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Survival and Growth of Brown Frog Juveniles Dispersing from Breeding Pond

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Abstract—In 1989 and 1990, the migration and survival rates and growth of *Rana temporaria* and *R. arvalis* juveniles were examined by means of the group marking method applied to recently metamorphosed individuals, and by recapture of juveniles along two different transects, each 700 m long. As compared with 1990, in 1989, juveniles of *R. arvalis* had smaller body size upon metamorphosis and higher density near the pond, with higher mortality rate in close proximity to it (up to 200 m) and higher survival rate at a considerable distance from the pond. In both years, the froglets that left the pond earlier had advantage of higher survival rate, but only at a distance from the pond exceeding 200 m. Among the early metamorphosed juveniles, larger individuals better survived in 1990, but not in 1989 (because of the higher density). Among the individuals that left the pond later, the survival rate was higher in large-sized juveniles in both years. Dispersing away from the pond, the juveniles attained larger average sizes in 1989, compared with 1990, and more completely compensated for the initial body size delay. The body sizes attained by the end of the season were the same for early small-sized and late large- and medium-sized individuals. In *R. temporaria*, the growth rate is higher than that in *R. arvalis* and compensation for the initially small body size of juveniles is practically complete.

The number of metamorphosed anuran juveniles sharply drops immediately after their leaving the pond. During this period of time, the survival of brown frogs much depends on their density, body size upon metamorphosis, and the time when they emerge onto land (see Lyapkov, 1995). These characteristics may exert prolonged influence, affecting the frogs’ survival rate till their sexual maturity (Ishchenko, 1971), as well as the size and age in the first breeding (Berven, 1982, 1990; Smith, 1987). The date when an individual leaves the pond may eventually determine the terms of its returning to water for breeding (Sinsch, 1997). The postmetamorphic growth rate of juveniles depends on their density near the water pool, initial body size, and time of leaving the pond (see Lyapkov, 1996a). As juveniles grow, they become less sensitive to their own density (Lyapkov, 1995, 1996a) and less vulnerable to some predators (Lyapkov, 1996b); in addition, the available forage range becomes wider (Lyapkov, 1990). The body size attained by the end of the warm season may also affect the juvenile’s survival rate during its first wintering (Lyapkov, 1997b).

Our long-term experiment carried out on an enclosed territory revealed a dependence of the mortality rates of brown frog juveniles shortly after leaving the pond on their initial body size, date of leaving the pond, and density (Lyapkov, 1995). It was revealed that the juvenile growth rates are affected by the same factors, and that *R. temporaria* juveniles grow, on the average, faster than those of *R. arvalis*, with small-sized specimens compensating for the initial body size delay more frequently (Lyapkov, 1996a).

However, owing to the limited space of our experimental plots (about 50 m between the point of release and the line of capture), the rate of migration from the pond increased with juvenile density. Therefore, at high initial density in experimental plots, the estimation of the time-specific mortality rate based on the proportion of recaptures and migration rate did not reflect adequately the real dependence of the mortality rate on the juveniles’ density (Lyapkov, 1995). For the same reason, the growth rates obtained under overcrowding conditions appeared to be much underestimated (Lyapkov, 1996a). In addition, the growth rates of juveniles that have left the plots and migrated to new places were poorly studied.

This study was aimed to evaluate under natural conditions the mortality and growth rates in freely dispersed juveniles of *R. arvalis* and to compare growth features in *R. arvalis* and *R. temporaria*. The bulk of *R. arvalis* population bred in a relatively big spawning pond. However, beginning in 1988, we observed a steady decrease in the number of adult frogs,

Table 1. The number of *Rana arvalis* juveniles leaving the pond

Sample	Size group	1989		1990		1991		1992	
		Nm	Nr	Nm	Nr	Nm	Nr	Nm	Nr
Early juveniles	Small	3980	188	682	56	34	–	41	–
	Medium	1615 (5140*)	70	1890	135	257	–	75	–
	Large	2610	77	624	58	185	–	49	–
Late juveniles	Small	2381	47	253	20	–	–	–	–
	Medium	1065	123	629	73	–	–	–	–
	Large	462	81	233	32	–	–	–	–
Total		12113	586	4311	374	476	15	165	6

Nm is the number of marked juveniles; and Nr, that of recaptured juveniles.

* The number of medium-sized juveniles that left the pond (for details, see text).

metamorphic survival, and, hence, the number of juveniles that left this pond (Cherdantsev *et al.*, 1997). This enabled us to examine the direct influence of the initial density on the migration and mortality rates of juveniles in relation to their body size and time of leaving the pond, and also on their growth as they dispersed. In this regard, the general goal of this study was to compare the density-dependent and density-independent factors affecting the mortality and growth rates of juveniles dispersing from the pond.

MATERIALS AND METHODS

The newly metamorphosed juveniles were collected on the banks of an overgrowing peat-bog located in an almost intact biotope 4 km away from the Moskva-river bank, at Zvenigorod Biological Station of Moscow State University. This pond is the main spawning place of *R. arvalis.* In addition, beginning in 1990, as many as 30–100 females of *R. temporaria* regularly bred in the pond. In 1989–1992, juveniles leaving the pond were collected every day, during the whole period of their emerging onto land, using a system of plastic fences with total length of 120 m, placed along the bank line of the pond. Depending on the maximum and minimum body lengths (varying between different years because of the different annual means, Tables 1 and 2), and on the type of body length distribution, all the examined juveniles were assigned to one of the three size groups: small, medium, or large. The distinctions between the size groups were drawn according to the body length distribution: the medium-sized group included individuals whose body length was equal or close to the modal value, whereas specimens with smaller or larger body length were assigned to small- or large-sized groups, respectively. In addition, depending on the time when the juveniles emerged onto land, these were divided, respectively, into categories of early (those that left the pond during 12.VI–2.VII.1989, and 26.VI–13.VII.1990), and late ones (7.VII–25.VII.1989, and 16.VII–13.VIII.1990). In this way, each specimen captured by means of plastic fences was marked, using one of the six group markers by cutting off digit phalanx of hind and fore limbs in certain combinations. Since we planned, in addition, to capture the previously marked adults returning to the same pond for breeding, we had to specifically mark the particular year of their leaving the pond as juveniles.

