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Jon LOMAN

Department of Animal Ecology, University of Lund, S–223 62 Lund, Sweden

GROWTH OF BROWN FROGS *RANA ARVALIS* NILSSON AND *R. TEMPORARIA* L. IN SOUTH SWEDEN

ABSTRACT: *Rana arvalis* Nilsson breed for the first time at an age of 3 or 4 years and a size of over 40 mm (snout-urostyle). They cease growing at a mean size of 54 mm. Corresponding values for *R. temporaria* L. usually are 2 or 3 years, 50 mm and 69 mm. The mean size of frog during its third winter is 40 and 62 mm respectively. Both species grow less fast at higher ages. Both species develop full-sized eggs more than a year before they breed for the first time. Mature females breed every year.

KEY WORDS: Growth, population dynamics, *Rana arvalis* Nillson, *R. temporaria* L.,Anura.

Contents

1. INTRODUCTION

Little information is available on the growth of European brown frogs (*Rana* part). Van Gelder and Oomen (1970) estimated the growth during the first two years of *Rana arvalis* Nilsson from the successive size distributions of animals caught continuously during several years. Kauri (1959) estimated the growth of *R. arvalis* and *R. temporaria* L. from the discontinuity in the relation: length of metatarsal tubercle/length of body. This is caused by the fact that the former continues to grow during the winter. The aim of the following study is to provide further information on the growth of these common frogs and to relate this to their age at maturity.

Both these two species are terrestrial as adults. They have a concentrated breeding period that in the study area falls in the end of March or beginning of April and lasts for up to two weeks. The young frogs metamorphose the same summer.

A preliminary summary of a part of the present study has been published previously (L o m a n 1976).

2. MATERIAL AND METHODS

The study was conducted in the vicinity of Stensoffa ecological station, University of Lund. This is situated in south Sweden (55° 40'N, 13° 30'E). Due to the presence of moist, ungrazed meadows close to suitable breeding ponds the density of brown frogs is high.

The growth of young frogs was estimated indirectly from the size distribution of frogs during different seasons. These frogs were caught in 24 trapping pits, 25 × 60 cm wide and 40 cm deep. Twelve pits were dug in a moist meadow, close to pond where both species breed and twelve in a moits birch-wood, 500 m from the meadow. These pit-falls were used from July 1972 to October 1974. Both habitats and all years are lumped in the compilations. This should increase the generality of the results.

The growth of older frogs was measured directly on individually marked (with toe-clipping) frogs that were recaptured either during the year of marking or the next. They were freed immediately after marking. They were captured by hand in a 50 × 50 m large plot in meadow habitat during the years 1972 through 1976. When calculating growth within one season, only growth intervals at least 20 days (*R. arvalis*) or 10 days (*R. temporaria*) were included. The latter is the faster growing of the two species. All measurements of length refer to snout-urostyle.

Weight of ovaries was measured on frogs caught August 21 to September 2, 1975. When comparing their size to that of animals caught during breeding migrations in the spring it is assumed that they did not grow any more before the winter. Only length of testes was measured and it turned out that this measurement was too crude to give any information on maturity of males. A 15 m long trapping trench was dug alongside a breeding pond. This was operated during the springs of 1973 and 1974.

One of the drawbacks with these data is that the breeding and non-breeding frogs did not belong to exactly the same populations and were not always measured during the same years. The breeding pond was situated 800 m away from the plot where the tagging was done and from which I have taken the non-breeding size distribution data. The ovary sizes were measured on frogs in the environment of this plot too. However, a breeding pond probably draws its frogs from a wide variety of habitats and should be fairly representative for the year in question. The mean size of the frogs in the tagging plot during summers of 1973 and 1974 was 46 and 48 mm (*R. arvalis*) and 56 and 57 mm (*R. temporaria*) as compared to 47 and 57 mm for the whole study period so these years do not seem to have been exceptional. Also, the habitat in which the tagging plot was situated seems to have been fairly representative for the whole range of habitats in the area (up to 3 km away). In 1974 22 plots were sampled by hand catching and the mean size of these animals were 44 (*R. arvalis*, $N = 42$) and 58 mm (*R. temporaria*, $N = 76$). All these samples were taken during the end of July and August and refer to frogs at least 40 (*R. arvalis*) and 50 mm (*R. temporaria*) in length.

3. RESULTS

3.1. GROWTH OF YOUNG FROGS

I have used the discontinuities in the size distributions to delineate probable age classes. With this method, the growth can probably be followed to the frogs' second winter. My age class grouping is indicated on Figures 1 and 2. During their first winter, the median size of *R. arvalis* were 22 mm and by their second 32 mm (Fig. 1). The median size of *R. temporaria* were 24 mm during their first and 50 during their second winter (Fig. 2). *Rana temporaria* are smaller at metamorphosis than *R. arvalis* but their metamorphosis occurred about two weeks earlier, last week of June and middle of July respectively. By winter they had grown about 12 mm as opposed to about 8 mm for *R. arvalis* (Table I). By June in their second summer *R. temporaria* had already increased to about 35 mm while most *R. arvalis* still were less than 30 mm (Figs. 1 and 2). The material on second-year *R. temporaria* is not very large but the low number of animals in the size 35–45 mm as compared to 45–55 mm during winter makes it very likely that most frogs are over 45 mm by their second winter and a median value of 50 mm seems likely. The aggregation of frogs around 50 mm in not due to a cessation of growth around this size, see below.

