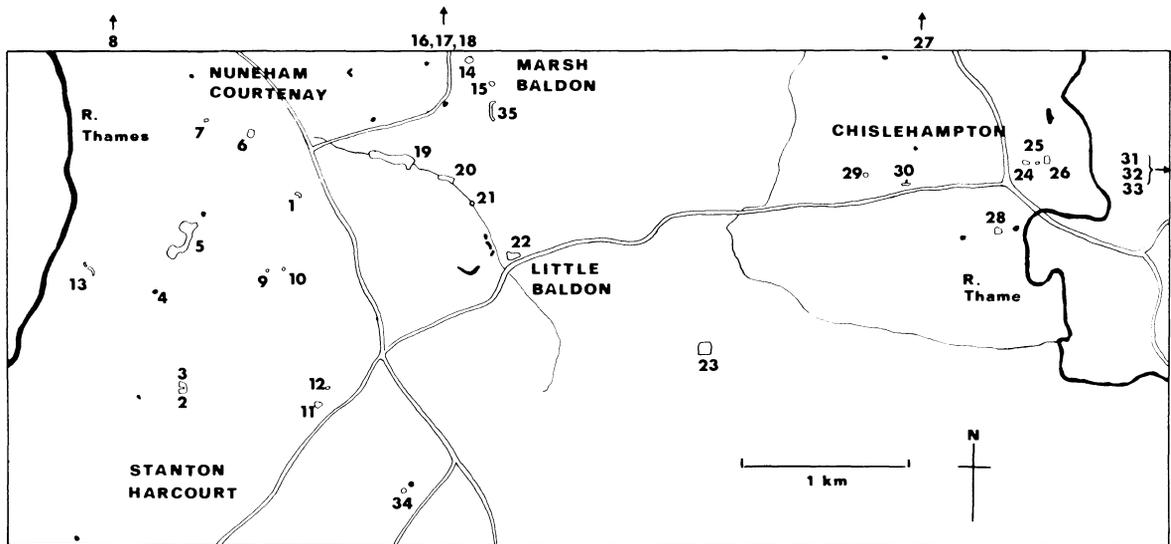


FIG. 1. Map of main survey area. Nuneham Courtenay Village is ≈ 12 km SE of Oxford on the A423 road. Solid lines represent rivers and streams, hollow lines roads. The ponds are named as follows: 1, NC Arboretum; 2, NC Venison South; 3, NC Venison North; 4, NC Deep; 5, NC Park Lake; 6, NC Church; 7, NC Upper Farm; 8, NC Lower Farm; 9, NC Cattle; 10, NC Bramble; 11, NC Wood Marsh; 12, NC Wood Pond; 13, NC Muscovy; 14, MB School; 15, MB Durham Leys; 16, MB College Farm; 17, MB Lane Deep; 18, MB Lane Shallow; 19, MB Upper Fish; 20, MB Lower Fish; 21, MB Far; 22, LB Farm; 23, LB Gravel Pit; 24, CH Riccia; 25, CH Barren; 26, CH Island; 27, CH Gotham; 28, CH Camois Court; 29, CH Marylands Willow; 30, CH Marylands Road; 31, Stadhampton (Shallow Glyceria); 32, Stad Reedmarsh; 33, Stad Newall's; 34, Burcot Farm. Ponds which are solid and unnumbered on the map have disappeared during the last 50 yr.

North pond is nearing the end of its life, with only a small area of open water grading into *Typha* swamp, and a much less diverse fauna dominated by *Asellus*. The lability of the small pond environment can also be illustrated by the South pond, where the area occupied by *Callitriche* (the principal oviposition site of the newts in this pond) was halved between 1972 and 1973.

Aquatic populations of breeding adults were sampled using underwater funnel traps, which were set during 1972 and 1973 in 28 of the ponds on the main study area. Terrestrial newts, because they are more dispersed, are more difficult to catch than breeding adults. Migrating animals were caught at NC Arboretum in a system of pitfalls and fence-traps (cf. Twitty et al., 1967). Immature terrestrial animals could not be captured in sufficiently large numbers at any locality on the main survey area, and were obtained instead by the inspection of surface cover around ponds in 2 nearby villages, Drayton and Appleton.

AGING TECHNIQUE

The basis of the aging technique employed for metamorphosed animals was the dissection of the frequency distribution of standard length. Standard length is the distance between the tip of the snout and the hinder margin of the cloaca. An attempt to identify meristic characters which varied with age was unsuccessful, although the testis is lobulate to some extent, larger animals usually having the more lobes (Humphrey 1922). Newts were anesthetized in a 1:8000 solu-

tion of MS-222® and measured on a flat surface with vernier calipers to a nominal accuracy of 0.1 mm. During the 1972 season at NC Arboretum, ≈ 600 recaptures were obtained 1 wk following a previous capture; the coefficients of variation of the difference between these successive measurements were only 0.55% (males) and 0.41% (females). There is no evidence that measurement was systematically biased towards any particular interval of measurement.

The frequency distributions of length in MSA populations are shown in Fig. 2. They are highly platykurtic, which is often an indication of complexity. When the raw data are smoothed by a simple 5-point moving average, the apparent polymodality of the distribution is striking, and suggests the existence of a number of distinct length classes, each of which comprises animals of the same age. These polymodal curves were dissected into their constituent normal distributions by the method of Harding (1949). The cumulative frequency distribution is plotted on probability paper, on which the cumulative normal distribution is a straight line. If the frequency distribution is polymodal, it will appear when plotted in this way to be made up of a number of short straight lines, separated by steps. The object of the analysis is to discover a pattern of distinct normal distributions which will sum to the observed polymodal distribution, and this is done by drawing straight lines on the probability paper such that they will sum to the observed cumulative frequency distribution. The mean of each constituent distribution is

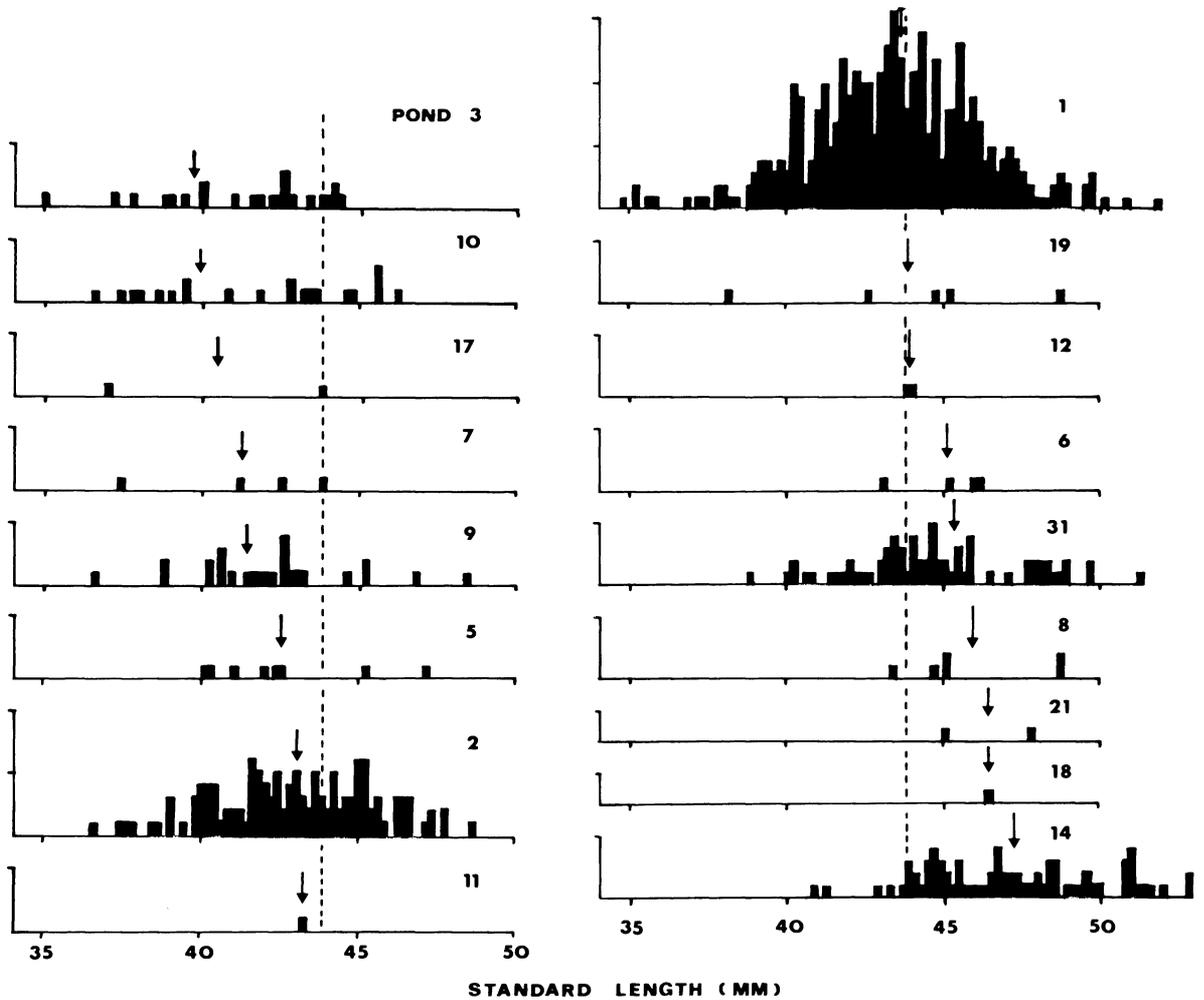


FIG. 2. Frequency distributions of samples of adult smooth newt ♂♂ from main study area (MSA) localities taken in 1972. Raw data lumped at 0.2 mm intervals of standard length. An arrow indicates the \bar{x} for each sample. Weighted mean of means shown by broken line through middle of diagram. One square indicates 1 individual; abscissas are divided at intervals of 5.

the value of length (x axis) at which the relevant straight line intersects the line of 50% probability (y axis); the slope of the line is used to estimate the standard deviation. The family of straight lines obtained in this manner can now be replotted onto arithmetic graph paper, where they appear as a family of normal curves; the area beneath each curve measures the number of individuals in each length-group. An example of such a dissection is shown in Fig. 3. The earliest mode in the length-distributions of juveniles (described below) will comprise 2nd-year animals, i.e., those which metamorphosed in the previous year, as the 1st year of life is invariably spent as an aquatic larva. Assuming that the increment between adjacent modes is 1 yr, later modes can be numbered sequentially. The early modes on the adult distributions can be identified from a knowledge of the immature distribution, remembering that adults will be rather larger than juveniles of the same age because of absorption of H_2O , and (in males) the growth of a cutaneous crest.

Later modes on the adult distribution can then be numbered. It was found that the earlier modes appeared themselves to be bimodal, and concluded that this was caused by the existence of two separate larval cohorts appearing ≈ 2 mo apart (Bell and Lawton 1975); this interpretation is supported by growth data—the disparity in size caused by 2 extra months' growth in the summer is the same as the difference between the 2 groups of juveniles in question—and by the fact that the bimodality was not observed in a population from Moor Monckton, near York, where it is known that only a single larval cohort developed in 1974 (Bell and Lawton 1975).