In 1989 (Tables 1 and 2), *R. arvalis* juveniles demonstrated the highest numbers, and, as a consequence, the majority of the individuals were not measured; they were only divided into size groups (small, 14 mm or less; medium, 15–16 mm; and large, 16 mm or more) and marked with group marks. In 1990, the fence-mediated juvenile harvest was 4 times less than that in 1989, which enabled us not only to mark the bulk of the individuals with group marks (small, 15 mm or less; medium, 16–17 mm; and large, 18 mm or more), but also to measure most of them with an accuracy of 0.5 mm. During the period of leaving the pond, the mean sizes of juveniles were seen to decrease, and, therefore, by the time when we finished marking the early juveniles, the highest values for small-, medium-, and large-sized specimens appeared to be 1 mm less. In addition, a few juveniles of *R. temporaria* also left the pond.

In 1991 and 1992, we repeated the fence-mediated captures of juveniles. However, the number of individuals that left the pond was much less compared with that in the two preceding years, the terms of metamorphosis were shorter (in 1991, from 2.VII to 2.VIII; in 1992, from 3.VII to 14.VIII). Therefore, all the juveniles that left the pond were marked as the early ones.

Migrating frogs were regularly captured on two slightly diverging permanent routes, running at a distance of 200 m from each other. Either route was 700 m long, with a layout accuracy of 10 m. The distance between the point of release of marked juveniles and the start of either route was 100 m. One route passed through an overgrown cutting in the wood, while the other run directly through fir- and mixed forest with several little clearings. We kept records every day, but started recording some days later than fence-mediated captures of juveniles began: in 1989, from July 12 to August 25; in 1990, from July 15 to August 22. In each route, the recorded width was not firmly fixed, and the distance, along which froglets were captured varied from 2 to 4 m, depending on the vegetation thickness. Each individual caught along the route was measured with an accuracy of 0.5 mm. In addition, we recorded the type of marking (or its absence), and the distance between the route start and the point of capture. In 1991 and 1992, we continued to make route recordings, but no relevant data are presented here: owing to the initially small numbers of marked froglets, the total amount of recaptured individuals was negligibly small (15 and 6 individuals, respectively).

While processing data on recaptures, each route was divided into four intervals: 0–100, 101–200, 201–300, and 301–700 m. In 1989, the numbers of individuals collected within each particular interval were similar in both the routes (with a 6% difference), and differed not very appreciably (53%) in 1990. In addition, the numbers of individuals collected at the remote intervals along each route (301–700 m) were much less as compared with those in the preceding intervals, and, therefore, the records from both the routes were summed. In order to count the numbers of frogs in each particular interval, some routine methods for interpreting recapture results were employed (Caughley, 1979). To analyze the dynamics of dispersal and mortality, proportions of recaptured specimens (relative to the number of juveniles marked with a given group mark) were determined from the estimates within each particular interval. The mean sizes of recaptured froglets within each group in either of the four intervals served as characteristics of the froglet group growth. The significance of differences between the proportions was determined by the *u*-test, and that of differences between the body size means, by the *t*-test. An analysis of variance with subsequent multiple comparisons (Scheffe-test) was used to compare several mean values. In material processing, spread sheets in Excel 7.0 and a package of statistical programs STATISTICA 5.0 were employed.

Table 2. Body length of *Rana arvalis* juveniles leaving the pond

Sample	Index	1989	1990	1991	1992
Early	*n*	200	1851	476	165
	L	14.47	16.02	16.24	17.66
	σ^2	2.26	1.78	1.63	3.70
	CV (%)	10.39	8.34	7.85	10.89
Late juveniles	*n*	126	1115	–	–
	L	13.24	15.47	–	–
	σ^2	1.97	1.66	–	–
	CV (%)	10.60	8.34	–	–

Note: *n*, sample size; *L*, mean value; σ^2, variance; and *CV*, coefficient of variation.

RESULTS AND DISCUSSION

Body Size of R. arvalis Juveniles upon Metamorphosis Their Numbers and Terms of Leaving the Pond

In 1989–1992, the mean sizes at metamorphosis were seen to increase annually, with the numbers of juveniles leaving the pond steadily decreasing. The juveniles of *R. arvalis* that left the pond in 1989 displayed the maximum numbers and minimum mean sizes (Tables 1 and 2). During this mass emergence onto land (12115 out of 15640 fence-captured individuals were marked), only one sample of early and one sample of late individuals were measured. The mean sizes of juveniles decreased: the former were significantly larger that the latter ($p < 0.001$, see Table 2).

In 1990, the number of fence-captured juveniles was 4 times less (Table 1). The mean body length in these was larger by 13% as compared with that in juveniles caught in 1989 (the differences were significant for both the early and the late individuals, $p < 0.00001$). During the whole season, a slight increase in the number of small-sized juveniles was observed along with a decrease in the number of medium-sized ones, and this, as in 1989, resulted in a decline in the mean size of all the individuals (Fig. 1). According to a two-way analysis of variance (henceforth a model with fixed effects and interaction is considered), the early juveniles were significantly larger than the late ones (factor “terms of leaving”: $F = 287.6$, $p < 0.00001$) on the background of distinctions between small-, medium-, and large-sized metamorphs (factor “initial size”: $F = 3787.7$, $p < 0.00001$). The interaction of the two factors was also significant ($F = 6.7$, $p = 0.001$), which corresponds to a redistribution of the size composition of the late metamorphs in comparison with the early ones (Fig. 1).

In 1991, only 476 juveniles of *R. arvalis* were fence-captured, and in 1992 as few as 165, i.e., 100 times less than in 1989 (Table 1). It is worth mentioning that the differences in the numbers of juveniles leaving the pond were determined by the significant differences in the rate of their survival till the end of metamorphosis (in 1989, 1990, 1991, and 1992, making, respectively, 1.89, 0.70, 0.06, and 0.015%), rather than by the number of egg clutches deposited into the examined pond (in the respective years we took into account as many as 2820, 2320, 2840, and 3560 clutches).

Beginning in 1991, the most likely reason for such a drastic drop in the survival rate could be an unusually high embryonic mortality rate caused by the deteriorated quality of water in the overgrowing pond (fall in pH and, presumably, oxygen deficiency). In 1991 and 1992, with the numbers of juveniles that left the pond being low, their mean sizes were even larger (compared with 1989, by 16 and 26%, respectively), with the maximum body length reaching 22 mm (see Table 2 and Fig. 1).

Dispersal Dynamics in R. arvalis Juveniles Related to Their Survival Rates

In 1989 (Table 3, Fig. 2), among the early juveniles, the proportion of initially large-sized ones recaptured at the interval of 0–100 m was significantly lower as compared with the corresponding proportions of the medium- ($p = 0.02$) and small-sized juveniles ($p = 0.0003$). However, as dispersal proceeded, these differences were leveled out to become not significant in the interval from 201 to 300 m. As a result, among the early juveniles, the proportion of specimens recaptured far from the pond was independent of their initial size. At the same time, the proportion of recaptures of late juveniles demonstrated a distinct dependence on the initial body size (Table 3, Fig. 2, 1989).