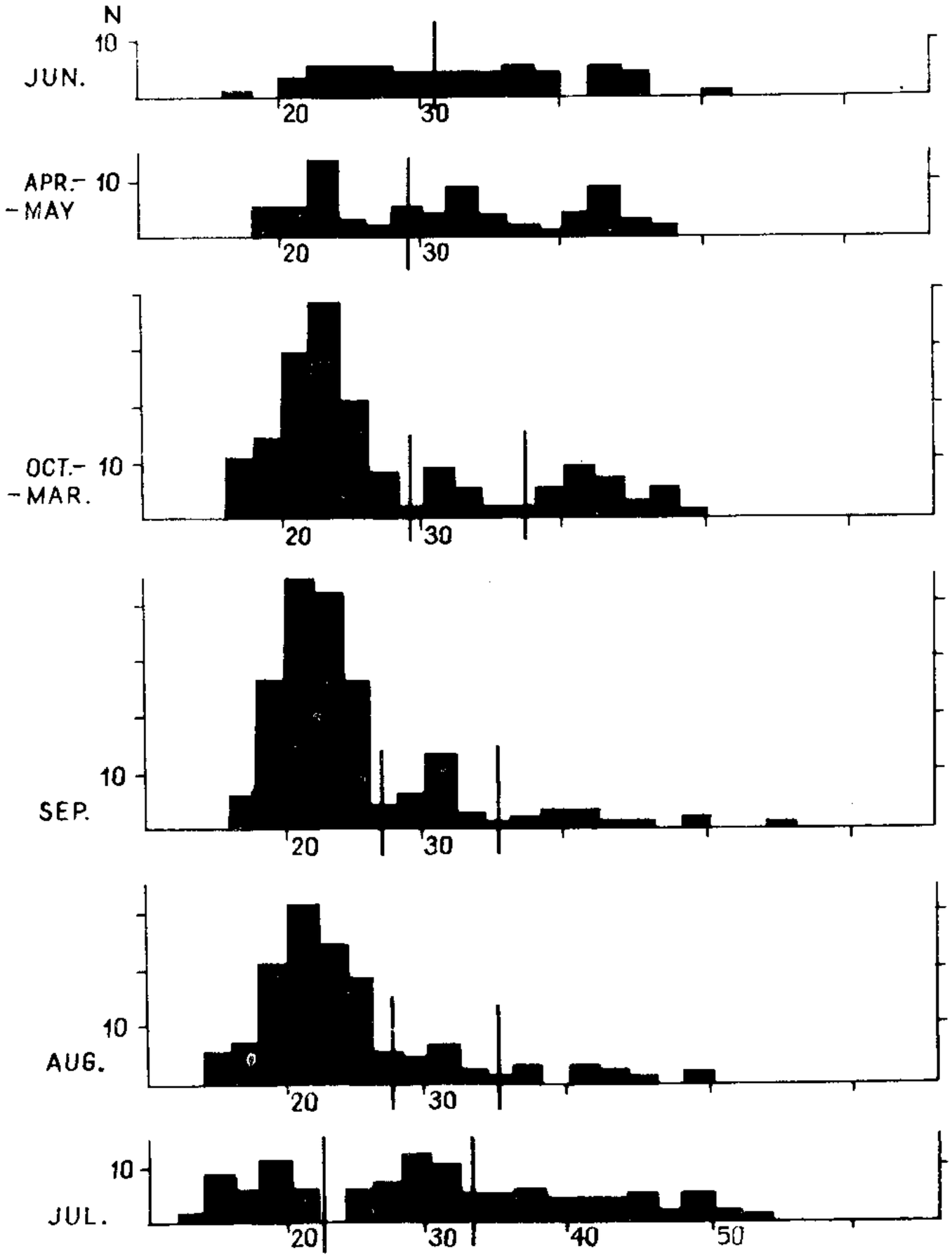

Fig. 1. Size distribution by 2– mm classes (30, e.g., represents 30 and 31 mm) of *Rana arvalis* Nilsson The frogs were caught in pit-falls from July 1972 to October 1974 incl. In each month or group of months frogs from all years and two sample sites are included. The vertical lines delimit the first and second age classes (exclusive of some overlap) according to my interpretation