A number of convergent lines of evidence suggests that the above interpretation is realistic. Of course, definitive evidence concerning the relationship of length to age can be obtained only by measuring animals of known age, but in salamanders, a crude separation of age-groups by length can usually be justified (e.g. Blanchard and Blanchard 1931), and the possibil-

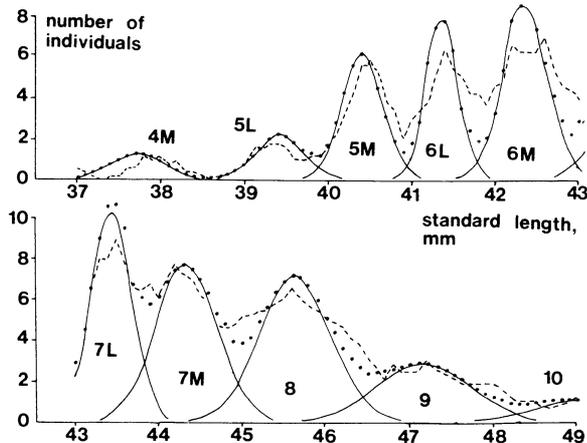


FIG. 3. Dissection of the NC Arboretum 1972 δ length frequency distribution into its supposed constituent distributions. The broken line is a simple 5-point moving average of the raw data; the unbroken lines are the supposed constituent distributions, whose sum is represented by the points. M and L refer to the age-classes contributed by the main and late oviposition periods respectively (see text).

ity of more sophisticated analysis is suggested by the results of Huheey and Brandon (1973), who found that 70–80% of variation in length in the salamander *Desmognathus ochrophaeus* could be explained by differences in age. A similar test would be to measure the length of marked animals in successive years. An attempt to do this at the NC Arboretum pond between 1972 and 1973 was largely unsuccessful, for reasons to be described later. However, 7 individuals caught in 1973 could be positively identified as animals caught in 1972. These had increased in length by an average of 1.05 mm, and because the extreme range of the length-frequency diagrams of Fig. 2 is ≈ 15 mm one might conjecture that adult newt populations contain 10 or 12 year-classes. This impression is supported by estimates of the annual rate of survival of adult smooth newts, which appears to be $\approx 50\%$ (see below). This rate of survival will determine the number of age-classes represented in a sample of given size. Suppose that the age of maturity is a , and that the last age-group is represented by a single individual aged w . Then it can be shown that in a sample of N individuals taken from a stationary population:

$$1 + (w - a) \sim [(-\log N(1 - p))/(\log p)] + 1,$$

where p is the annual rate of survival, and the expression $1 + (w - a)$ is the number of year-classes in the adult population. The sample of adult males taken at N.C. Arboretum in 1972 has $N \approx 400$ and $p \approx 0.5$, so that $1 + (w - a) \sim 9$, with unknown variance.

A number of other observations are consistent with the hypothesis that smooth newt populations include a substantial number of age-classes. For example, the distribution of length within a population may vary considerably from year to year, as it did at NC Ar-

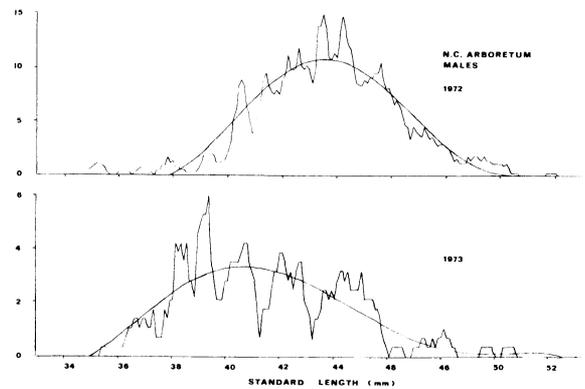


FIG. 4. The change in the length-distribution of δ from the NC Arboretum pond between 1972 (upper figure) and 1973 (lower figure).

boretum between 1972 and 1973 (Fig. 4). Not only did the mean length of male newts decrease by >2 mm (>20 standard errors), but the third moment of the distribution changed from significant negative to significant positive skew; changes of the same magnitude occurred in females also. These changes can easily be explained in terms of age-specific mortality. Some newts hibernated in the pond, and others on land; those hibernating in the pond were of much smaller average size and are thought to have been younger animals, about to reproduce for the first time. The winter of 1972–1973 was exceptionally dry, and if this caused extra mortality it would do so only amongst those newts which hibernated on land. This would selectively remove larger animals from the population, which would cause the observed changes in mean length and in skewedness. Of course, this necessarily implies the presence of several year-classes in the population.

The existence of very large differences in mean length between the populations in a small area (Fig. 2), although conceivably caused by differences in growth rate, can be interpreted in the same way, as the result of differences in age structure. Moreover, this interpretation can be supported by straightforward biological evidence at M.B. School, which is a very highly polluted pond; it was found to contain $> 10\times$ as much phosphate, and $>30\times$ as much potassium, as NC Arboretum, as the result of receiving raw sewage. Consequently, it is highly dystrophic, and larvae placed in water from this pond died within 1 h; no living larvae were caught during 3 yr of sampling at this pond, and it is presumed that none can survive. If adult populations consist of several age-classes, the result of total larval mortality will be eventually to abolish recruitment to the adult population, and thus to shift the adult age structure successively to the right, biasing it in favor of older animals. This would cause an increase in the mean length of animals in the population, which is what is observed.

It seems that length-frequency analysis correctly in-

TABLE 1. An attempt to predict certain population parameters at NC Arboretum in 1974, using an interpretation of the age structure derived from the length frequency distribution. In the final column, *P* is the two-tailed probability that at least as large a discrepancy between prediction and observation in 1974 would have been caused by chance. Since no prediction of sample size was possible, it was not felt to be permissible to calculate confidence intervals for predicted values of parameters in 1974. The probabilities in the final column would be increased if any finite variances were assigned to the predicted values, giving further support to the hypothesis

Sex	Parameter	1973 Observed	1974 Predicted	1974 Observed	<i>P</i>
♂♂	Sample size	195	...	45	...
	Mean length	41.5253 ±0.0905	43.052	43.048 ±0.085	0.98
	Variance	8.3607	5.7443	5.2167	0.50
	Skewedness	-0.4298 ±0.1755	+0.1754	+0.2189 ±0.3735	0.90
	Kurtosis	-0.3554 ±0.3510	+0.1408	-0.6338 ±0.7470	0.33
♀♀	Sample size	80	...	17	...
	Mean length	40.7366 ±0.1317	43.033	42.840 ±0.160	0.23
	Population number	294.6	321.6	293.5	0.70

icates the number of age-classes present in smooth newt populations. It remains to be shown that the dissected modes of the length frequency distributions actually represent age-classes, and can be used to measure the population age structure.

Some formal analysis is possible if one treats length frequency distributions as time series, although it should be understood that this is only an analogy. First, the "trend" of the data is removed to obtain a stationary series. A number of simple tests which discriminate between random data and data which are structured in some way, are given by Kendall (1973), and all of these confirm the existence of structure in the distributions. For example, the expected number of turning points (i.e., points which are either greater or less than both the neighboring points) in a random series of 80 observations is $(\frac{2}{3})(80 - 2) = 52$, with standard deviation $[(16 \times 80 - 29)/90]^{1/2} = 3.75$; the observed number of turning points in the length-frequency distributions of the 4 largest samples of male newts is in all cases significantly fewer than expected, the \bar{x} being 40.5 ± 3.6 . Autocorrelation analysis was attempted but gave disappointing results, presumably because the period of the fluctuations in frequency diminishes from the left to the right of the length frequency distributions. Indeed, this reduction in the absolute distance between adjacent modes from left to right, which is evident in all the distributions, is independent evidence of the reality of the modes, since it is consistent with a Brody-Bertalanffy growth curve (von Bertalanffy 1938; Brody 1945), but is not expected in a random series.

The particular interpretation of the length-frequency

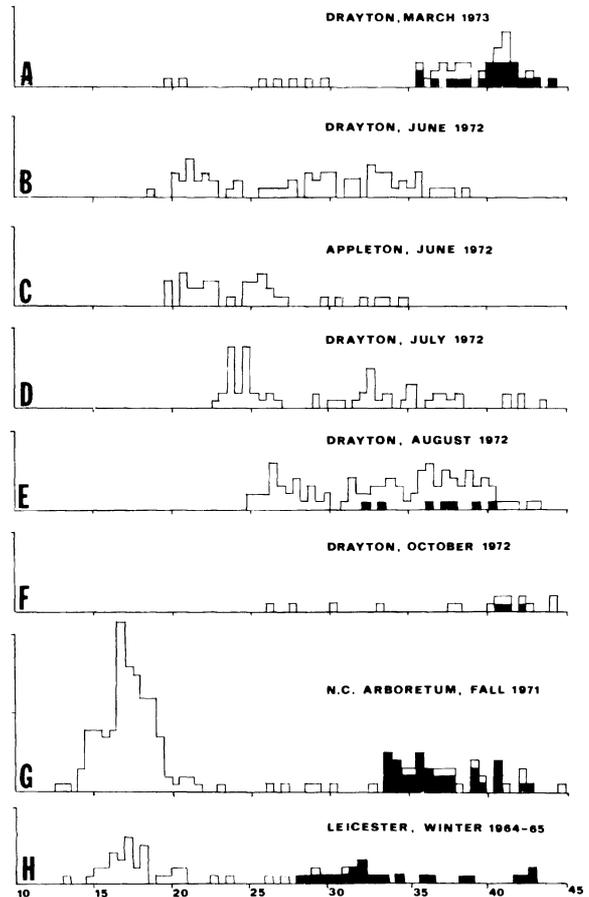


FIG. 5. Standard-length frequency distributions of samples of terrestrial newts. (a) Drayton, March 1973 (migrating adults and some juveniles); (b) Drayton, June 1972 (juveniles only); (c) Appleton, June, 1972 (juveniles only); (d) Drayton, July 1972 (juveniles only); (e) Drayton, August 1972 (juveniles and some newly mature adults); (f) Drayton, October 1972 (juveniles and migrating adults); (g) NC Arboretum, September-October 1971 (metamorphosing juveniles, juveniles and migrating adults); (h) St. Margaret's Mill, Leicester, October 1964-March 1965 (juveniles and breeding adults). One square represents 1 individual; solid squares represent individuals shown by dissection to be sexually mature.

distributions as age structures, based on the sequential numbering of modes described above, can be tested as follows. In certain circumstances, a knowledge of the population age structure enables one to calculate the number of animals of given age, their annual rate of survival and of growth in size, and the schedule of maturity. These parameters are further discussed below; their calculation depends strictly on the validity of the technique used to characterize the age structure. Once they have been obtained, future states of the population can be predicted. The NC Arboretum population was considered to be a suitable subject, as it was thought to have been seriously disturbed in 1972-1973, and in following years would presumably return to some new equilibrium. Table 1 shows the result of

TABLE 2. Age structures of large samples of adult newts from MSA localities in 1972 and 1973. Obtained from length frequency data

Year	Locality	Sex	N	Age (yr)								
				3	4	5	6	7	8	9	10	11+
1972	NC Arboretum (1)	♂♂	358	1	13	46	87	95	71	30	7	8
		♀♀	414	1	5	36	111	115	51	40	27	28
	NC Venison South (2)	♂♂	131	0	4	21	44	44	13	4	0	0
	MB School (14)	♂♂	66	0	0	1	2	21	9	8	11	14
	Stadhampton (31)	♂♂	70	0	0	6	12	31	5	6	7	3
♀♀		106	0	7	8	18	22	16	22	8	5	
1973	NC Arboretum (1)	♂♂	155	1	15	60	36	34	2	4	2	1
		♀♀	59	4	7	18	14	9	3	2	0	2
	CH Riccia (24)	♂♂	222	2	15	60	82	49	6	6	2	0
		♀♀	84	6	6	22	32	14	3	0	0	1

an attempt to predict the mean, variance and higher moments of the distribution of length, and the population size, of the 1974 population. These predictions are compared with estimates based on the measurement of a small sample of animals trapped in the pond during the first half of May 1974. It can be seen that the predictions are adequately justified by observation.