In the interval from 0 to 100 m, large-sized juveniles occurred most frequently, whereas medium-sized individuals were found more seldom (with significant differences between recapture proportions, $p < 0.001$), and small-sized ones were even more rare (these differed significantly from both large- and medium-sized specimens, $p < 0.001$). With further dispersal, the proportion of recaptures of large-sized juveniles decreased at the highest rate, that of medium-sized juveniles decreased more slowly, and that of small-sized froglets even more so.

Between 301 and 700 m, distinctions between the size groups diminished (with those between medium- and large-sized specimens becoming not significant), but were not leveled out completely, so that the relationship remained as before: large- and medium-sized individuals being found more frequently as compared with small-sized ones.

In the beginning of dispersal, the proportion of all recaptured early juveniles is much less than that of all recaptured late ones (in the interval of 0–100 m, the differences are significant, $p < 0.00001$). However, in the interval from 301 to 700 m, the proportion of the early recaptured juveniles is rising ($p = 0.014$). Since juveniles that left the pond in 1989 demonstrated the highest number and density (Table 1), their dispersal rate was presumably equally high (Lyapkov, 1995). Therefore, the majority of early individuals dispersed rather quickly and were not captured in the interval from 0 to 100 m. As a result, the observed pattern (Fig. 2, 1989) reflects changes in the proportion of recaptures of both the early and the late juveniles only within remote intervals.

In 1990 (Table 4, Fig. 2), among the early juveniles, large-sized ones constituted the most frequently recaptured group already in the interval from 0 to 100 m (the distinction from medium-sized individuals was significant, $p = 0.037$), this advantage persisting as far as to the last interval (with significant difference from small-sized individuals, $p = 0.011$). At the beginning of the routes, medium-sized froglets were captured more rarely than small-sized ones (not significant difference), but farther (301–700 m, $p = 0.039$) they left the small-sized ones behind, firmly holding the second position. Among the late juveniles, a strict correlation between the proportion of recaptures and the initial sizes of individuals was established even in the interval from 0 to 100 m (small–medium: $p = 0.05$), and then (with slight fluctuations between medium- and small-sized individuals) remained constant to the route end.

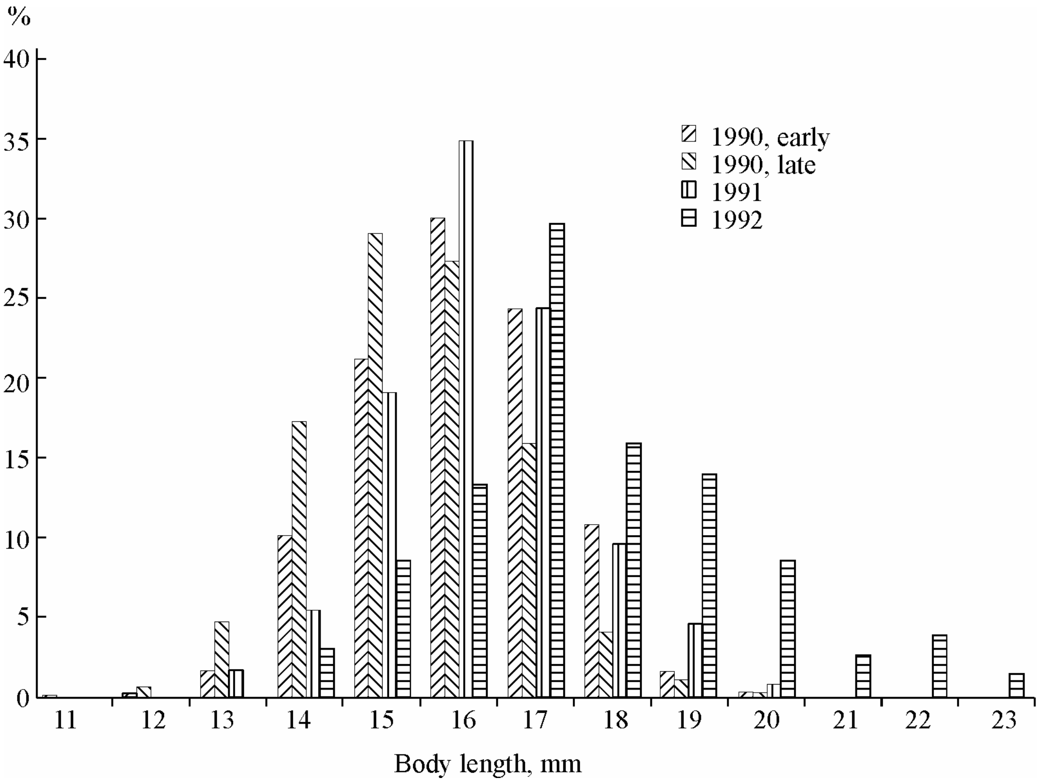

Fig. 1. Distribution (%) of the initial sizes (body length, mm) in juveniles that left the pond in 1990–1992.

In 1990, the proportion of recaptures of all the late juveniles exceeded that of all the early ones only in the interval from 0 to 100 m (p = 0.0005). Within 201–300 m, the proportion of all the recaptured early juveniles was higher than that of all the late ones (p = 0.0075); exactly the same correlation was preserved in the interval from 301 to 700 m (Fig. 2, 1990).

A comparison between the proportions of recaptures in two years does not make it possible to reveal any unequivocal dependence on either the density of juveniles or their initial sizes. It will be recalled that juveniles that left the pond in 1989 were smaller than those that emerged onto land in 1990, but the number of the former was 4 times higher. On the assumption that the survival of juveniles may be adversely affected by their initial smaller sizes and higher density, a lesser proportion of recaptures of both the early and the late juveniles in 1989 would be expected. At the same time, similar proportions of recaptures of the early juveniles were recorded in the interval of 301–700 m for these two years. As already noted, the estimates of the juvenile survival rate in this remote interval most adequately corresponded to the real situation. In the late juveniles, examined in the interval from 301 to 700 m, no significant differences were also recorded, the proportion of recaptures within all the three size groups in 1989 being higher than in 1990.