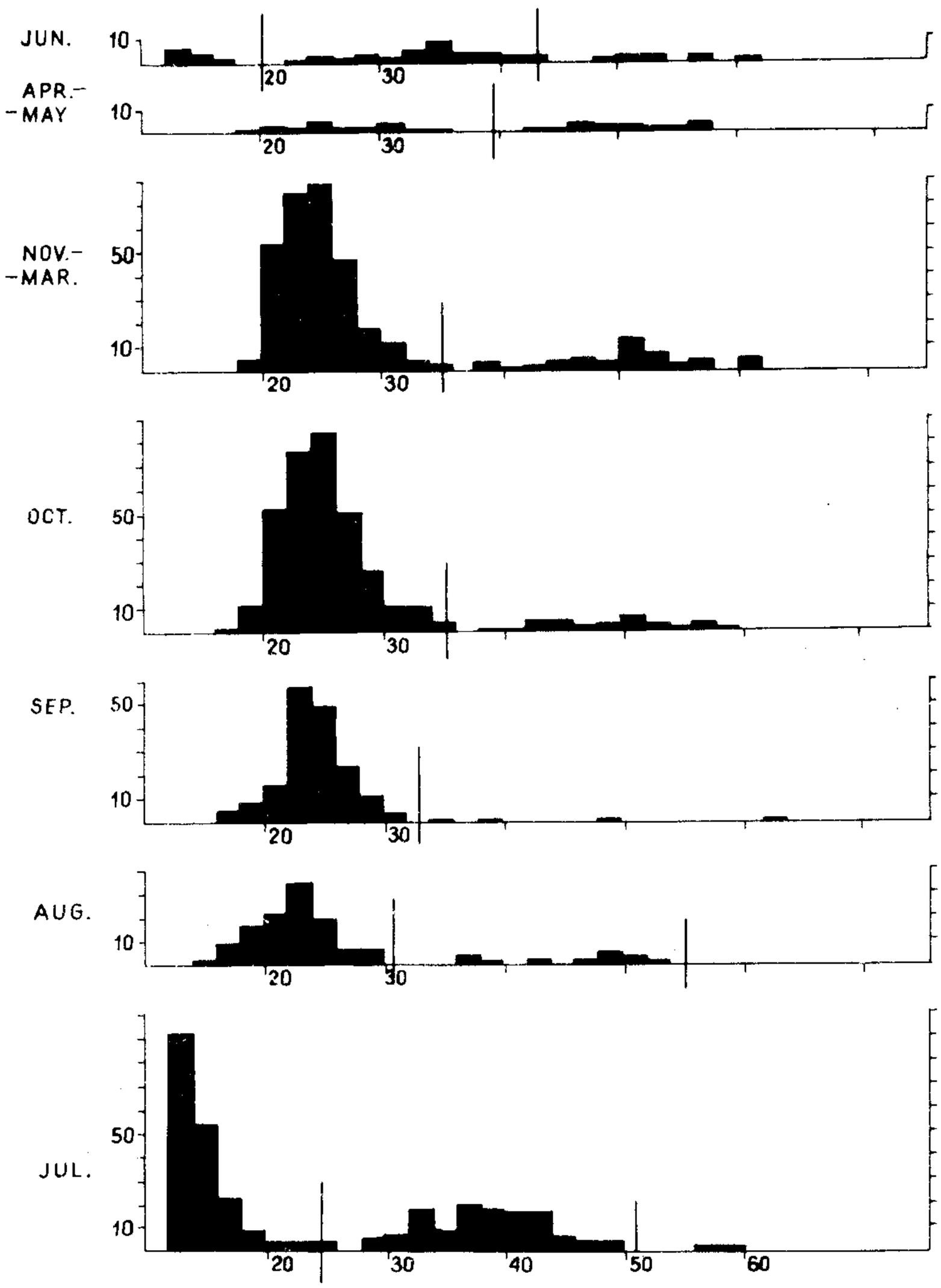

Fig. 2. As Figure 1 but for *Rana temporaria* L.

Table I. Size of juvenile brown frogs during their first summer and autumn

Frogs are regarded as juveniles up to the following lengths: *Rana arvalis* Nilsson – July – 22 mm, Aug. – 27 mm, Sept. – 27 mm, Oct. – 29 mm, Nov. – 29 mm, *R. temporaria* L. – July – 26 mm, Aug. – 30 mm, Sept. – 32 mm, Oct. – 32 mm, Nov. – 32 mm

Species	Average size and numbers	July	Aug.	Sept.	Oct.	Nov.
R. arvalis	$\bar{x}$ (mm)	17.2	20.7	21.3	21.3	22.4
	N	33	107	146	85	23
R. temporaria	$\bar{x}$ (mm)	14.3	22.0	23.6	24.0	24.0
	N	182	116	170	315	292

3.2. GROWTH OF OLD FROGS

In both species the differences between the growth rates of females and males were insignificant (Table II). Also, there was no difference between the mean size of all females and

Table II. Growth rates during summer and early autumn of adult brown frogs
Frogs at least 38 mm (*R. arvalis*) and 48 mm (*R. temporaria*) at the start of the measured growth intervals are included

Species	Groups and periods	Growth rate (mm/d)	*N*	Mean size of included frogs at the beginning of the growth interval (mm)
R. arvalis	All (July 9–Oct.7)	0.03	19	47
	Females	0.03	11	47
	Males	0.03	8	48
R. temporaria	All (July 9–Oct.7)	0.08	53	54
	Females	0.09	21	53
	Males	0.07	32	54
	Growth interval completely within the period July 9–Aug. 31	0.11	17	53
	Growth interval completely within the period Aug. 29–July 10	0.01	12	56