THE POPULATION AGE STRUCTURE

The terrestrial population

Immature animals can be recognized by dissection, or, more conveniently, by their presence on land during the breeding season. Figure 5 shows the seasonal cycle in the composition of the terrestrial population in the immediate vicinity of the pond. In mid-March, most of the animals found on land are mature animals which have recently emerged from hibernation; a few immature individuals are present, but most become active only after the adults have migrated to the water, which they appear to do almost immediately. In April, May, the early part of June, and sometimes later, the only individuals found on land are immature. They are rejoined by the adults during July. A second migration of animals which are coming into breeding condition occurs during October. Immature animals and a part of the adult population appear to enter hibernation towards the end of September. There are two major influxes of metamorphosing larvae, main cohort animals emerging in early August and late cohort animals in late September.

During the breeding season, when the terrestrial population consists exclusively of immature animals, the youngest individuals are the most frequent. This leads to a simple interpretation of the age structure of immature animals: the number of metamorphosed animals is reduced as they grow older by mortality and by recruitment to the mature population.

The aquatic population

The age structure of large samples of breeding adults was obtained by dissecting the length-frequency dis-

tribution. In different populations, modes tend to occur in the same regions of the distributions, as would be expected if growth rate does not vary much between populations (see below). Results from large samples are shown in Table 2. It can be seen that the age structure of mature animals is quite different from that of immature animals. The central, rather than the youngest, year-classes are the most frequent, as one would expect from the appearance of the length-frequency distribution. This observation is discussed in the next section.

It was not possible to establish the stable age structure of any population. However, it seems plausible that the stable structure will typically fall near the middle of Fig. 2, in the region occupied by the 2 largest populations, NC Arboretum and NC Venison South. Moreover, after severe disturbance during the winter of 1972-1973, the NC Arboretum population in 1974 showed a tendency to return to the 1972 structure (Table 1).

During the period of study, the age structures of the MSA populations were found to be exceedingly variable. In the first place, different populations, even nearby populations, may have very different age structures, the best example being the senile population at MB School. Secondly, the age structure may differ considerably in successive years. One of the most remarkable events observed during the course of this study was the failure of the spring migration and the consequent reduction in population size at NC Arboretum in 1973. The data of Table 2 show that the additional mortality responsible for this change was not random with respect to age: the modal year-class was the 7th in 1972 but the 5th in 1973, and the proportion of the population represented by males 8 yr or older fell from 33% in 1972 to 6% in 1973. This change was probably quite general: the age structure of the total MSA sample shifted in the same way as the NC Arboretum sample, and animals were much more difficult to catch both in the MSA ponds and on land at Drayton. This change can be explained satisfactorily

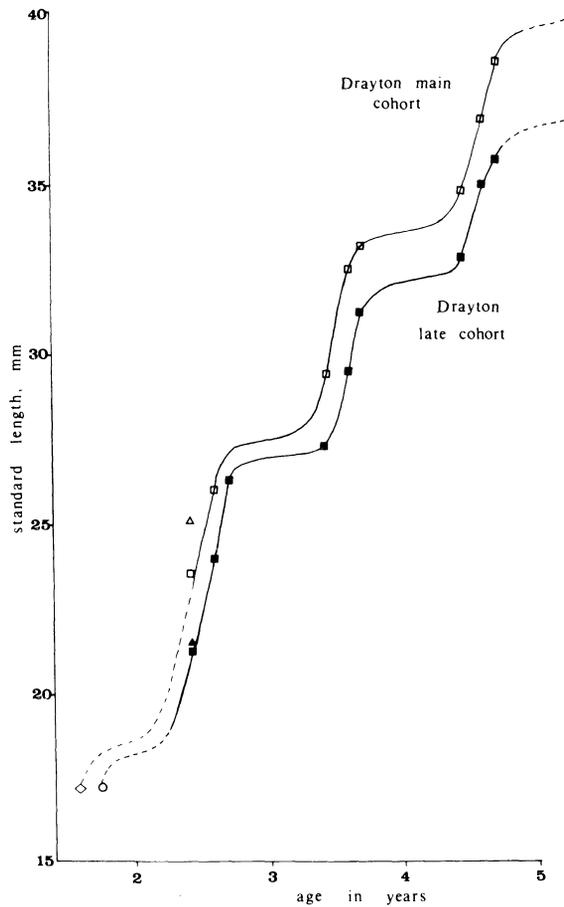


FIG. 6. A growth curve for juvenile newts: o, juveniles metamorphosing from NC Arboretum late cohort, 1972 ($N = 170$); ■ Drayton late cohort juveniles ($N = 85$); □ Drayton main cohort juveniles ($N = 58$); △ Appleton late cohort juveniles ($N = 16$); ▲ Appleton main cohort juveniles ($N = 15$). Plotted points are modal values of dissected standard length frequency distributions.

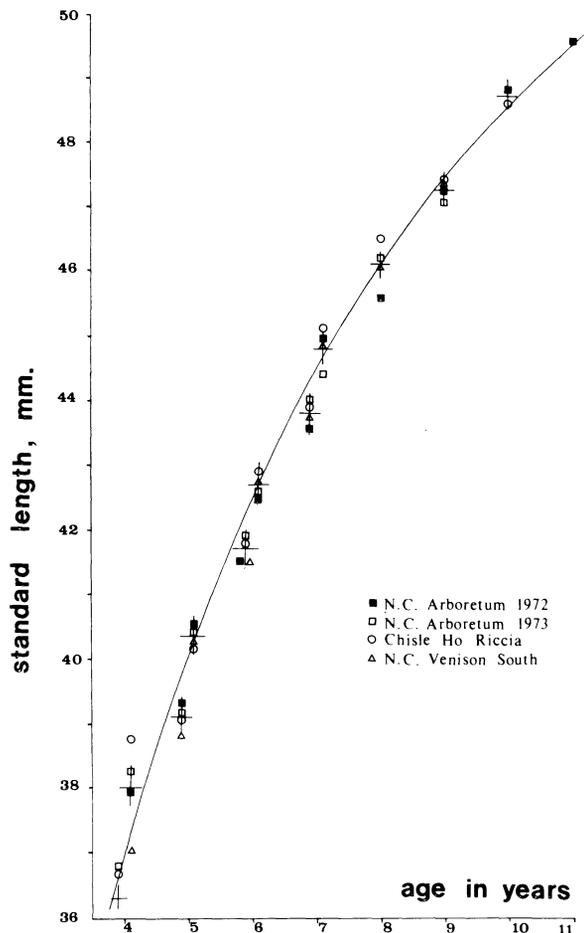


FIG. 7. A growth curve for adult ♂♂: ■ NC Arboretum, 1972 ($N = 357$); □ NC Arboretum, 1973 ($N = 155$); △ NC Venison South, 1972 ($N = 131$); ○ CH Riccia, 1973 ($N = 222$). Plotted points are modal values of dissected standard length frequency distributions.

in the following way. The mature animals caught during migration to the pond in autumn 1972 were, on the average, much smaller than spring migrants, and their age structure suggests that they were individuals which had recently become mature and which would breed for the first time in the following year. These adults could be caught in the pond throughout the winter. The winter of 1972-1973 was notable for a prolonged drought, during which the soil dried out to a considerable depth. This is thought to have killed most of the adults and immature newts hibernating on land, leaving the autumn migrants, hibernating in the water, unaffected.

The two sexes usually have slightly different age structures, although they vary in space and time in the same way. In general, female smooth newts seem to mature at about the same age as males, but survive better, so that their age distribution has a longer tail.

GROWTH

The modal length of animals of given age can be obtained from the dissected length-frequency distributions, and used to construct growth curves.

Figure 6 shows the growth of juveniles; the 2 separate curves represent individuals derived from the 2 separate larval cohorts (Bell and Lawton 1975). Growth is rapid during the summer months and ceases during the winter, when the animals are in hibernation and do not eat. The growth of adult males is shown in Fig. 7. Growth continues throughout life, although the rate of growth declines with age; this situation is usual in poikilotherms. Estimates of growth in length have been given previously by Smith (1964) and by Gislen and Kauri (1970); neither account agrees with the other or with the data presented here, but neither describes how the age of the material was determined. Mature animals measure slightly more than juveniles of the same age because of changes in cloacal mor-

phology which occur as the animals come into breeding condition. No consistent differences were observed either between years or between populations.

Growth in length appears to be much steeper in *Triturus* and in the related North American genus *Notophthalmus* (cf. Healy 1974) than in *Desmognathus* (cf. Tilley 1974). It is this rapid growth, and the fact that the growth curve does not level off as quickly as in *Desmognathus*, which has made it possible to define year-classes by length-frequency analysis in *Triturus*.

SURVIVAL

In 1972 and 1973, mark-release-recapture censuses were carried out at several MSA localities, where the newts were marked by clipping digits according to a code which enabled individual recognition of nearly 1,000 animals; regeneration was slight after 6 mo and some animals could be recognized after more than a year. The conditions under which such a census provides valid population data have been listed by Southwood (1966), and can be shown to hold in this case (Bell 1973).

The results of the census among the adult males at the Arboretum pond in 1972, analyzed by the method of Jolly (1966), provide an estimate of daily survival of 0.9979 ± 0.0060 . Similar results were obtained for females (0.9959), and for males in 1973 (0.9978) at this locality. This suggests an annual rate of survival of ≈ 0.45 . By itself this estimate is unsatisfactory, however, both because it assumes that the survival of the aquatic and terrestrial phases is equal, and because a small error in the estimate of daily survival would accumulate as a large error in the estimate of annual survival.