The noticed decrease in the proportion of recaptures may result from the following three factors: mortality, migration rate (juveniles commonly strive to move away from the spawning pond as far as possible), and a mere drop in density due to juveniles' dispersal over the permanently growing territory. To estimate the role of the last factor, we used a simple model that could account for the drop in density by only the growing area of the territory on which the juveniles distributed when migrating away from the pond. We assumed that juveniles migrated in a radial direction from the point where they originally emerged onto land; in our case this is the point where the marked specimens were released. The distance between the point of release on the pond bank and the starting points of each of the two routes was about 100 m (Fig. 3a). Therefore, the area of the plot (S_0) adjoining the start of the recorded routes was estimated as the area of a sector with radius R_0 = 100 m, i.e. $S_0 = \pi R_0^2 \alpha$, where α is an angle determining the lateral (radial) demarcation lines of the

Table 3. Survival and growth of *Rana arvalis* juveniles in 1989

Group of juveniles	Distance from the pond, m								
	0–100	101–200	201–300	301–700	Release	0–100	101–200	201–300	301–700
	Survival rate (% of recaptured juveniles)				Mean body length (mm)				
Early small-sized	4.72	3.32	1.68	0.78	12.50	19.10	19.88	20.89	23.97
medium-sized	4.33	3.16	1.49	0.99	14.52	19.03	21.44	22.13	24.47
large-sized	2.95	2.03	1.30	0.57	16.49	19.96	20.61	22.84	25.37
All early	4.08	2.88	1.52	0.76	14.47	19.29	20.39	21.63	24.44
Late small-sized	1.97	0.92	0.25	0.13	12.50	18.30	19.28	23.50	23.50
medium-sized	11.55	4.23	1.88	0.56	14.46	19.23	20.62	22.46	23.92
large-sized	17.53	10.61	4.76	1.30	16.53	19.50	21.19	22.94	23.75
All late	6.42	2.97	1.23	0.38	13.24	19.12	20.53	22.79	23.77
All marked	–	–	–	–	13.99	19.19	20.44	22.03	24.31
All unmarked	–	–	–	–	13.99	19.48	21.75	23.77	24.64

Note: Numbers of particular groups of juveniles are given in Table 1.

sector of dispersal. Similarly, the area of plot 1 (S_1), which contains the 1st interval (0–100 m), is determined as the area of a sector with radius R_1=200 m: $S_1=\pi R_1^2\alpha$. Similarly are determined the areas of plots 2, 3, and 4 (S_2, S_3, S_4), i.e. areas of sectors with radii R_2=300 m, R_3= 400 m, and R_4=800 m, including, respectively, the intervals 101–200, 201–300, and 301–700 m. Then, the density of the *i*-th group of juveniles (whose number is N_i and does not change as they migrate), when they reach the border of the 1st and 2nd intervals, i.e. on a plot of area S_1, will make $P_1 = N_i/S_1$; when they reach the borders of the 2nd and 3rd intervals, the density will become $P_2=N_i/S_2$, and, with further dispersal, the respective densities will be:

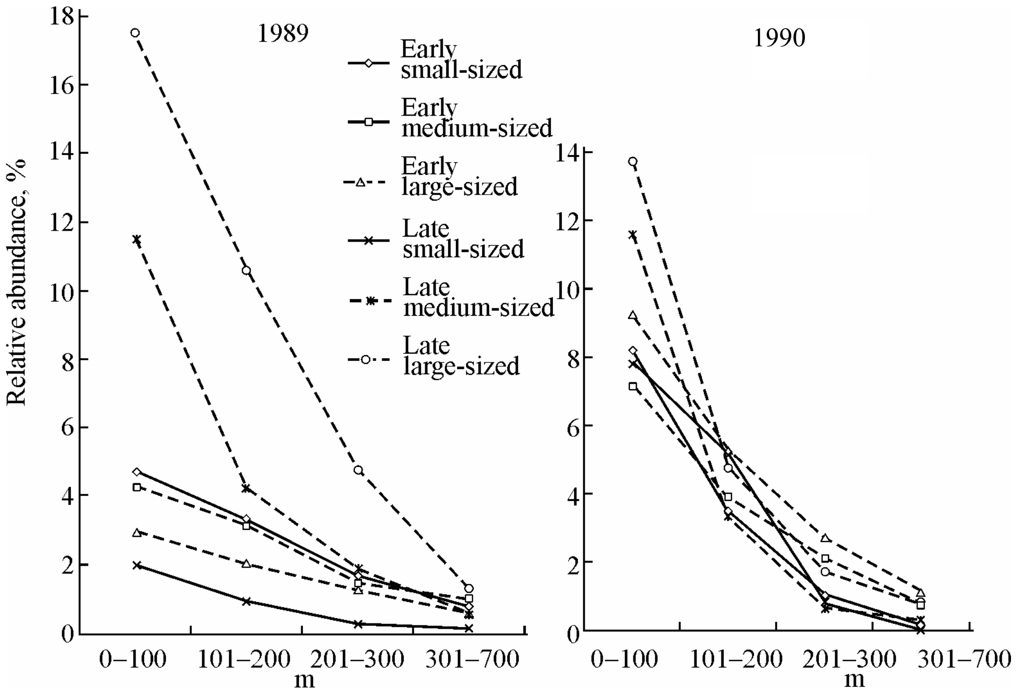

Fig. 2. Dynamics of relative numbers of recaptured *Rana arvalis* juveniles in the course of their dispersal away from the pond in 1989 and 1990. Abscissas: intervals along the recording routes, m. Ordinates: number of recaptured juveniles related to the number of marked juveniles of a given group (%).

Table 4. Survival and growth of *Rana arvalis* juveniles in 1990

Group of juveniles	Distance from the pond, m								
	0–100	101–200	201–300	301–400	Release	0–100	101–200	201–300	301–700
	Survival rate (% of recaptured juveniles)				Mean body length (mm)				
Early small-sized	8.21	3.52	1.03	0.15	14.33	18.63	19.94	21.67	24.00
medium-sized	7.14	3.92	2.12	0.74	16.03	19.06	20.59	21.96	22.86
large-sized	9.29	5.29	2.72	1.12	17.64	20.96	21.44	22.80	23.14
All early	7.79	4.10	2.00	0.69	16.02	19.34	20.63	22.12	23.00
Late small-sized	7.91	5.14	0.79	0.00	13.74	17.43	18.18	20.00	–
medium-sized	11.61	3.34	0.64	0.32	15.48	18.63	20.06	21.00	23.50
large-sized	13.73	4.72	1.72	0.86	17.31	20.19	20.57	20.00	21.50
All late	11.21	4.04	0.90	0.36	15.47	18.94	19.57	20.33	22.50
All marked	–	–	–	–	15.81	19.18	20.26	21.90	22.92
All unmarked	–	–	–	–	15.81	19.68	21.12	22.25	23.50

Note: Numbers of particular groups of juveniles are given in Table 1.