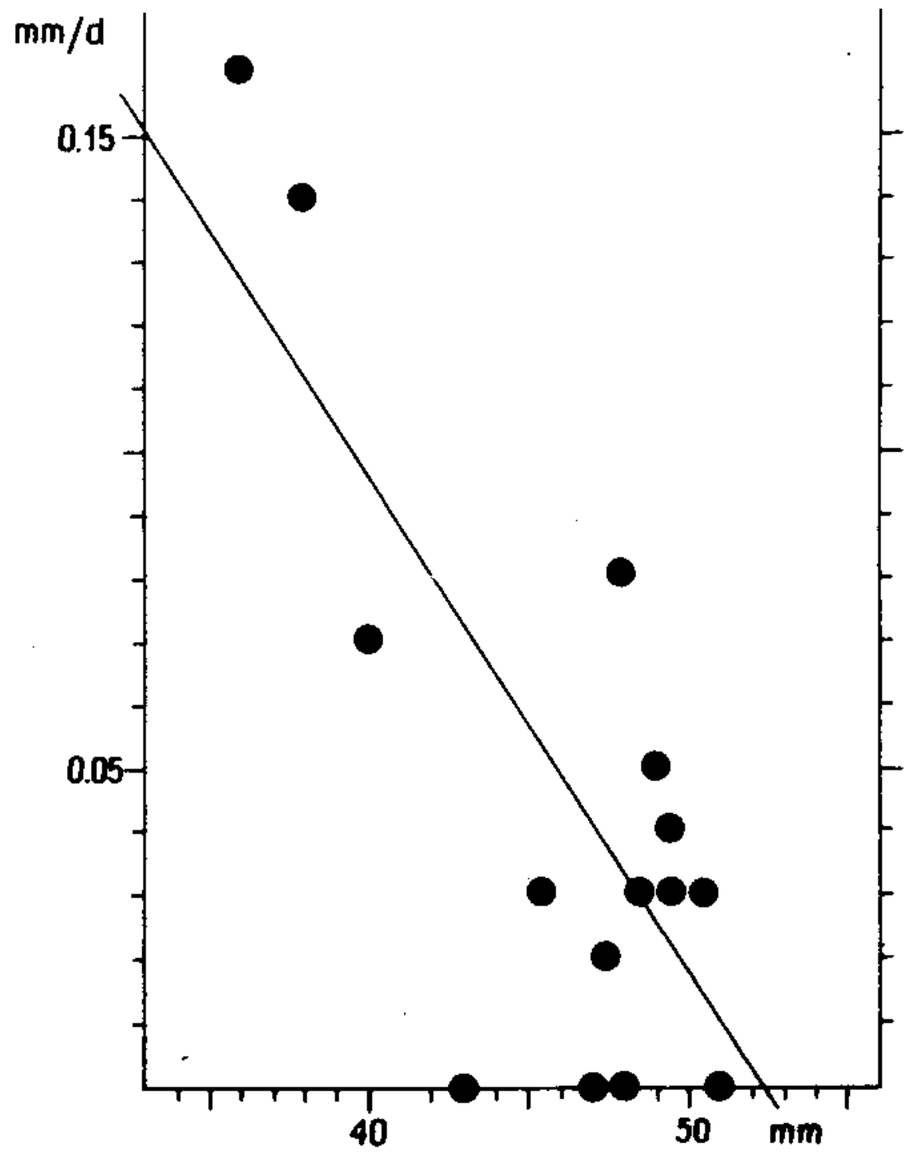

Fig. 3. Growth (mm/d) plotted against original size (mm) for *R. arvalis* caught twice in the same growth season. Only growth intervals at least 20 days long are included. Data from four years combined. The regression line is described by $G = -0.0078\,L + 0.41$ (G – growth in mm/d, L – initial length in mm); $r = -0.75$; $P < 0.001$

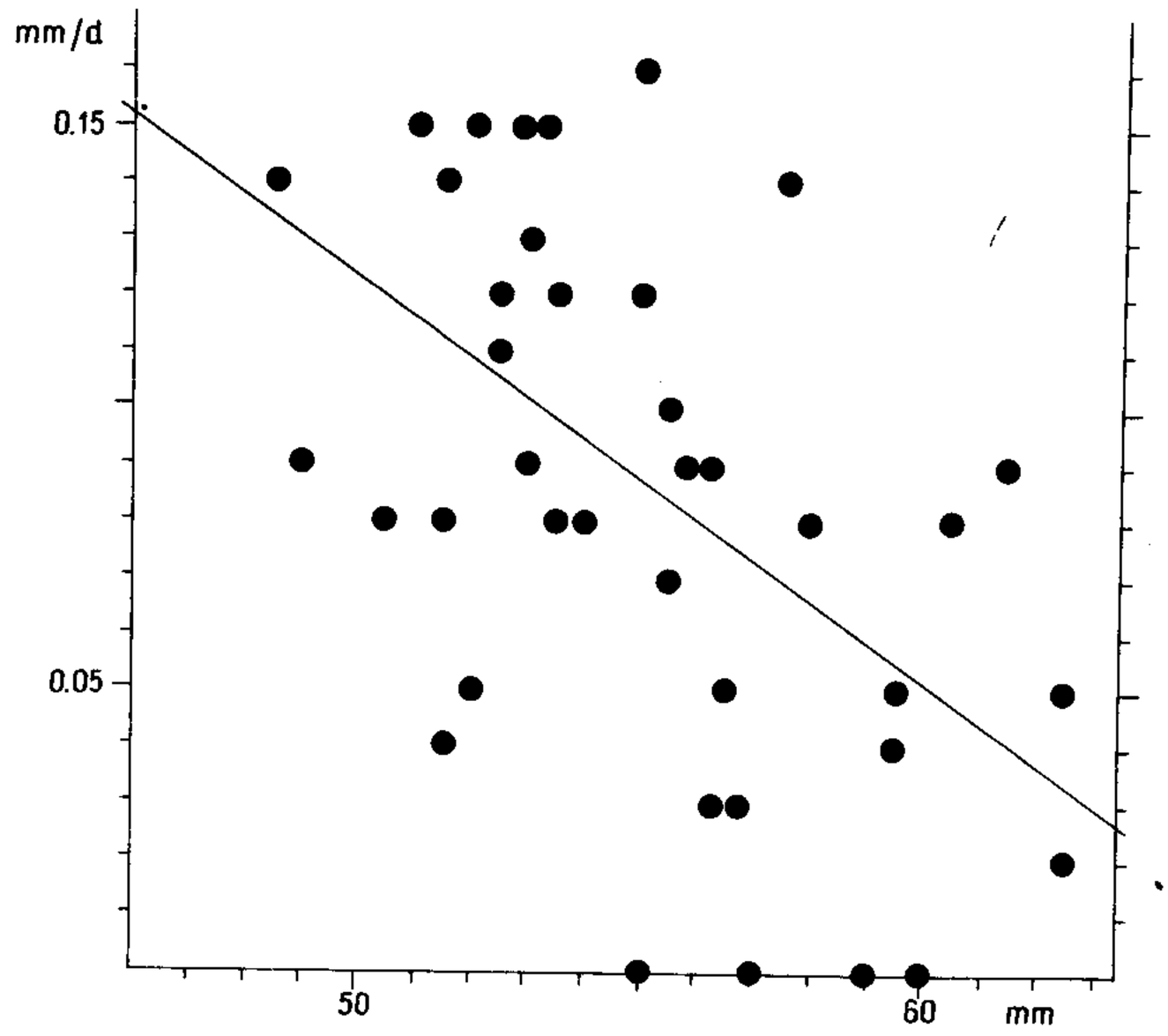

Fig. 4. As Figure 3 but for *R. temporaria*
Only growth intervals at least 10 days long are included. The regression line is described by $G = -0.0071\ L + 0.48$; $r = -0.54$; $P < 0.001$