An alternative approach is to equate the survival curve with the regression of the frequency of animals of given age. This procedure follows from the age-structure equation discovered by Sharpe and Lotka (1911), but, as Tilley (1973) emphasizes, involves the assumptions that the population is stationary in size and stable in age structure. There are some indications that the Arboretum population had reached a quasi-stable age structure in 1972 (see above). At the end of May 1971, the estimate (trellis method of Fisher and Ford 1947) of total population size was 999.0 ± 544.6 ; the corresponding estimate for 1972 was $1,006.7 \pm 220.4$. There is thus no evidence of any overall change in population number. These arguments are by no means conclusive, but fortunately the effect of small changes in population number or in the age structure on the estimate of survival will be small. The results for the Arboretum population are shown in Fig. 8. They suggest that the annual rate of survival of adult males is ≈ 0.45 , and that of females ≈ 0.55 ; these estimates are in reasonable agreement with the census results, which of course rely on quite different assumptions. The difference between the survival regressions of males and females is significant at the 5%

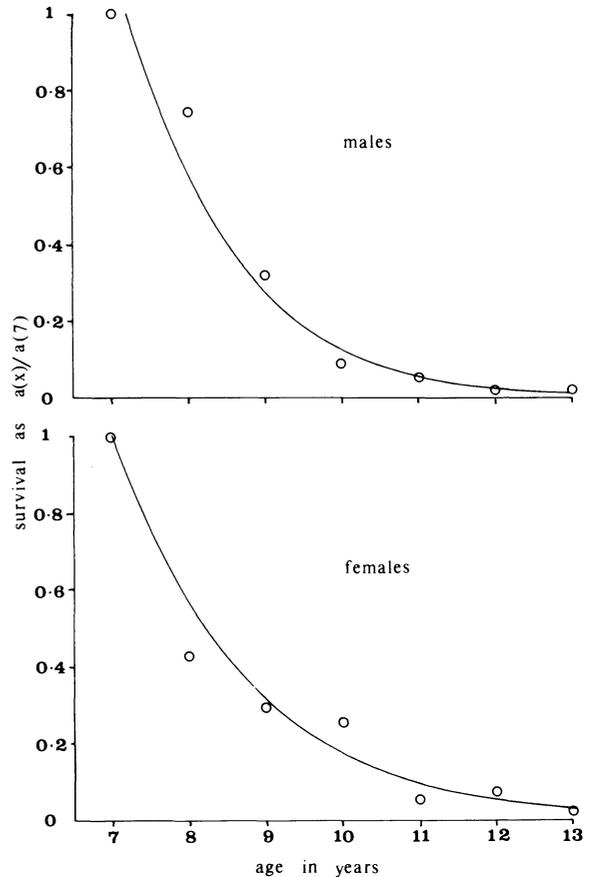


FIG. 8. Survival curves for adult newts based on the age structure of the NC Arboretum population in 1972: $\delta\delta$: $\log Y = -0.344X + 2.18$; ♀♀ : $\log Y = -0.257X + 1.55$. Standard errors of regression coefficients are 0.155 and 0.162, respectively, so that the difference between the 2 curves is significant at the 0.05 level ($t_{11} = 2.56$).

level ($t_{11} = 2.56$), the greater mortality of males being caused, presumably, by their bright epigamic coloration and conspicuous breeding display. The survival curves are semilogarithmic, implying a constant rate of mortality throughout at least the greater part of adult life, the so-called Type III curve of Slobodkin (1961).

Hagstrom (1973) has developed a technique of recognizing individual newts by the ventral pattern, which does not change with age. He estimates the annual rate of survival of adult smooth newts in a Danish population to be ≈ 0.50 (Hagstrom, 1973 and *personal communication*).

The calculation of the schedule of maturity (see below) led to estimates of the annual rate of juvenile survival of ≈ 0.73 for males and 0.85 for females. These figures may not be really different, and the annual rate of juvenile survival can be taken to be $\approx 80\%$.

THE AGE AT FIRST REPRODUCTION

The fact that the most frequent age class in adult populations is centrally located might be interpreted in

TABLE 3. Schedules of maturity in 2 populations. Method of estimation given by Bell (1973). The variances of the estimates are unknown

a	Proportion of animals first reproducing at age a:			
	NC Arboretum		Drayton	
	♂♂	♀♀	♂♂	♀♀
2	0	0	0	0
3	0+	.0066	.1419	.1372
4	.0740	.0163	.7112	.4048
5	.2296	.2070	.1159	.4581
6	.3795	.5457	.0311	0+
7	.3169	.2244	0+	0+
8	0+	0+	0+	0+
Age (\bar{x}) at maturity	5.94	5.97	4.04	4.32

1 of 3 ways. First, very small adults may be more difficult to catch, and would then be under-represented in the samples. But samples which are thought to comprise almost the whole population (e.g. Stadhampton, described below) have the same type of age distribution. Secondly, all the populations might be far from age-structure equilibrium, but in order for this to explain the distributions, all the populations would have to be skewed in the same direction, a rather unlikely assumption.

The remaining possibility is that the age at maturity is variable. If different individuals may reproduce for the first time at different ages, the earlier adult year-classes would be supplemented by the recruitment of animals from the immature population as well as being eroded by mortality. This would explain the "normal" appearance of the age structure; it would also explain the overlapping of the length distributions of mature and immature animals. The most frequent age-class in most populations in 1972 was the seventh, whilst the earliest was thought to represent 3-yr-old animals; thus, maturity may occur at any age between 3 and 7, and perhaps exceptionally occurs outside these limits. At Stadhampton, almost all (171/180) of the population was removed during 1972, so that the 1973 population should have consisted almost entirely of animals reproducing for the first time. Only 6 males were caught in 1973, all of which were aged between 3 and 5.

It is concluded that the apparently anomalous age structure of adult smooth newt is generated by variation in the age at maturity. This finding is in complete agreement with the work of Healy (1974), who shows that individuals from inland populations of the salamandrid *Notophthalmus viridescens* become mature at between 4 and 8 yr of age. This study also found that the age of maturity varied between populations, a phenomenon previously reported for *Gyrinophilus prophyriticus* (Bruce 1972) and for *Desmognathus ochrophaeus* (Tilley 1973). Gislen and Kauri (1970) give data for Swedish smooth newts (from museum material) which are consistent with those from the English

populations reported here, and which seem to imply variation in the age at maturity either between or within populations. They show that among terrestrial juveniles, the smallest individuals are the most frequent, while among sexed animals, the central length classes are the most frequent; moreover, the immature distribution overlaps that of sexed animals.

The schedule of maturity was estimated indirectly from the adult age structure, using an iterative technique described by Bell (1973). The results, shown in Table 3, suggest that there may be variation between, as well as within, populations. It has not been possible to calculate the variance of the parameters listed in this table, so that the reality of this variation must remain in doubt. However, a population in Leicestershire included many individuals which appeared to be breeding for the first time at the age of 2 yr (Fig. 5), a condition which seems to be unknown in Oxfordshire.

FECUNDITY

Mean female fecundity

Ninety adult females (≈80% of the total female population; see below) were collected from the Stadhampton locality (Pond 31) between 17 March and 18 April 1972. After storage in alcohol for ≈2 mo, their ovaries were dissected out and put into Gilson's medium (Ricker 1968). After ≈3 mo they had hardened sufficiently to break up easily with shaking and gentle pipetting. The ovarian oocytes were then examined under a microscope and found to be continuously distributed with respect to size, ranging from large yolked oocytes apparently about to be ovulated to very small primary oogonia. For convenience in counting, 4 classes were recognized: (1) large yolked oocytes (LYO) apparently ready for ovulation, together with ovulated eggs found in the oviducts; (2) small yolked oocytes (SYO), which included all eggs smaller than the first class which showed any tinge of yolk; (3) large unyolked oocytes (LUYO), which although as large as the smallest yolked oocytes had no tinge of yolk; and (4) small unyolked oocytes (SUYO), which included all the other unyolked oocytes which were visible under the binocular microscope. Yolked oocytes were counted directly. Unyolked oocytes were estimated by 2 methods: a quadrat method using a sheet of graph paper placed beneath the petri dish containing the eggs, and a Lincoln Index technique based on the known number of yolked oocytes.

Age-specific changes in the number of oocytes per female are shown in Fig. 9. There is no evidence that the total number of visible germ cells changes with age, but the number of yolked oocytes increases markedly.

The total number of eggs laid by a female each year is thought to be equal to the total number of yolked oocytes (LYO plus SYO); the large yolked oocytes are those laid in each of the 2 major oviposition periods. The evidence for these statements is as follows. First,

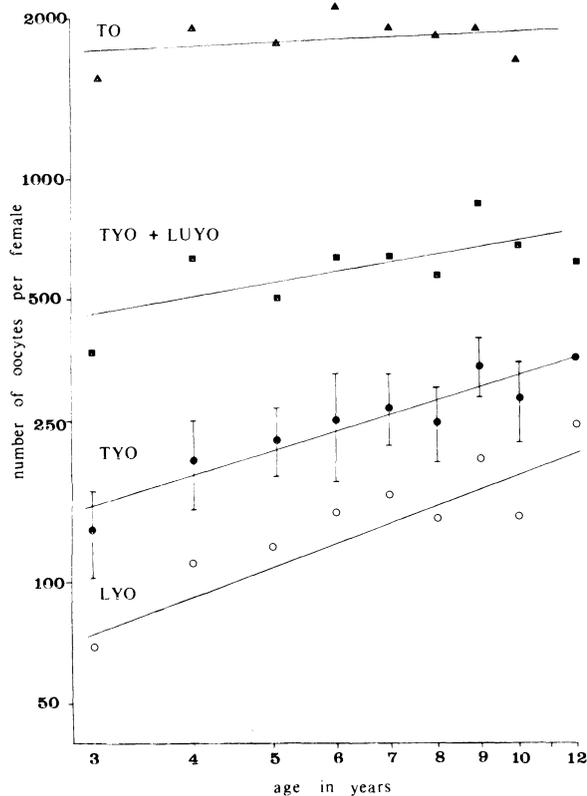


FIG. 9. Estimates of fecundity of ♀♀ at Stadhampton, 1972: ▲ total oocytes (TO), $Y = 0.0912X + 3.2726$; ■ yolked and large unvolked oocytes (TYO + LUYO), $Y = 0.3515X + 2.4930$; ● total yolked oocytes (TYO), $Y = 0.6074X + 1.9009$; ○ large yolked oocytes (LYO), $Y = 0.7533X + 1.5137$. In regression equations, Y and X are log fecundity and log age in years respectively. All regression coefficients are significantly different from zero at the 0.05 level or better, except that for total oocytes. The bars around the TYO plots are ± 1 standard deviation.

the large yolked ovarian oocytes are only slightly smaller than eggs found in the oviducts, which are about to be laid. Secondly, the rate of decrease in the number of large yolked oocytes during the breeding season leads to a correct estimate of the length of an oviposition period (Bell and Lawton 1975). Thirdly, the large yolked oocytes comprise about half the total number of yolked oocytes ($12.874/21.914 = 0.587$ in the Stadhampton material; see Bell and Lawton 1975). Finally, the number of eggs laid by females in the laboratory agrees with the number of large yolked oocytes inferred from the Stadhampton material (Fig. 10).