$P_3=N_i/S_3$ and $P_4=N_i/S_4$. On the other hand, since no captures were made between the point of release and the route start, the truly observed density is given by:

in plot 1: P_1^1,

in plot 2: $[P_1^2(S_1-S_0) + P_2^2(S_2-S_1)]/(S_2-S_0)$,

in plot 3: $[P_1^3(S_1-S_0) + P_2^3(S_2-S_1) + P_3^3(S_3-S_2)]/(S_3-S_0)$,

in plot 4: $[P_1^4(S_1-S_0) + P_2^4(S_2-S_1) + P_3^4(S_3-S_2) + P_4^4(S_4-S_3)]/(S_4-S_0)$,

where P_1^i, P_2^i, P_3^i, and P_4^i are the estimated densities in the 1st, 2nd, 3rd and 4th intervals, respectively.

The upper index $i = 1$ means that the density was estimated at the time when juveniles dispersed in a plot of area S_1, i.e. when they reached the borders of the 1st and 2nd intervals. Similarly, the upper indices "2", "3", and "4" correspond to the moments when the specimens dispersed in plots of areas S_2, S_3, and S_4, respectively. From these formulas it also follows that the relation between the theoretical and real density values is independent of the angle α commonly used in density calculations. In our estimations (Fig. 3), $\alpha = 120^\circ$.

A comparison between the model-based and real values of density (Figs. 3b and 3c) showed that in 1989 the expected results exceeded the real ones in each juvenile group in plots 1 and 2 (including the 1st and 2nd intervals). In the 3rd interval, the expected value for the late juveniles coincided with the real one, while in the 4th interval the real values exceeded the expected ones for both the early and the late juveniles. Such a density dynamics may be a consequence of the combined effect of dispersal and mortality: surviving juveniles can actively move away from the pond to the remote intervals; therefore, the density there either continues to fall down but more slowly (the late juveniles), or even increases (the early ones).

In 1990, a similar pattern was observed with lower initial density (Fig. 3b), but the real densities were observed to exceed the expected ones as early as beginning with the 2nd interval. Results of these comparisons suggest that the juveniles' mortality is especially high in early dispersal, and the mean density (over the whole occupied territory) may be eventually stabilized only owing to a sharp fall in mortality as the surviving juveniles migrate further to a rather long distance.

It is to be noted that the terms of recaptures in the remote interval (301–700 m) suggest similar migration rates in small-, medium-, and large-sized juveniles of *R. arvalis*. In 1989, both small- and large-sized juveniles were first captured among the early metamorphs at a distance of 300 m or more 17 days after the last marking of small-sized individuals, whereas medium-sized froglets were caught only 4 days later. Among the late juveniles, large-, medium- and small-sized specimens were first captured at the same interval 17, 18, and 22 days, respectively, after the last marking. In 1990, among the early froglets, the first large- and

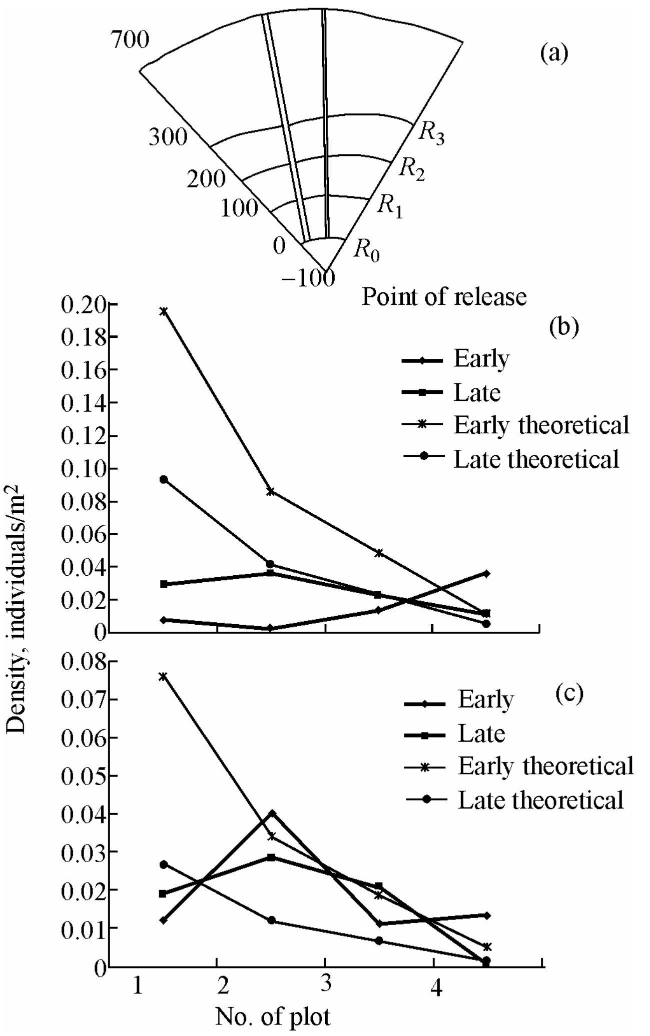

Fig. 3. Theoretical and real densities for juveniles dispersing from the pond: (a) diagram used for constructing a dispersal model: double lines denote recording routes, single lines designate the limits of intervals; figures show distances (m) from the origin of routes, R_0, R_1, R_2, R_3, R_4 mean distances from the points of release to the borders of the respective intervals (for details see the text); (b, c) comparison between theoretical and real densities in 1989 and 1990, respectively.

medium-sized individuals were caught in the same interval 18 days after the last marking, and small-sized ones only 3 days later. In 1990, the late small-sized specimens made an exception: none of them was recaptured farther than 300 m away, and, therefore, a comparison between the proportions of recaptures of juveniles of all three size groups within each interval looks quite correct.

Thus, in 1989, the high density near the pond much more strongly affected the early juveniles, among which distinctions in proportions of recaptured small-, medium-, and large-sized individuals were practically equal (Fig. 2). In 1989, the late juveniles were not exposed to the high density pressure, and for these the proportions of recaptured small-, medium-, and large-sized individuals exactly corresponded the juvenile dimensions, with this correlation preserved as they dispersed.

In 1990, a similar dependence on the initial size was observed among the late specimens in the interval 0–100 m, farther these distinctions were retained, although becoming not significant. In addition, the smaller the density of dispersing juveniles, the higher their survival owing to the earlier terms of metamorphosis.

According to the patterns of the revealed survival and dispersal dynamics (see Fig. 2), once juveniles get over a zone of maximum density (the first 100 m or so between the point of release and the route start) their mortality rate decreases, but does not go to zero. At the same time, the density of juveniles (evaluated by the total number of individuals recaptured in each interval, Table 5) sharply drops as they disperse, and thus their mortality becomes progressively less density-dependent. In 1989 and 1990, in the interval from 0 to 100 m, the survival rate in all the early juveniles was, respectively, 4.1. and 7.8%, the corresponding values for the late ones being 6.4 and 11.2%. However, in the same years, the share of individuals that reached the last interval (related to the number of those that reached the first interval) was 18.5 and 6% in the early individuals, and 8.8 and 3.2% in the late ones, respectively. In other words, with higher juvenile density near the pond (in 1989, as compared with 1990) their rate of mortality obviously increases in the immediate vicinity of the pond, and drops as juveniles disperse, which is true for both the early and the late individuals.