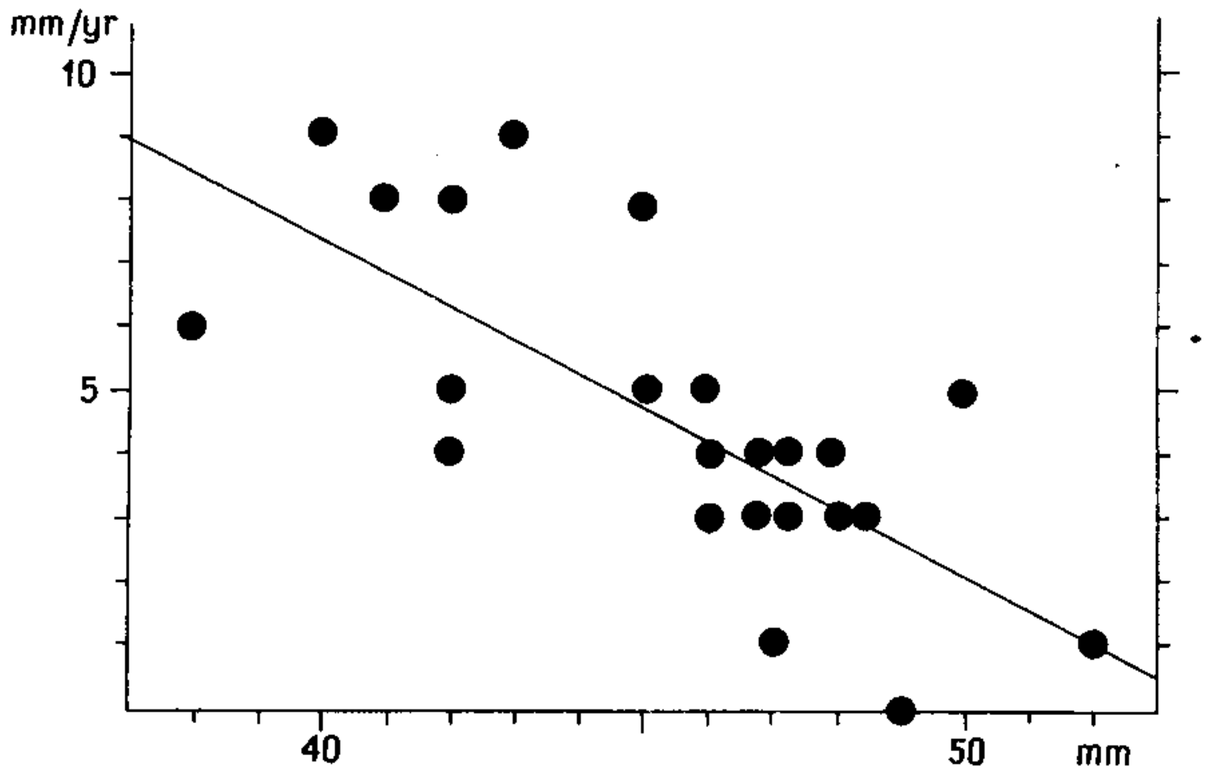

Fig. 5. Growth (mm/yr) plotted against original size (mm) for *R. arvalis* caught in successive years
Data from Figure 3 have been used to add or subtract length from measured increases so the values refer to exactly one year. Data from five years combined. The regression line is described by $G = -0.53\ L + 28.4$ (G – growth in mm/yr, L – initial length in mm); $r = -0.71$; $P < 0.001$

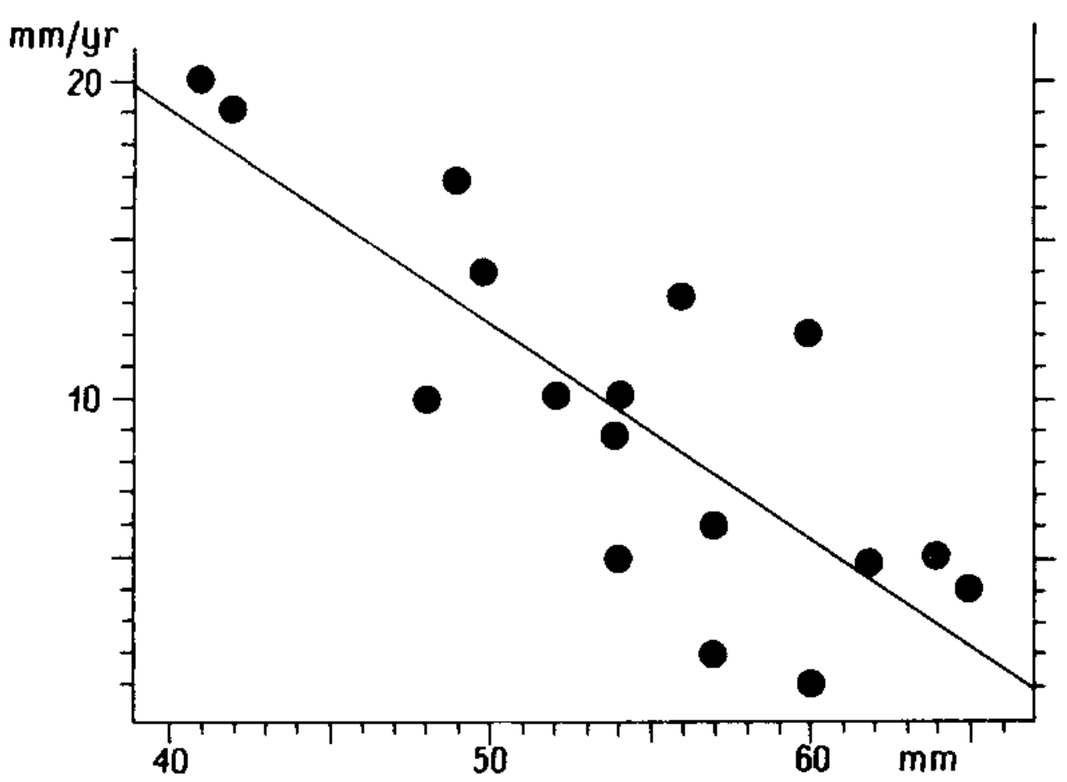

Fig. 6. As Figure 5 but for *R. temporaria*
The regression line is described by $G = -0.67 + 45.8$; $r = -0.81$; $P < 0.001$