It was concluded that the mean annual fecundity of females of given age is estimated by the total number of yolked ovarian oocytes. Since the Stadhampton females were collected during the main oviposition period, however, the observed number of large yolked oocytes declined in samples taken at successively later dates, when age-specific effects had been eliminated. This decline was presumably caused by oviposition. It

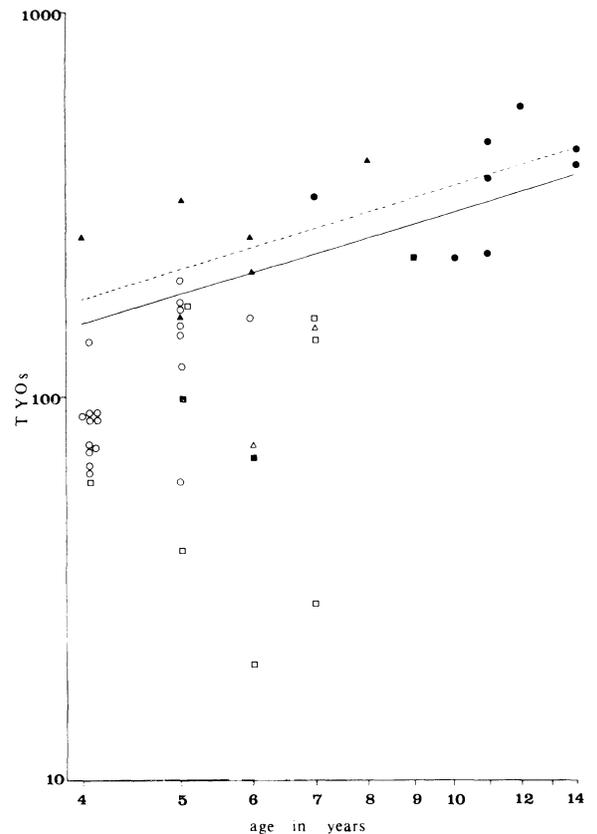


FIG. 10. Fecundity (as total yolked oocytes) of individuals from populations other than Stadhampton at different times of the year: ● MB School aquatic adults, April 1972 ($N = 8$); ○ Drayton terrestrial spring migrants, March 1973 ($N = 19$); ■ NC Arboretum terrestrial autumn migrants, October 1972 ($N = 3$); □ NC Arboretum terrestrial summer emigrants, July 1972 ($N = 7$); ▲ twice the number of eggs laid by ♀♀ in the laboratory ($N = 6$); △ Drayton terrestrial nonbreeding individuals, June 1972 ($N = 2$; 58 other juveniles in same sample were unsexed). The unbroken line is the Stadhampton TYO regression (Fig. 9); the broken line is the same regression, corrected for oviposition (see text).

was found that the sample of 17 March had on the average, 15% more LYO than the mean value for females of given age taken over all sampling dates. A minimum estimate of the number of eggs laid per female during a single oviposition period is thus 15% greater than the mean number of LYO counted in the Stadhampton females; total annual fecundity is $2 \times$ this figure, because most adult females participate in 2 oviposition periods per season.

This estimate will be used in subsequent life-table calculations. But it is an unbiased estimate of mean age-specific female fecundity only if the survival of zygotes after having been laid does not depend on the age of the mother; this assumption may not hold for newts. The occurrence of age-specific effects on egg and larval survival was suspected when it was observed that the diameter of LYO (which is highly correlated with their weight) increases with female age.

An experiment was performed to test the hypothesis that differences in oocyte size will affect later development. Eggs divided into 2 batches were cultured in the laboratory; one batch was laid by 4 females of <42 mm standard length, and the other by 4 females of >44 mm standard length. These eggs were cultured in a single glass trough divided by a double gauze partition, so that as far as possible they developed under identical conditions. No difference in survival between the 2 batches of eggs was noticed, but the eggs from the larger females hatched more quickly (23 vs. 25.7 days, significance of difference not testable) and gave rise to larger larvae (8.94 vs. 8.15 mm; $t_{196} = 3.09$, $P < .01$). These differences will almost certainly influence larval survival.

The cycle of oocyte maturation

A number of small series of animals from other localities were dissected. The results, shown in Fig. 10, allow the cycle of oocyte maturation to be outlined.

Nineteen adult females captured during the 1973 spring migration at Drayton had significantly fewer yolked oocytes than would be expected from the Stadhampton regression, as did 3 Arboretum females collected during the 1972 autumn migration. I conclude that female newts must pass some time in the water before they are able to mature a full complement of oocytes. Seven females caught as they emerged from the Arboretum pond after breeding in July 1972 also had fewer yolked oocytes than the Stadhampton (Pond 31) animals, as one would expect. The results from 8 breeding females captured at the School pond (Pond 14) and from females from various localities which were allowed to lay eggs in the laboratory, agreed with the Stadhampton results. Two of 26 juvenile females collected at Drayton in June 1972 possessed a few yolked oocytes; it seems likely that these individuals would breed for the first time in the following year.

These results suggest a reconstruction of the cycle of oocyte maturation, which can only be tentative because of the small sample size involved. Yolked oocytes are always present in the ovaries of mature females, and perhaps in those of females which are about to mature. After migration to the water, some time (≈ 40 days for spring migrants) passes before the full complement of oocytes is yolked. Oviposition of course reduces this number, but the maturation of oocytes apparently proceeds at a diminished rate throughout the breeding season. Similar conclusions were reached by Hurlbert (1970) from a study of *Notophthalmus viridescens*. He found that pond-overwintered females could breed earlier in the season than land-overwintered females, causing the length-frequency distribution of emerging juveniles to be bimodal in some populations. In *Triturus vulgaris* a similar situation occurs, the autumn migrants being solely responsible for an early period of oviposition,

because they alone are capable of maturing a batch of oocytes in early spring. However, this early period seems to be rather unsuccessful in most years, and the bimodality of the larval population, and of the early age-classes of metamorphosed individuals, is caused by the 2 major peaks of oviposition later in the season, to which all surviving females contribute (Bell and Lawton 1975).

In 1972, almost all members of the Stadhampton population were captured (see below). In 1973, only 8 individuals were captured there, 7 of which could have been reproducing for the first time. It is concluded that both males and females breed annually.

Male fecundity

A male which was kept in the laboratory and mated to a new female every day produced at least 1 spermatophore each day for 25 days, at which point the experiment was terminated (Halliday 1974). It is likely, therefore, that females are the demographically limiting sex; that is, that the reproductive output of the population is determined by the number of fertilizable female gametes. Male fecundity is thus of little demographic consequence, but it may still influence other population processes, including evolutionary change.

The age-specific schedule of male fecundity will depend on the breeding system of the smooth newt, which is unknown. Females which have already been fertilized and which have begun to lay eggs will still participate in courtship, but the fate of the male gametes following their entry into the female is unknown. Since there would be no point in such behavior if additional spermatophores had no function, it is speculated that the eggs laid during a single oviposition period by a single female may have been fertilized by several males.

There is no parental care after the egg has been wrapped in the leaf of a water plant by the female. There is no postreproductive period of life.

The simplest estimate of male fecundity (defined as the number of gametes fertilized by a given male) assumes that all males are equally successful in competing for females, and is the product of average female fecundity and the ratio of females to males. This number is ≈ 420 for the Arboretum population. However, there is the possibility that age-specific effects may exist. These are discussed at length by Bell (1973), but lack empirical support.

The energy cost of reproduction

The maturation of the gonads and their maintenance in subsequent years, must impose an energy burden on the animal, and if the total amount of energy that a newt can assimilate is limited, then putting energy into gonadal growth implies the withdrawal of energy from somatic growth. It is well known that the fecundity of female urodeles is related to body size. Thus, an animal which reproduces for the first time in a given year

TABLE 4. Results of microbomb calorimetry. All comparisons between the 3 different types of tissue are significant beyond the 1% level, except that the energy content of somatic and testis tissue has $t_{8} = .05$ ($P > .90$). Total wet weight of ♀♀ increases with age as: $Y = 0.2634X + 0.94$, where Y is weight in grams and X is age in years (data from Arboretum, 1972; $N = 291$). Ovary weight is related to age as: $Y = 34.71X + 40.9$, where Y is ovary weight in milligrams and X is age in years (data from Stadhampton, 1972; $N = 90$)

Material	dry wt/wet wt	kJ/g (ash-free dry wt)
Somatic ; 8 samples of whole animal less gonads.	0.2202 ± 0.0196	21.86 ± 1.20
Testis ; 2 samples each comprising 2 organs each from 12 animals.	0.1584 ± 0.0071	21.81 ± 0.72
Ovary ; 12 ripe ovaries from 6 females.	0.3157 ± 0.0405	24.15 ± 0.71

y will be less fecund in the following year ($y + 1$) than an individual of the same age which reproduces for the first time in year ($y + 1$), because the latter, having been able to devote more energy to somatic growth, will be larger in year ($y + 1$). This implies that the schedules of fecundity of individuals which reproduce for the first time at different ages will be different.

The energy content of fresh somatic and gonadal tissue was measured with a Phillipson Microbomb Calorimeter® (Phillipson 1964). These measurements are given in Table 4, together with the wet weights of the whole animal and of the gonads and the dry : wet weight ratio of each. Both the energy content and the dry : wet ratio of ovarian tissue is greater than that of somatic tissue, so that a cost of reproduction in terms of potential future fecundity will exist in females. But testis tissue seems to have the same energy content per unit dry weight as somatic tissue, and because it has a lower dry : wet weight ratio will actually be cheaper to produce. However, the total energy cost of reproduction in the male may still be fairly large, because a certain quantity of tissue is 'exported' as spermatophores, and because the cost of the breeding display (including the cost of growing a crest) may be appreciable.

Using the data of Table 4, we can calculate for females the loss in weight in a given year caused by breeding in the preceding year. If this loss is associated with a corresponding loss in the rate of increase in fecundity with age, then it can be used as the basis for calculating the age-specific fecundities of females which reproduce for the first time at different ages. For example, consider those females which become mature in the 3rd year of life. From the data presented above, we have total dry weight: 0.3105g; ovary dry weight: 0.0348g; somatic energy content: $(0.3105 - 0.0348) \times 21.86 = 6.02$ kJ; ovary energy content: $0.0348 \times 24.15 = 0.84$ kJ. If the 0.84 kJ de-

voted to ovary production were used in somatic growth, it would be sufficient to produce $(0.84/21.86) = 0.0385$ g of somatic tissue, assuming equal growth efficiencies for ovarian and somatic tissue. An individual which did not reproduce in its 3rd year of life would therefore weigh $0.3105 + 0.0385 - 0.0348 = 0.3142$ g, and would thus be $(0.3142/0.3105) = 1.012\times$ as large. If the simple relationship between weight and fecundity that has been postulated holds, then it will also be $1.012\times$ as fecund. In fact, it is known that surviving adult females mature a batch of oocytes $2\times$ each year, so that an immature 3-yr-old would weigh $0.3105 - 0.0348 + (2 \times 0.0385) = 0.3527$ g, and would be $(0.3527/0.3105) = 1.136\times$ as fecund in the following year.

From the regression of total yolked oocytes on age (Fig. 9), mean female fecundity at age 4 is estimated to be 178.5. From the schedule of maturity (Table 3), the fraction of animals which mature at age 3 is 0.004, so the fraction which mature at age 3 and survive to reproduce again at age 4 is $0.55 \times 0.004 = 0.0022$. The fraction of the population which reproduces for the first time at age 4 is 0.0096. Mean female fecundity at age 4 (i.e., $b[4]$), estimated from the regression of Fig. 10) is the weighted mean fecundity of females reproducing at age 4 which first reproduced at ages 3 (i.e., $b[3,4]$) and 4 (i.e., $b[4,4]$). Thus:

$$b(4) = [0.0022 b(3,4) + 0.0096 b(4,4)] / (0.0022 + 0.0096).$$

Since $b(4,4) = 1.136 b(3,4)$ this equation can be solved to yield $b(3,4) = 160.7$ and $b(4,4) = 182.5$. These calculations can then be continued to obtain all values of $b(x,y)$ up to and including $x = y = 7$. Thereafter the fecundity of all animals is assumed to increase at the same rate, ignoring the possibility of long-term effects on potential fecundity of repeated reproduction. The results of these calculations are shown in Fig. 11 which suggests that the effect of early maturity is to lower fecundity by a considerable amount in later life.