On the whole, our estimates of the share of recaptures compare well with the relevant data of other observations made on unfenced territories: 3.1 and 4.2% in *Rana pipiens* (De Benedictis, 1974), and 9.3% in *Bufo woodhousei* (Breden, 1987).

Juvenile Growth

In evaluating the growth rates of juveniles, we started from the evident relation: the farther a given juvenile moved away from the pond, the longer it survived on the land.

In 1989, the mean sizes of the early juveniles of *R. arvalis* changed in such a way that the distinction between small-, medium-, and large-sized individuals became less and less obvious (Fig. 4, 1989).

The strongest compensation for the initial small body size was revealed within the interval 0–100 m, and, as a result, distinctions between all the three size groups vanished to not significant already at the start of dispersal. As the growth proceeded, these distinctions were further enhanced, but in the interval 301–700 m they were obvious only between small- and large-sized individuals. The same pattern of compensation for the initial body size delay occurred in the late juveniles as they grew. The only difference was that complete compensation was attained later, rather than in the interval 0–100 m: distinctions between all the three groups were not significant in the interval 301–700 m. The difference between the early and the late juveniles was estimated by the three-way analysis of variance. The influence of the factor "interval" (0–100, 101–200, 201–300, and 301–700 m) was significant ($F = 102.3$, $p < 0.00001$); the influence of the factor "initial size" (small, medium, large) was also significant, but weaker ($F = 6.0$; $p = 0.0025$). However, the influence of terms of leaving the pond (early or late) was not significant ($F = 0.3$, $p = 0.57$). A comparison between medium-sized specimens showed that the early juveniles examined in the intervals 0–100 and 301–700 m were slightly larger than the late ones (Table 3); but these distinctions were not significant.

In 1989, in addition to marked specimens (a total of 586), 689 unmarked juveniles were captured along the routes. The terms when these latter metamorphosed were unknown. Therefore, these juveniles were compared with all the early and all the late specimens, and also with the early and late ones taken together (Table 3). The two-way analysis of variance (the factors "interval" or "mark", i.e., the presence or absence of marking) revealed significant differences between the marked and unmarked specimens ($F = 42.1$, $p < 0.00001$), along with a significant increase in the mean sizes as juveniles dispersed ($F = 271.3$, $p < 0.00001$). In the interval 0–100 m, unmarked and marked specimens differed only not significantly. Farther, the former were seen to grow faster than the latter, and, therefore, in the intervals 101–200 m and 201–300 m their distinctions were significant ($p < 0.00001$ in both cases). However, in the interval 301–700 m the marked individuals caught up the unmarked ones to make eventually the size distinctions between these two again not significant.

Unlike 1989, no complete compensation for the initial small body size was observed in 1990 (Fig. 4, 1990). Within the intervals 0–100 and 101–200 m, some obvious significant differences remained among the early juveniles between small- and large-sized specimens, to become eventually not significant. Among the late juveniles in the interval 0–100 m, the large ones significantly differed from medium- and small-sized individuals. Within the interval 101–200 m, significant differences were recorded between all the three size groups, to be lost farther, in the interval from 201 to 300 m. Distinctions between the early and late juveniles were estimated by the three-way analysis of variance. The influence of the factor "interval" (100, 200, 300 m) was significant ($F = 19.8$, $p < 0.00001$), as was that of the initial body size ($F = 10.9$, $p = 0.00003$). In other words, the mean body length within each size group of juveniles increased as they dispersed, with the distinctions between these groups retained. At the same time, the influence of the terms of metamorphosis was also significant ($F = 18.9$, $p = 0.00002$), which was manifested in larger body sizes of the early specimens as compared with the late ones (distinctions between the large juveniles being significant) in the interval 201–300 m. Thus, unlike the situation in 1989, the early juveniles obtained some obvious gain in size in 1990.

Table 5. Variation of juvenile density in 1989 and 1990 (number of individuals per square meter)

Year	Group	Distance from the pond, m			
		0–100	101–200	201–300	301–700
1989	Early	0.8375	0.5900	0.3125	0.0388
	Late	0.6275	0.2900	0.1200	0.0094
1990	Early	0.6225	0.3275	0.1600	0.0138
	Late	0.3125	0.1125	0.0250	0.0025

As it was done in 1989, in 1990, unmarked individuals were captured along the routes (a total of 425) and compared with the marked ones (a total of 374). The former had similarly high growth rates in the interval 0–100 m, and farther, according to their mean sizes, they were the closest to the early juveniles. This similarity, taken together with the sharp drop in the number of juveniles that have left the pond by the beginning of marking of late specimens, suggests that according to the terms of metamorphosis the majority of unmarked juveniles may belong to the early individuals. A two-way analysis of variance (factors "interval" and "mark") revealed significant differences between the marked and unmarked juveniles