G= -0.67L + 45.8

males caught during the five years in the tagging plot: *R. arvalis*, females 47.3 mm ($N = 153$), males 47.2 ($N = 134$) (animals at least 40 mm included), *R. temporaria*, females 57.0 ($N = 96$), males 56.5 ($N = 174$) (animals at least 50 mm included). *R. temporaria* had practically ceased growing in September (Table II). Too few *R. arvalis* were caught at least twice that late to make a similar analysis. Both species grew less the larger the individuals were (Figs. 3 and 4). This was also clear from the data on frogs caught in successive years (Figs. 5 and 6).

3.3. SIZE AT MATURITY

These is a clear discontinuity between frogs with small (as a percentage of total body weight) and large ovaries. The large ovaries contain pigmented eggs while the smaller do not, or at most single ones. The switch from small to large ovaries occurs between a length (during the winter after the large ovary is formed) of 32 to 36 mm (*R. arvalis*, Fig. 7) and 39 to 44 mm (*R. temporaria*, Fig. 8). From the size distribution of animals that participated in breeding migrations it is, however, clear that all females with large ovaries did not take part in the breeding (Figs. 7 and 8). The smallest animals captured during breeding migrations were 40 mm (*R. arvalis*) and 50 mm (*R. temporaria*). If the distribution of all animals at least 40 and 50 mm is compared to that of those that took part in the breeding migrations, and presumably bred, it is suggested that only from a size of 50 mm (*R. arvalis*) and 57 mm (*R. temporaria*) did all animals breed (Figs. 7 and 8).

As the distribution of relative ovary sizes for larger frogs was relatively homogeneous (Figs. 7 and 8) it is probable that, having bred once, the females breed every year.

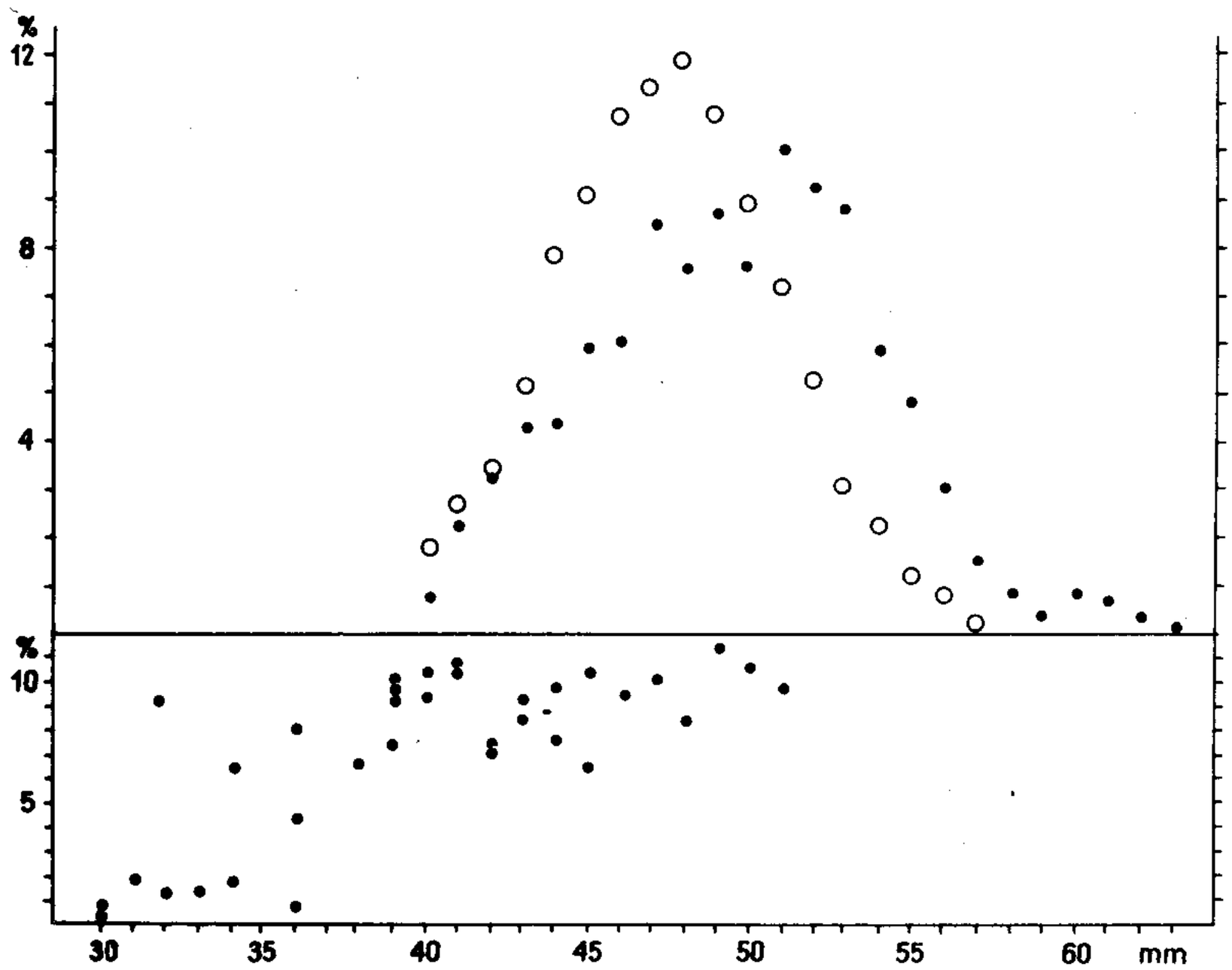

Fig. 7. Lower part of the diagram gives the size of the ovaries from *R. arvalis* in percent of total weight plotted against length of the female. The animals were captured and measured August 21 to September 2 1975. On the upper part, the solid spots give the size distribution of frogs that were caught in pitfalls during their breeding migration in 1973 and 1975 (N = 102 and 74 respectively). The open spots give the size distribution of all frogs caught by hand in a meadow plot during the summers (July 20 to October 6) of 1972 to 1976 inclusive. Using Figure 3 and assuming that no growth takes place after September 1, the lengths have been recalculated to correspond to the expected winter size. Animals at least 36 mm long were measured and those with an expected winter size of at least 40 mm were included in the Figure. The total sample size is 274 animals