POPULATION NUMBER

The distribution of population size within a species is an ecological parameter of considerable interest, but one which has rarely been measured. During the breeding season, adult newts are aggregated in sharply distinct populations whose size can be measured relatively easily. It is natural to sample only those ponds known to contain newts and to avoid this bias an attempt was made to census all the ponds on the main survey area. However, differences between the ponds made it necessary to employ several different methods of estimating population number.

At Stadhampton, an attempt was made to remove all the adults from the pond for dissection. When the number of animals caught on a given occasion is plotted against the total number caught on previous occasions, the total number in the population can be esti-

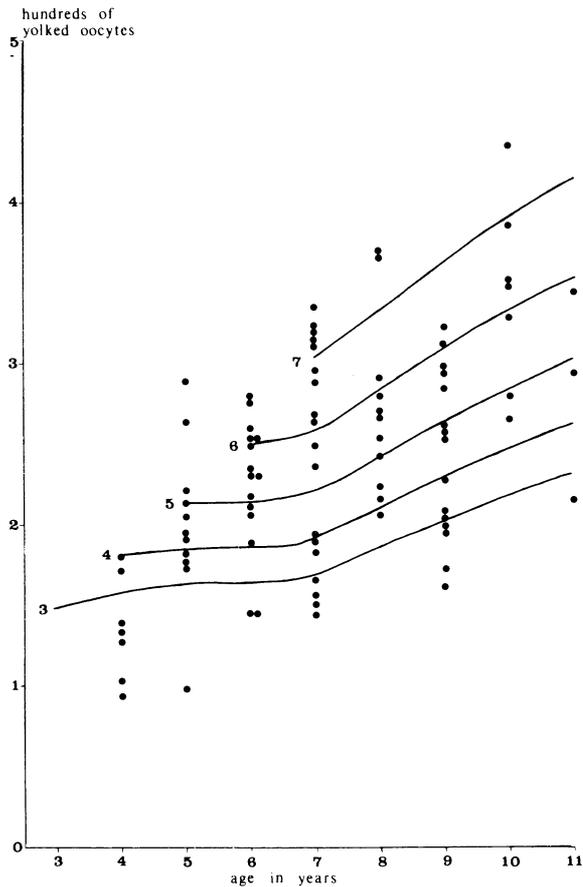


FIG. 11. The fecundity schedules of ♀♀ which mature at different ages. Derivation of theoretical curves is explained in text; plotted points are raw data from Stadhampton.

mated by fitting a curve to the plotted points and reading the cumulative total beyond which the number of animals subsequently caught is zero (Hayne 1949). This method can also be used to check the results of mark-recapture censuses, since marked animals can be equated with animals previously "removed" from the population. The operation of such a census itself has been defended above. Stochastic estimates (Jolly 1966; Seber 1965) were used whenever possible, but when sample sizes were small, one of the deterministic versions of the Lincoln Index (Lincoln 1930) was used instead (calculating formulae for several methods given by Southwood 1966). When no recaptures were made, an estimate could still be made by using a special case of the hypergeometric distribution (Bell 1974; but see Edwards 1975). Finally it was found that these estimates of population number were highly correlated with the rate of capture in underwater traps (Bell 1973). This provided a means of estimating the size of populations which could not be estimated in any other way, and was used extensively in 1973.

The results are shown in Table 5. Figure 12 shows that adult population number is distributed lognor-

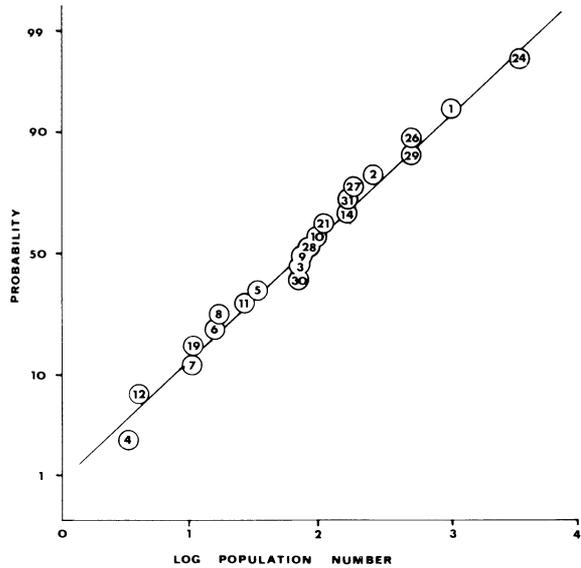


FIG. 12. The lognormal distribution of population size. Data are from Table 5. Numbers identify populations listed in legend to Fig. 1.

mally with a mean of 72.5. The density of adult newts on the main survey area in 1972 was 310/km².

THE SEX RATIO

Ovary and testis become morphologically distinct shortly after metamorphosis, and all transformed individuals can be sexed by dissection after their first winter. No completely reliable method for sexing juveniles using only external characters was discovered. A series of juveniles from Drayton and Appleton gave the results found in Table 6. This sex ratio (as males/total) is 0.478 ± 0.055 and thus does not differ significantly from equality. Table 6 has $\chi_3^2 = 0.96$, $P > 0.8$; there is therefore no difference between the age-classes. Nor was there any difference between the 2 localities. It is concluded that among juveniles, the sexes are present in equal numbers.

The census data reported above provided information on the sex-ratio of adult populations. The Stadhampton material showed no change in the sex ratio as the population was depleted, showing that hand-netting catches the two sexes in the proportions in which they occur. But where independent estimates of the numbers of males and of females were available, for example at the Arboretum pond, these were very different from the numbers caught in the underwater trap, which seemed to be biased in favor of males. The real sex ratio being known in these populations, a simple correction was devised by which the true sex ratio could be estimated from the trap sex ratio in populations where only the trap sex ratio was known. The results, shown in Table 7, show that there is a preponderance of females in most populations. The greater mortality of adult males has been noted above, and

TABLE 5. The size of populations on the main survey area. P is the estimate of population size. The sample size includes all captures, whether or not they refer to different individuals, and so need not necessarily be smaller than the estimate of population size; total sample size is 3,058. The sizes of the Chislehampton populations which were discovered in 1973 were multiplied by 3.9 to estimate their 1972 values from these data for Fig. 14, a simple correction factor based on the reduction in size of the Nuneham Courtenay and Marsh Baldon populations between 1972 and 1973 (see Bell, 1973). Ponds from which no recaptures were recorded were trapped throughout the season in question. N = sample size

Year	Locality	N	$P \pm sd$	Method
1971	NC Arboretum (1)	191	999.0 \pm 544.6	Trellis
1972	NC Arboretum (1)	1,298	1,006.7 \pm 220.4	Jolly's
	NC Venison South (2)	202	242.9 \pm 131.9	Jolly's
	NC Venison North (3)	28	71 \pm 60.2	Lincoln Index
	NC Deep (4)	1	3.3	Trap-ratio
	NC Park Lake (5)	11	31	Nil-recapture
	NC Church (6)	6	16	Nil-recapture
	NC Upper Farm (7)	6	10	Nil-recapture
	NC Lower Farm (8)	6	15.7	Trap-ratio
	NC Cattle (9)	43	71 \pm 56.6	Lincoln Index
	NC Bramble (10)	34	94	Nil-recapture
	NC Wood Marsh (11)	11	25	Nil-recapture
	NC Wood Pond (12)	3	4	Nil-recapture
	NC Muscovy (13)	0	0+	...
	MB School (14)	105	154.3 \pm 58.4	Lincoln Index
	MB Durham Leys (15)	0	0+	...
	MB College Farm (16)	0	0+	...
	MB Lane Deep (17)	5	5+	(one netted sample)
	MB Lane Shallow (18)	1	1+	(one netted sample)
	MB Upper Fish (19)	5	11	Nil-recapture
	MB Lower Fish (20)	0	0+	...
Stad Shallow Glyceria (31)	171	180	removal	
Stad Reedmarsh (32)	0	0+	...	
Stad Newall's (33)	5	5+	(netted sample)	
Burcot Farm (34)	0	0+	...	
1973	NC Arboretum (1)	315	294.6	Jolly's
	NC Venison South (2)	11	34.7	Trap-ratio
	NC Venison North (3)	2	7.4	Trap-ratio
	NC Park Lake (5)	0	0+	...
	NC Church (6)	0	0+	...
	NC Wood Marsh (11)	6	20.0	Trap-ratio
	NC Wood Pond (12)	0	0+	...
	MB School (14)	36	55.7	Trap-ratio
	MB Far (21)	0	0+	...
	LB Farm (22)	0	0+	...
	LB Gravel Pit (23)	0	0+	...
	CH Riccia (24)	351	881.2	Trap-ratio
	CH Barren (25)	0	0+	...
	CH Island (26)	50	125.3	Trap-ratio
CH Gotham (27)	26	42.0	Trap-ratio	
CH Camois Court (28)	13	20.0	Trap-ratio	
CH Marylands Willow (29)	48	120.7	Trap-ratio	
CH Marylands Road (30)	1	15.9	Trap-ratio	
1974	NC Arboretum (1)	62	293.5	Trap-ratio

would of course result in a deficiency of males in most populations. If this is so, year-classes after the 7th should contain increasing proportions of females. The Oxfordshire collections from all localities between

TABLE 6. Sex ratios of juvenile newts from Drayton and Appleton, obtained by dissection

Age (yr)	♂♂	♀♀	Total
2	26	25	51
3	8	12	20
4	7	7	14
5	3	4	7
total	44	48	92

1971 and 1973 yielded the results found in Table 8, for which $\chi^2 = 68.67$, $P < .001$. It is concluded that the greater mortality of males causes an age-specific trend in the sex ratio, and thereby a deficiency of males in the adult population as a whole.

MOVEMENTS

Figure 13 shows the number of adult newts caught on the banks of the Arboretum pond during 1972 and the early part of 1973, and around a small pond in Oxford during spring 1971. This can be interpreted very simply. Most adults move into the pond in the latter half of March—the spring breeding migration, which is well known in the literature (e.g., Smith

TABLE 7. Sex ratio of MSA and other populations. Samples used are very nearly, but not quite, identical with corresponding samples of Table 5; total sample size = 4,452. Sex ratios are all calculated as $\delta\delta$ /total. The trap ratio (sex ratio of animals in traps) is biased in favor of $\delta\delta$, but may be multiplied by 0.63 to estimate the real sex ratio (Bell, 1973); hand-netted samples need no adjustment. The "small populations" of 1972 are NC Deep, NC Church, NC Upper Farm, NC Lower Farm, NC Wood Pond and MB Upper Fish. The exceptional sex ratio recorded at NC Wood Marsh in 1972 may have been an accident of sampling, because 3 $\delta\delta$ and 3 ♀♀ were caught in 1973

Year	Locality	$\delta\delta$	♀♀	Total	Trap ratio	Real ratio
1963-65	Leicestershire	393	356	749	...	0.525
1971	Oxfordshire	86	128	214	...	0.402
	Rye St. Anthony, Oxford	10	16	26	...	0.385
1972	MSA: NC Arboretum (1)	815	483	1,298	0.628	0.395
	NC Venison South (2)	162	40	202	0.802	0.505
	NC Venison North (3)	16	10	26	0.615	0.388
	NC Park Lake (5)	9	2	11	0.818	0.516
	NC Cattle (9)	29	6	35	0.829	0.522
	NC Bramble (10)	20	12	32	0.625	0.394
	NC Wood Marsh (11)	1	9	10	0.100	0.063
	MB School (14)	86	19	105	0.819	0.516
	Stad Shallow Glyceria (31)	68	103	171	...	0.398
	6 small populations	21	5	26	0.808	0.509
	Drayton	44	3	47	0.936	0.590
	Appleton	42	23	65	0.646	0.407
1973	MSA: NC Arboretum (1)	235	80	315	0.746	0.470
	MB School (14)	30	6	36	0.833	0.525
	CH Riccia (24)	248	100	348	0.713	0.449
	CH Island (26)	36	10	46	0.783	0.493
	CH Gotham (27)	16	4	20	0.800	0.504
	CH Camois Court (28)	10	4	14	0.714	0.450
	CH Marylands Willow (29)	33	6	39	0.846	0.533
	All others	18	10	28	0.643	0.405
1974	NC Arboretum	45	45	62	0.726	0.457
	Moor Monckton, York	385	203	588	0.655	0.413
	Brownmoor Farm, York	36	3	39	0.923	0.581

1964). The migration lasts for about a month. In early July, the adults leave the pond. There is a second breeding migration in the autumn, which seems to have escaped the attention of earlier authors, although it is well known on the continent (e.g., van Gelder 1973). In 1972, the autumn migration was unusually prolonged because the animals were forced to remain on the banks of the pond until it filled with water in early December. The age structure of the autumn migrants suggested that they were individuals which were about to reproduce for the first time (see above).