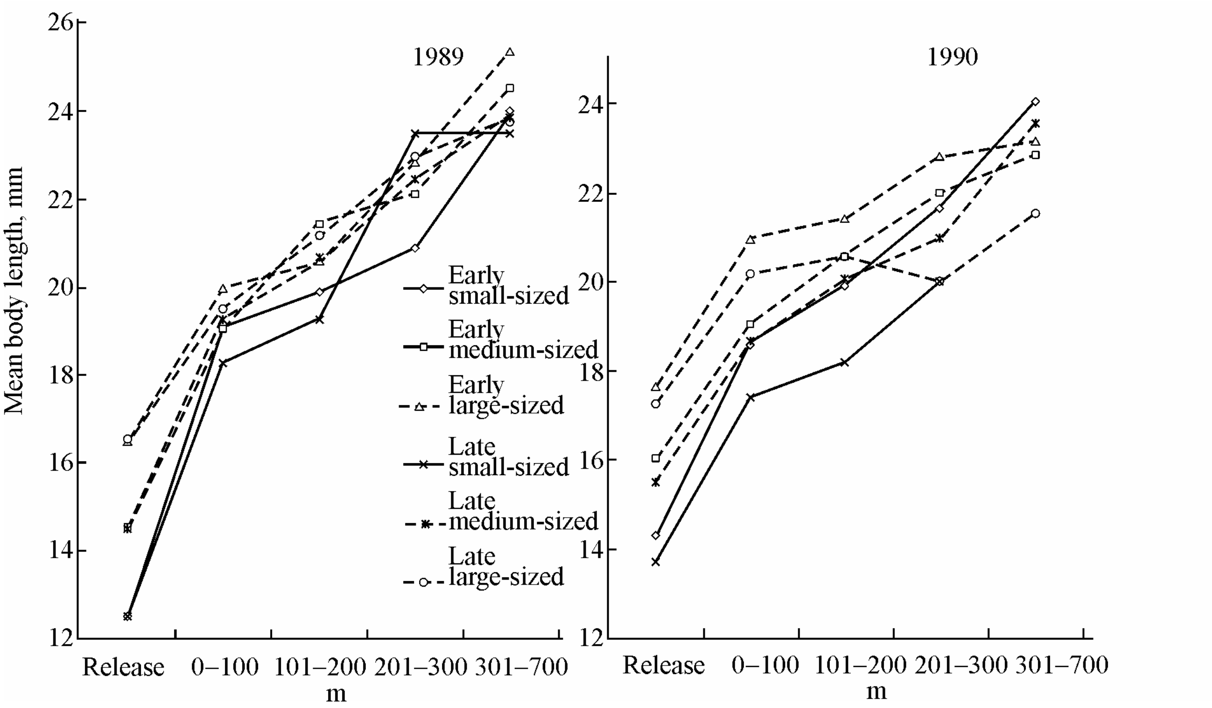

Fig. 4. Variations of the mean body lengths within each size group of *Rana arvalis* juveniles in different intervals in 1989 and 1990.

($F = 10.5$, $p = 0.001$), along with a significant increase in their mean sizes in the course of their migration ($F = 108.3$, $p < 0.00001$). Since the late juveniles grew somewhat more slowly than the early ones, unmarked juveniles were larger than all the marked individuals. However, this difference was significant only in the intervals 0–100 m ($p = 0.006$) and 101–200 m ($p = 0.0004$). Thus, in 1989 and 1990, the marked juveniles could compensate for their growth delay as compared with unmarked ones early in the dispersal (see Tables 3 and 4), which makes it possible to conclude that the mark itself slightly affected the growth rate in froglets that migrated some long distance away from the pond.

To evaluate characteristic features of juvenile growth in 1989 and 1990, we used a design of the four-way analysis of variance ("year" is the 4th factor, the other three being the same as in a comparison within one year). Significant differences between the years were revealed ($F = 14.9$, $p = 0.00012$): in 1989, the juveniles attained, on the average, larger body sizes. It is worth mentioning that they got this advantage (as in the case of survival) in spite of their initial small sizes and higher density. In addition, significant interactions were revealed: "interval × year," and "terms of metamorphosis × year." The former means that in 1989 the juveniles examined in the remote intervals attained larger sizes, while the latter implies (as already mentioned) an incomplete compensation among the late individuals in 1990 (Fig. 4).

In 1990, apart from juveniles of *R. arvalis*, those of *R. temporaria* also left the pond. The number of the latter was much lower than that of the former, constituting about 5% among the early specimens and being close to zero among the late ones. On dividing these into three size groups, the same body length limitations were used, as with *R. arvalis*. The mean values of the initial sizes within the corresponding groups of small-, medium- and large-sized individuals appeared essentially the same in these two species (see Tables 4 and 6). In the routes, we captured only those juveniles which were marked on leaving the pond as the early ones (136) and also unmarked individuals (109). Unlike *R. arvalis, R. temporaria* displayed complete compensation for the initial body size delay (Table 6, Fig. 5). In the interval 0–100 m, significant differences were retained between large- and small-sized juveniles only ($p < 0.048$) to become not significant as they dispersed farther.

Higher growth rates in *R. temporaria* are revealed when these two species are compared using a design of the three-way analysis of variance (factors "initial sizes," "interval," and "species"). Small juveniles of *R. temporaria* catch up with small ones of *R. arvalis*, as early as in the interval 101–200 m. The higher growth rates in *R. temporaria* are retained up to the route ends. Among medium-sized juveniles, significant differences are revealed as early as in the interval

Table 6. Juvenile growth of *Rana temporaria* (mean body length, mm) in 1990

Group of juveniles	Distance from the pond, m				
	Release	0–100	101–200	201–300	301–700
Early small-sized	14.33	20.50	22.13	23.87	25.29
medium-sized	16.03	21.31	23.07	24.75	27.47
large-sized	17.64	23.80	22.89	24.11	26.33
All early	16.02	21.87	22.69	24.24	26.36
All unmarked	16.02	22.72	22.57	23.83	26.00

0–100 m, becoming more pronounced farther. Similar distinctions are seen also between large-sized specimens (within 201–300 m these distinctions are not significant because of the small sample sizes, compare Figs. 4 and 5). The higher growth rates of juveniles in *R. temporaria*, compared with *R. arvalis*, under similar environmental conditions, mean the existence of interspecific differences for this character. Similar results have been obtained previously on examining the fenced plots (Lyapkov, 1996a, 1997a).

Direct comparison of growth rates in the early and the late juveniles is not quite correct. These two juvenile groups grow at different times, but this difference could not be taken into account since we did not mark each individual. When the late juveniles reached the interval 301–700 m, the early ones, which had already migrated even farther by this time, should have exceeded the former in size, but we do not know by how much, since no regular captures were performed at the long distances. Only rare specimens were occasionally caught farther than 700 m from the pond.

For a more correct comparison between the early and late juveniles, and between the early juveniles of the two species, we summarized the data for all intervals obtained by the end of the recapture period: in 1989, from 6.08 to 25.08; in 1990, from 7.08 to 22.08 (Table 7, Fig. 6). We assumed that juveniles captured within these periods of time had already attained comparatively large body sizes, and, therefore, distinctions between different groups were expected to be most clearly pronounced. In 1989, significant differences were recorded between the early and late juveniles of *R. arvalis* (two-way analysis of variance, factor “terms of leaving the pond”: $F = 46.1$, $p < 0.01$), i.e. larger sizes were attained by those individuals which earlier metamorphosed. Differences between the size groups were also significant, but weaker ($F = 9.6$, $p < 0.01$). Among the early juveniles, medium- and large-sized ones differed not significantly from one another, whereas among the late ones all the three size groups differed significantly. In 1990, significant differences were also revealed between size groups among the early and late individuals: the initially large- and small-sized juveniles attained, respectively, the maximum and minimum body sizes. In addition, no significant difference was found between the early small-sized and late large-sized individuals (in 1989 and 1990), and also between the early small-sized and late medium-sized ones (in 1990).