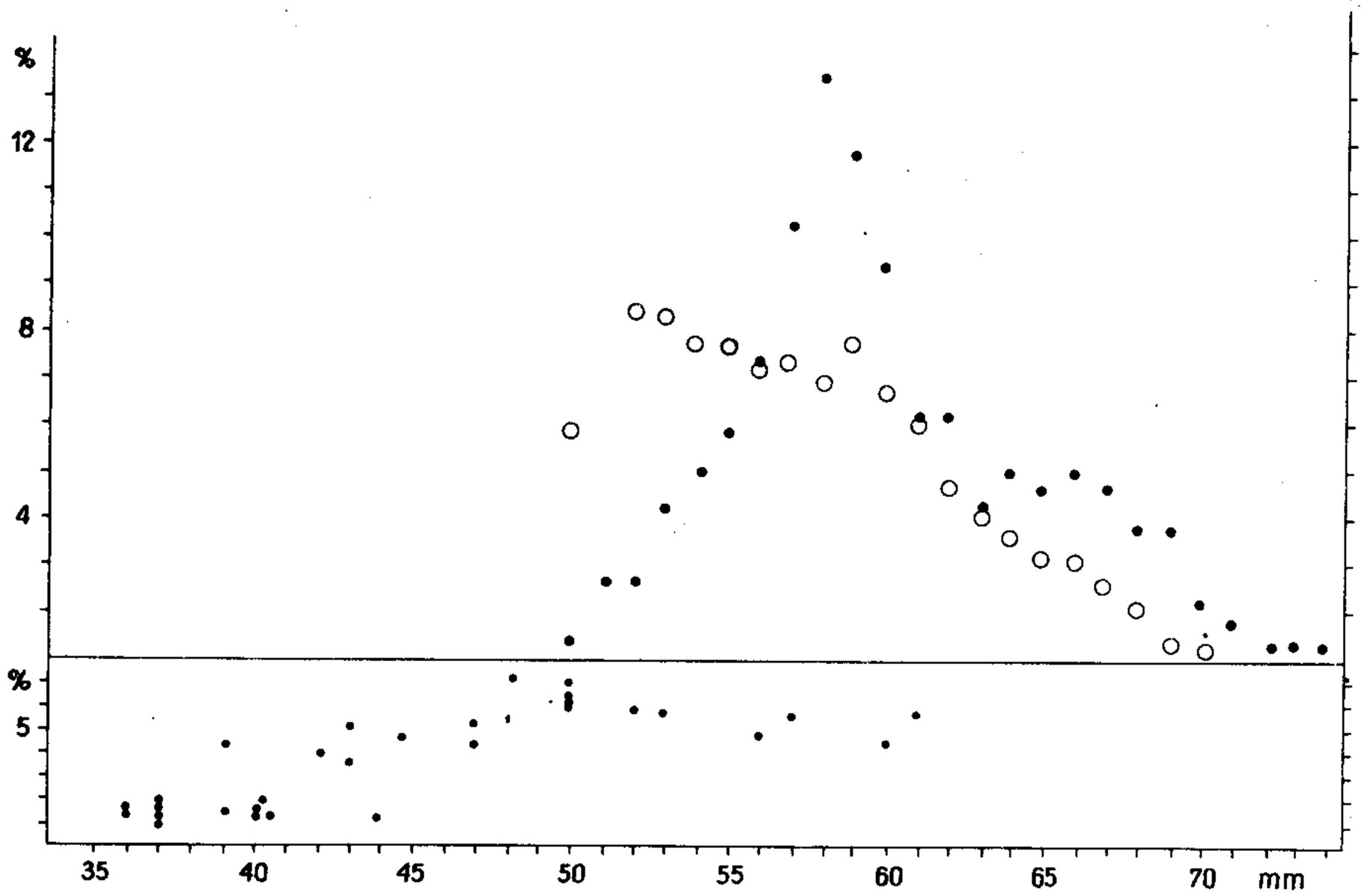

Fig. 8. As Figure 7 but for *R. temporaria*

The number of breeding frogs was 49 and 23 for 1973 and 1974 respectively. The total number of non-breeding animals caught 1972–1976 is 270. Animals over 46 mm long were measured and those with an expected winter size of at least 50 mm included. As a frog that is 46 mm by July 20 can be expected to have an winter length of 52 mm the classes of 50 and 51 mm are somewhat underrepresented. This will however decrease the difference between the two distributions

4. INTERPRETATIONS AND COMPARISONS

The growth pattern of anurans is not well known. The model that seems to fit the available data best, mine as well that of other studies, is one where every individual frog grows, at a decreasing rate, to an individual definite size. A similar pattern, the logistic growth curve, was assumed by Standaert (1967 after C l a r k e 1974). For larger frogs the decline in growth rate with size will be nearly linear. I have used this in my model as my data are not sufficient for a more detailed analysis. According to my data, an average *R. arvalis* will cease growing at a length of 53 mm (data from within on growth period, Fig. 3) or 54 mm (data from successive growth periods, Fig. 5) and an average *R. temporaria* at 68 mm (Fig. 4) or 69 mm (Fig. 6). The largest measured individuals in the populations were 56 mm and 70 mm respectively ($N = 287$ and $N = 270$).