On 21 July 1972, 61 marked juveniles were released at a point 22.5 m from the edge of the pond at Drayton; they had all been captured within 100 m of this point on the previous day. A sample taken 35 days later yielded the results found in Table 9.

A second sample on 11 October yielded two recaptures from 17 animals: one was within 1 m of the point of release, the other 10-12.5 m away. A ring of 180 small pitfall traps 50 m from the edge of the Arboretum pond caught only 5 newts in 21 mo, while >200 were caught in 70 pitfalls within 5 m of the pond. It seems that newts usually settle near the pond in which they were born, and afterwards move around very little.

However, newts are known to be able to colonize a substantial proportion of newly dug ponds within a few years of their construction (Warwick 1949), and there-

fore some phase of the life history must be capable of dispersal. The classical mechanism is the transport of eggs on the feet of waterfowl, but it does not seem to be appreciated that, because of their high rate of mortality under natural conditions, enormous numbers of eggs would have to be transported to ensure the appearance of even a very few adults. The transport of larvae seems inherently less likely. Of $\approx 2,500$ adults marked by toe clipping in MSA ponds in 1972, none were recaptured in different ponds in 1973. Frequent migration should tend to make the age structure of nearby ponds similar, but they are often very different. It is tentatively suggested that movement between populations may be caused predominantly by the infrequent migration of juveniles. In 1972, the 2 Venison ponds, which are only a few metres apart, supported a large and a small population of newts respectively; the

TABLE 8. The age-specific trend in the sex ratio among adult newts. All Oxfordshire localities, 1971-1973

Sex	Age (yr)							Total
	up to 7	8	9	10	11	12	>12	
$\delta\delta$	1,185	183	90	51	20	11	7	1,547
♀♀	751	97	83	58	32	12	22	1,055
Total:	1,936	280	173	109	52	23	29	2,602

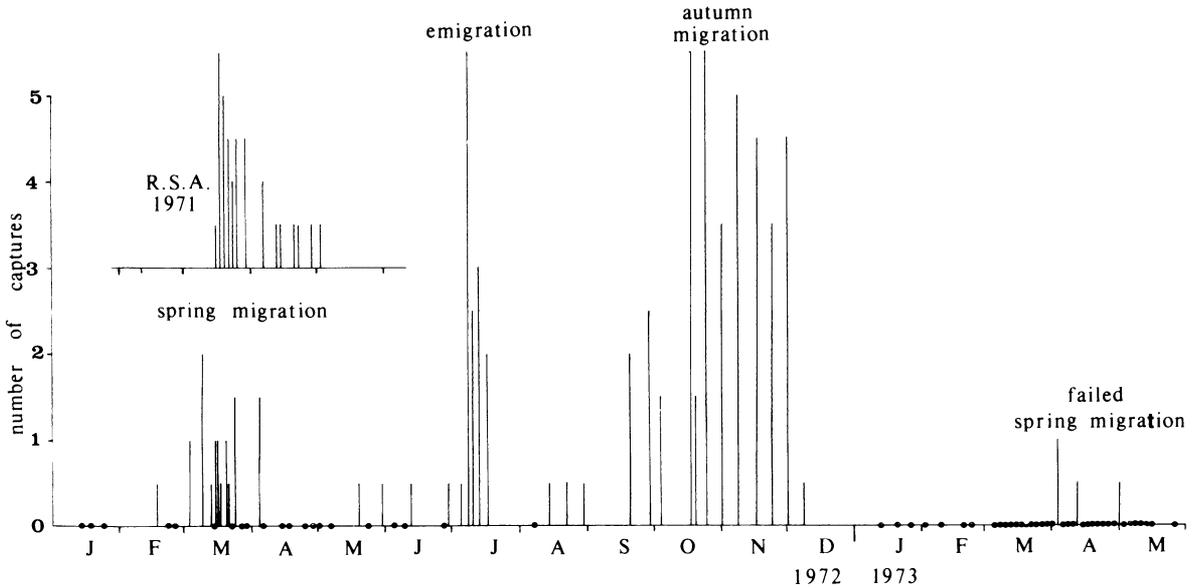


FIG. 13. Terrestrial activity at NC Arboretum, 1972–1973, and at a small pond in Oxford, 1971. Solid circles indicate no captures.

smaller population contained more younger adults than the larger populations, which is what would be expected if exchange of individuals between the populations consisted largely of juveniles. Similarly, very small populations are usually comprised of much younger (smaller) adults than average, which would be expected if they are maintained largely by the infrequent immigration of juveniles. These facts are capable of bearing other interpretations, however, and can be accepted only with reserve.

Hibernation was not observed. Most terrestrial animals disappeared during October, the youngest juveniles disappearing first. Autumn migrants and overwintering larvae are active to some extent

throughout the winter, since they are sometimes caught in underwater traps at this time.

DISCUSSION

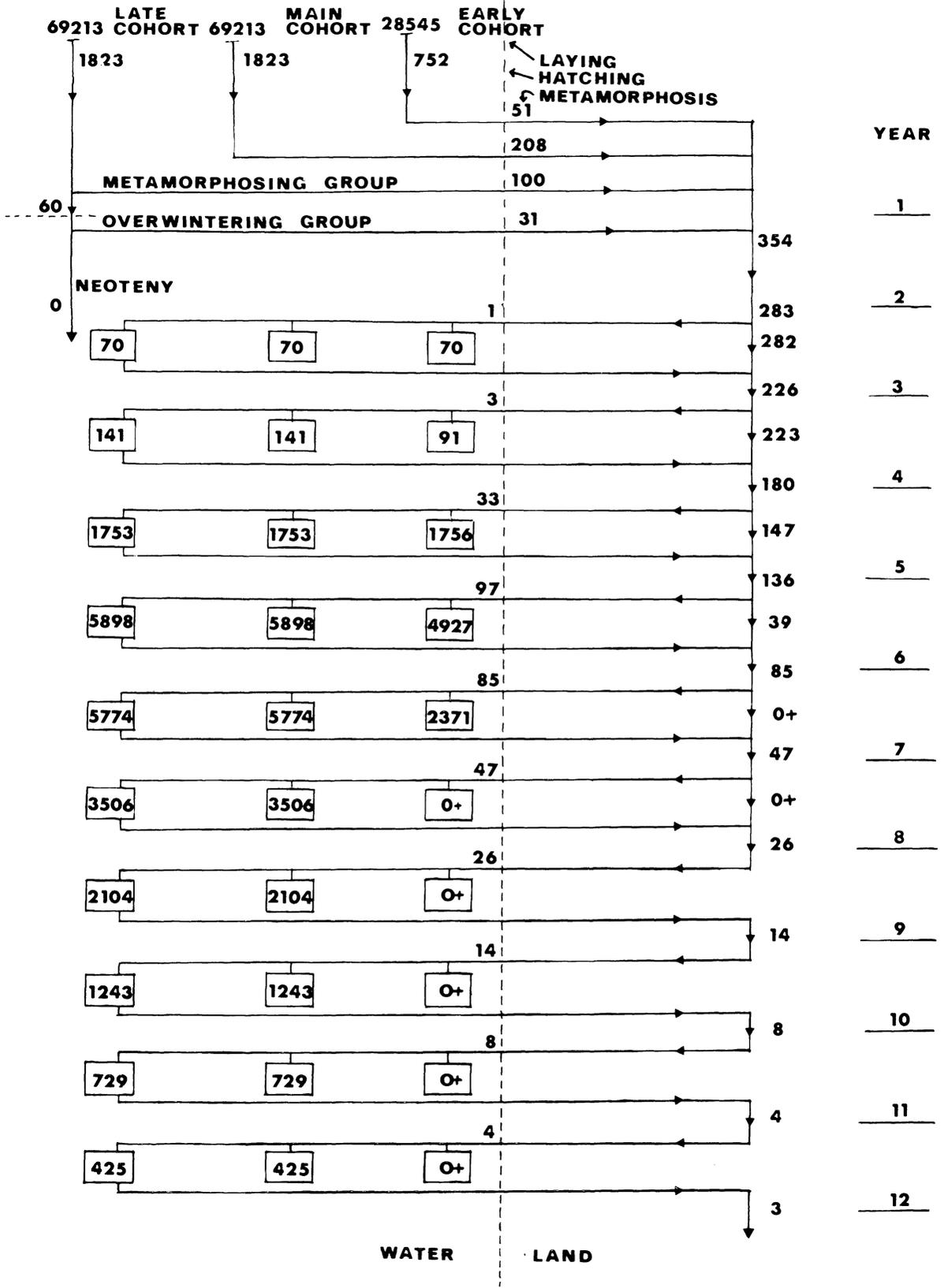
The principal events of the life history are summarized in Fig. 14, where an attempt has been made to estimate the frequencies of different types of behavior (further data in Bell and Lawton 1975).

The essential feature of the life history is a shuttling to and from the water, but this basic pattern is capable of considerable variation. An individual may take any one of the many possible "routes" through the life history, depending on whether it is born into the main or the late larval cohort; whether it metamorphoses in the same year, or overwinters in the pond; whether it matures early or late in life; and so forth. Any such route passes through several distinct ecological niches, without passing through them all; thus, the niche occupied by a larva in the pond during winter can be experienced only by an overwintering late cohort larva, which thereby loses the opportunity of experiencing the niche occupied by a larva participating in a mass metamorphosis. A more extreme exam-

TABLE 9. Movement of marked juveniles at Drayton. Explanation in text

Parameter	Distance (in metres) from point of release						Total
	0	2.5	5	7.5	10	>10	
Total captures	13	16	6	14	32	22	103
Recaptures	4	3	0	0	0	0	7

FIG. 14. Flow diagram for the life history. The early, main and late cohorts are derived from the 3 separate oviposition periods in each breeding season. Each cohort is started with the number of eggs laid during the relevant oviposition period by a population of 1,000 ♀♀ which have the age structure and the schedule of maturation of the NC Arboretum population in 1972. Numbers next to lines represent the number of surviving ♀♀ using a particular pathway, calculated from rates of survival measured at NC Arboretum; for example, 97 of the 136 ♀♀ estimated to survive until the 5th year of life enter the water to breed, while the remaining 39 have not yet matured and remain on land. The numbers in boxes represent the output of ♀ zygotes by mature ♀♀ calculated from the fecundity of Stadhampton ♀♀. Net reproductive rate can be calculated as the ratio of output to input of zygotes = $54839/166971 = 0.328$. This seems much too low, and is thought to have been depressed by abnormally heavy predation on the eggs and early larvae by the caddis fly, *Limnephilus*, during 1972 and 1973. The generation period of the population is ≈ 7.6 years.



ple is provided by neoteny. Moreover, each route apporitions its time differently between the niches through which it passes; thus an individual which matures late in life will spend comparatively little time as a breeding adult in the pond. A newt cohort might be thought of as navigating a landscape of ecological niches. Each individual may "choose" from a large but finite number of routes, which differ not only in the niches through which they pass, but also in the time that they take to traverse different parts of the territory. This situation is common to most animals; newts are interesting because their niches are discontinuous. This is why the number of possible routes, although large, is not infinite. In Fig. 14 there are at least 33 possible routes.