Table III. Estimated average sizes of frogs at different ages
The estimations are based on data from Figures 1, 2, 5 and 6 and are commented in the text. Size in mm length (snout-urostyle)

Species	Metamorphosis	Winter 1	W 2	W 3	W 4	W 5	W 6
R. arvalis	14	22	32	40	47.5	51	52.5
R. tempararia	13	24	50	62	66	67.5	68

A hypothetical growth curve that is consistent with my data is given in Table III. Up to a size of 32 mm (*R. arvalis*) it is based on Figure 1. I have had difficulties to estimate their growth during the second full summer. I have put it at 8 mm as it is not likely that they should grow more (in mm/year) than during their first full summer and assuming that they grew less would imply (Fig. 5) that they grew more during their third than during their second full summer. From 40 mm on Table III is based on Figure 5. Up to a size of 50 mm (*R. temporaria*) Table III is based on Figure 2 and from then on Figure 6.

If the average lengths in Table III are compared to the data on ovary size and size of breeding frogs, the following conclusions emerge:

– Some females of *Rana arvalis* have developed ovaries with mature eggs by their second winter at a size of 32 to 36 mm. Some however do not do so until their third winter as e.g. the 36 mm long female with immature ovaries (Fig. 7) that hardly is in her first winter (Fig. 1). To judge from Figure 1, few, if any, frogs are 40 mm by their second winter so probably no two-year old ones breed. At an age of three years many, probably those that had mature eggs the year before, breed. Comparison of the upper two size distribution on Figure 7 indicates that some frogs in the size interval 40–47 mm do not breed. These are probably fast growing three years old frogs. It seems less likely that they are slow-growing four years old ones.

The conclusion that some, perhaps all, young frogs have large, apparently mature eggs, but do not breed until the next year is further confirmed by an other, independant observation. During breeding time, 3 specimens, 35 mm long, of *R. arvalis* were found well away (> 300 m) from all breeding congregations. As they were strikingly thick I dissected them and found 185–405 mature eggs. This strategy is explained if the risk of predation during breeding migration and breeding is large. It might then be more profitable for a female frog to spend one more year in relative security and the lay a larger clutch than to stand the risks involved in breeding if she anyhow only will produce a small clutch.

Most of *Rana temporaria* are over 40 mm by their second winter and have then developed mature eggs (Figs. 2 and 8). Most probably do not breed until one year later at a size of more than 55 mm. Those 50–55 mm long frogs that breed are either fast maturing two years old ones or, more probably, slow growing three years old ones. It seems likely that the strategy of delayed breeding occurs also in *R. temporaria.* This species probably breeds at an earlier age than *R. arvalis,* three years as opposed to three or four years of age.

Van Gelder and Oomen (1970) recorded a faster growth of *R. arvalis* in the Netherlands than I found in south Sweden. Their results indicate that the animals reached a length of 28 mm by their first winter and 40 mm by their second. Kauri (1959) found that *R. arvalis* from south Sweden reached 24 mm by their first, 37 mm by their second and 52 mm by their third winter. He found that *R. temporaria* from south Sweden reached 40 mm by their first, 60 mm by their second and 80 mm by their third winter. However, the step-wise relation on which his age class grouping is based is not very clear and the method may be less safe than the one I have used, especially for higher ages. The ecological vicariant of these species in North America is *Rana sylvatica* Le Conte. This was studied by Bellis (1961) in northern Minnesota. These frogs metamorphose, like the ones studied above, in the middle of the summer. Females bred in the spring nearly three years later, also this in agreement with the Swedish species. The males however bred one year earlier. There was no indications of such a difference between the sexes for *R. arvalis* and *R. temporaria.* Another difference is that *R. sylvatica* nearly completely ceased growing by the time of sexual maturity while this only occurred at least one year later for the two species studied here.

Thomas Madsen, Sten Nordström and Sten Rundgren have given helpful comments to the manuscript.

5. SUMMARY

The growth of *Rana arvalis* Nillson and *R. temporaria* L. was studied by analyzing the size distribution of young frogs captured continually for a succession of years (Table I) and with help of recaptures of marked adult frogs (Figs. 1, 2, Table II). The development of ovaries from frogs of different sizes was analyzed (Figs. 7, 8). Both species breed in spring. *R. arvalis* grow to 40 mm (mean value) by the third winter and cease growing altogether at a size of 54 mm (Table III). The corresponding values for *R. temporaria* are 50 mm and 69 mm (Table III). *R. arvalis* breed for the first time at an age of 3 or 4 years. *R. temporaria* do so at an age of 3, or in some cases possibly at 2 years. Both species may develop full-sized eggs more than a year before they breed for the first time. Mature females breed every year.

6. POLISH SUMMARY

Badano wzrost *Rana arvalis* Nilsson i *R. temporaria* L. analizując rozkłady długości młodych żab odławianych stale w ciągu kolejnych lat (tab. I) oraz stosując ponowne odłowy znakowanych żab dorosłych (rys. 1, 2, tab. II). Analizowano rozwój jajników pochodzących z żab o różnych wymiarach (rys. 7, 8). Oba gatunki rozmnażają się na wiosnę. *R. arvalis* dorasta średnio do 40 mm przed trzecią zimą, przestając rosnąć po osiągnięciu 54 mm (tab. III). Analogiczne wartości u *R. temporaria* wynoszą 50 i 69 mm (tab. III). *R. arvalis* zaczyna rozmnażanie w wieku trzech lub czterech lat, natomiast *R. temporaria* w wieku trzech lat, a nieraz nawet dwóch. U obu gatunków mogą rozwijać się jaja normalnej wielkości przeszło rok przed początkiem rozmnażania. Dojrzałe samice rozmnażają się co roku.

7. REFERENCES

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