The complexity of the life history might influence the behavior of large populations in two ways, by increasing the quantity of genetic variation and by enhancing numerical stability. In the first place, the presence of several distinct ecological niches in the environment relaxes the conditions under which simple genetic polymorphisms are stable (Levene 1953), especially if individuals are able to "select" the niches that they occupy (Maynard Smith 1970). This effect may be strengthened by the fact that individuals occupy the available niches for varying lengths of time. Giesel (1972a) has argued that the effect of fluctuations in age structure, which are so pronounced in newt populations, will be to retard the loss of genetic variation under selection, and it is possible but unproven that such fluctuations may be capable of maintaining quasistable polymorphisms. Since nearby ponds are usually dissimilar, a population may be further enriched by migration. These effects will be opposed by the skewed sex ratio and, of course, by the small effective size of most populations. Secondly, the long generation period and the occupation of several distinct niches may moderate fluctuations in population size, since a disaster in any one niche will not cause the extinction of the entire population. The dampening of fluctuations in population size caused by the "spreading of risk" is discussed by Reddingius and den Boer (1970).

A stable population size and a rich store of variation are, of course, extraordinarily convenient properties for a species which inhabits a heterogeneous set of changeable habitats, but it is possible to argue that all the major features of the life history have evolved through individual selection. For example, after attaining maturity, smooth newts breed in every subsequent year for as long as they survive, rather than making a single suicidal reproductive effort. The conditions under which selection will favor iteroparity (breeding repeatedly) rather than semelparity (breeding only once) have been investigated by Cole (1954), Gadgil and Bossert (1970), Charnov and Schaffer (1973), Goodman (1974) and Bell (1976), among others. The consensus view is that iteroparity will be likely to

evolve when survival during the 1st year of life is low, and when maturity is delayed; both conditions are satisfied by smooth newts. More precisely, it is possible to calculate the increase in fecundity necessary to equate the fitness of semelparity with that of iteroparity, the presumption being that semelparity is unlikely to evolve if it would necessitate an "unreasonable" increment in fecundity. For an annual species, Charnov and Schaffer (1973) show this increment to be about p/s , where p is the average annual rate of survival of adults, and s the rate of survival during the 1st year of life. A semelparous smooth newt breeding in its 1st year of life would have to produce $\approx(0.55/0.0025) = 220$ more eggs in order to match the fitness of an iteroparous individual which first bred at that age. Delayed maturity will increase this figure. But the annual production of somatic tissue by mature newts is equivalent to only ≈ 1.13 kJ, or ≈ 0.047 g of ovarian tissue. If all of this were utilized in reproduction, it would be sufficient to produce only ≈ 50 more eggs. To produce 220 extra eggs at the age of 3 yr would involve metabolizing $>80\%$ of the total body weight, long before which the animal would be dead. Thus, in smooth newts, there are straightforward reasons for the evolution of iteroparity. Murphy (1968) and Hairston et al. (1970) have also shown that iteroparity may be an appropriate response to environments which fluctuate with a period shorter than the length of a generation, as small ponds sometimes do.

In certain circumstances, and especially in colonizing organisms which have high intrinsic rates of increase, the age at first reproduction may be the single most important determinant of fitness, and selection is expected to make its variance very small (Lewontin 1965). The existence of delayed maturity and of extensive variation in the age at maturity of the smooth newt is therefore puzzling. However, although in general fitness is maximized by maturing as soon as possible, this may not be true in at least one set of circumstances commonly encountered in nature. Consider a species in which fecundity increases with age, and in which juveniles survive better than adults. An individual which reproduces for the first time in a given year realizes a part of its potential fitness, at the cost of reducing the probability that it will survive until the following year. Further, by delaying maturity until the following year, its fecundity when it did reproduce for the first time would be greater, since fecundity is known to increase with age. Clearly, it might be advantageous to delay maturity, depending on the ratio of juvenile to adult survival, and on the rate at which fecundity increases with age. Some undefined joint function of juvenile survival and of the rate of increase in fecundity with age will determine whether it is advantageous to delay maturity or to mature as soon as possible, and this function may therefore take values at which some intermediate maturity age is optimal. This problem has been explored theoretically by Bell

TABLE 10. The relative fitness of ♂♂ and ♀♀ which reproduce for the first time at different ages. Fitnesses are calculated from life tables, as explained in the text

Sex	Age (yr)				
	3	4	5	6	7
♀♀	0.940	0.973	0.980	0.990	1.000
♂♂	...	1.000	0.951	0.924	0.913

(1976, personal observation). A further possibility is that selection may act differently in the two sexes, since the rate of increase of fecundity with age is likely to be different in males and in females. Using data on survival and fecundity presented above, the fitness (as a relative finite rate of increase) of maturing at a given age can be calculated, giving the results found in Table 10.

The calculation for males assumes that mating is partially assortative with respect to age, so that male fecundity increases with age, and if this assumption is discarded, late maturity becomes even more disadvantageous. In females, however, delayed maturity may be favorably selected if age-specific fecundities are influenced by an energy cost of reproduction. Thus, selection may act in different directions in the two sexes, if the energy cost or reproduction in males is negligible. This would tend to retard the loss of genetic variation from the population, and in certain circumstances will support a stable polymorphism (Owen 1953; Bennett 1957; Haldane and Jayakar 1964).

Similar arguments can be advanced to explain the other major features of the life history. For example, Bell (1976) has discussed the adaptive significance of dividing oviposition into two major periods in each breeding season. The autumn migration of newts which are about to reproduce for the first time is more difficult to interpret. The observed behavior is phenotypically intermediate between the two extremes of autumn migration in every year of adult life, and spring migration every year. Autumn migrants gain somewhat in fecundity by contributing exclusively to a third, early oviposition period (Bell and Lawton 1975), but probably suffer more mortality in the water than they would have done on land. These factors will influence net fitness, and one extreme strategy or the other will be fittest; it is not possible for an intermediate strategy to be more fit than both extremes. It is easy to show that, being phenotypically intermediate, the observed pattern of migration is also intermediate in fitness between the two extremes. However, which extreme strategy is the more fit will depend critically on rates of survival during the life history, which appear to vary considerably from year to year. The observed behavior may be more fit than one extreme in a given year, and more fit than the other extreme in the following year. On average, it might be a strategy which involves the least risk in a fluctuating environment.

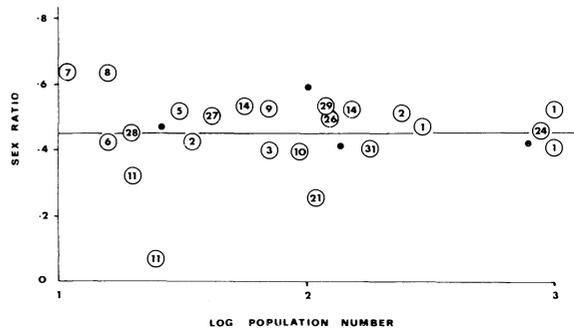


FIG. 15. Relationship of the sex ratio to population number. Data are from Tables 5 and 7. Numbers identify populations listed in legend to Fig. 1; more than 1 value indicates data for >1 year. Solid circles refer to populations not on the main survey area. The horizontal line is the weighted \bar{x} adult sex ratio of all populations.

Only in the case of the sex ratio is it possible to test the two competing hypotheses of individual and group selection in a wholly satisfactory manner. Several authors have suggested that an equal sex ratio at maturity benefits the population by maximizing reproductive output and genetic variance, and has evolved through group selection (e.g., Crew 1927; Kalmus and Smith 1960); skewed sex ratios may regulate reproductive output or allow faster initial adaptive response to a changing environment (e.g., Wynne-Edwards 1962; Giesel 1972b). Edwards (1960) has strongly criticized these interpretations, and it is now established that individual selection will normally result in an equal sex ratio at some time between birth and the end of parental care (Fisher 1958; Bodmer and Edwards 1960; Leigh 1970). Data for smooth newt populations supports this interpretation, the sex ratio being equal in juveniles and skewed in adults. Williams (1966) suggested an ingenious test of the two theories. If group selection operates to maximize reproductive output, the sex ratio will be nearly equal at low population densities when it is important to maximize the probability that two randomly chosen individuals are not of the same sex, and will thereafter decline as population density increases, since a few males are capable of inseminating the entire female population. If group selection acts to regulate population size at some intermediate optimum, then the proportion of males will increase with increasing population density. If only individual selection is effective, an equal sex ratio will be maintained at all population densities. Andersen (1961) surveyed the available data and concluded that there was no evidence that group selection was capable of influencing the sex ratio. Figure 15 presents data for newt populations on the main survey area. No precise data are available for population density, but, in general, large bodies of water support small newt populations, while the largest populations are found in quite small ponds. The 2 largest and the 2 smallest populations shown on this figure are certainly

the two densest and the two least dense respectively. The sex ratio is not correlated with population size, and so is probably influenced primarily by individual selection.

In conclusion, different life-history strategies can be shown to possess different fitnesses, and if they are to some extent under genetic control they will respond to individual selection. Verbal and numerical arguments suggest that the major features of the observed life history are compatible with this interpretation although these arguments are demonstrably weak, except in the cases of iteroparity and the sex ratio. Natural selection on the level of the individual will have statistical consequences at the level of the population, and it has been suggested above that these consequences will include increased genetic variation and numerical stability. Although these are obviously relevant to the problems faced by an animal which occupies an unstable environment, it is not necessary to postulate that they have arisen through group selection, or that they constitute biotic adaptations.

ACKNOWLEDGMENTS

I received constant help and encouragement from my supervisor, Dr. J. H. Lawton. The detailed analysis of the length frequency distributions presented here was stimulated by criticism from Professor M. H. Williamson and from Dr. J. Beddington. I am especially grateful to John Byrne, who wrote and ran autocorrelation and trend-fitting programs, besides giving a great deal of salutary advice. I am also indebted to Mr. K. Burras of the University of Oxford Botanic Garden for permission to sample at the Arboretum pond. Useful criticism has come from Harm Gross, Paul Handford, John Pernetta, Tom Reimchen and Dr. H. N. Southern, and I am grateful to Bob Abel for teaching me the technique of bomb calorimetry. This work was supported by a Christopher Welch Scholarship from the University of Oxford.

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