A comparison of the data obtained in 1990 for the two species (two-way analysis of variance, “species” being the second factor) demonstrated that the early juveniles of *R. temporaria* attained, on the average, larger body length than did those of *R. arvalis,* which left the pond in the same terms ($F = 63.4$, $p < 0.01$). In addition, in *R. temporaria*, the initially small-sized juveniles demonstrated the maximum growth rate in contrast to the initially large-sized ones, which had the minimum growth rate. As a result, in *R. temporaria*, the attained mean body length in the three size groups did not differ significantly from each other (Fig. 5).

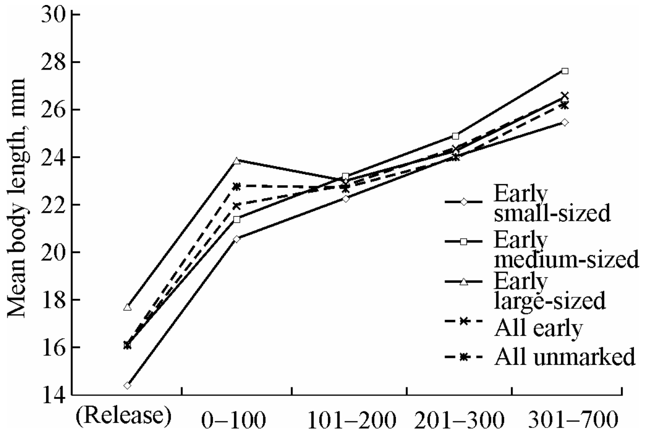

Fig. 5. Variations of the mean body lengths within each size group of *Rana temporaria* juveniles in different intervals in 1990.

Table 7. Juvenile sizes (L_t, mm) in *Rana temporaria* (T) and *R. arvalis* (A) attained during dispersal

Year	Group of juveniles	Nr		L_t					
		T	A	T			A		
				mean	min	max	mean	min	max
1989	Early small-sized	–	67	–	–	–	22.80	17.0	28.5
	medium-sized	–	12	–	–	–	25.25	18.5	30.0
	large-sized	–	21	–	–	–	24.10	20.0	30.0
	Late small-sized	–	33	–	–	–	19.58	15.5	25.0
	medium-sized	–	79	–	–	–	21.33	17.5	26.5
	large-sized	–	50	–	–	–	22.31	18.0	26.0
1990	Early small-sized	13	20	25.77	22	31	20.50	18.0	24.0
	medium-sized	21	52	25.19	18	32	21.67	17.0	26.0
	large-sized	10	15	25.70	20	32	23.27	21.0	26.0
	Late small-sized	–	17	–	–	–	18.41	16.0	20.0
	medium-sized	–	50	–	–	–	19.68	15.0	24.0
	large-sized	–	25	–	–	–	20.64	18.0	24.0

Note: Nr is the number of recaptured specimens; dashes denote lack of data on *R. temporaria.*

Let us briefly summarize the main results concerning the juvenile growth.

In 1989, the juveniles of *R. arvalis* demonstrated higher growth rate, compared with 1990: in the interval 301–700 m they attained, on the average, larger sizes and compensated for the initial body size delay more completely. The attained larger body sizes may account for the higher juvenile survival in 1989 (compared with 1990).

In 1990, the growth delay of the late juveniles, compared with early ones, was in fact even greater, if account is taken of the later terms when the former left the pond.

The body sizes attained by *R. arvalis* are consistent with their initial size and terms of leaving the pond, the early small-sized juveniles being equal to the late large-sized, and also to the late medium-sized individuals.

The growth rate in *R. temporaria* is higher than that in *R. arvalis* (Fig. 5).

The initial body sizes being equal, the mean sizes attained by *R. temporaria* juveniles in the course of dis-

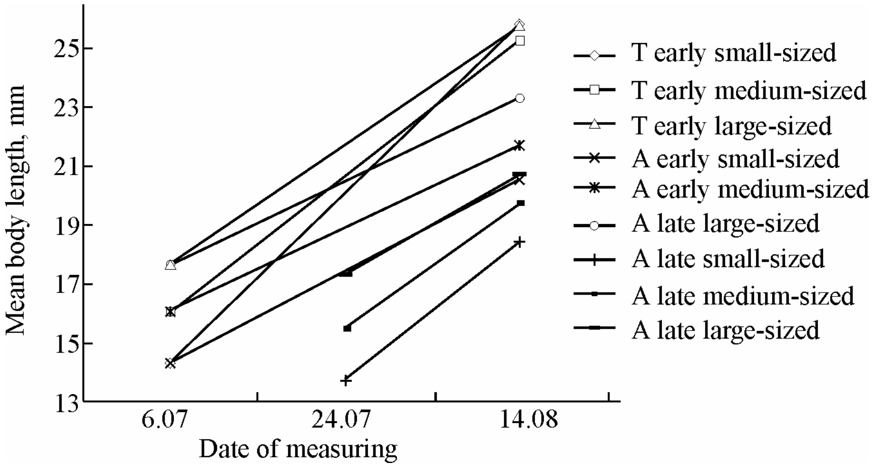

Fig. 6. Sizes (body length, mm) attained by the time of recapture in juveniles of *Rana temporaria* (T) and *R. arvalis* (A) in 1990 (for details, see the text).

persal exceeded those attained in the fenced plots (Lyapkov, 1996a) and in large terraria (Lyapkov, 1997a), whereas in *R. arvalis* the corresponding values, on the whole, coincided. This confirms our previous observations (Lyapkov, 1997a) that in contrast to *R. temporaria*, the overall growth rate of *R. arvalis* juveniles is lower during the whole active period and before the first wintering.

CONCLUSION

It is generally agreed that the biological significance of juveniles' dispersal from spawning ponds consists in that the froglets can find access to some remote zones rich in food, where they, further, replenish other local settlements (or establish new ones) and use other ponds for breeding (Dole, 1971; Sinsch, 1997). The mobility and stamina of juveniles depends on their body sizes attained by the end of metamorphosis, and, therefore, the initially large-sized individuals must migrate faster away from the pond (John-Adler and Morin, 1990). To reduce the mortality caused by density-independent factors, the migrating juveniles have to grow as fast as possible (Cohen and Alford, 1993). However, many anuran species belonging to different taxonomic groups, such as toads (Breden, 1988), true frogs (Moravec, 1990; Tucker, 1995), or brown frogs (Ishchenko and Ledentsov, 1985; Lyapkov, 1996a), are characterized by fast growth rate immediately after metamorphosis, slowing down after the first or second wintering. As far as we could judge from published evidence, such processes as dispersal and growth of froglets after leaving the pond have never been related to each other. Moreover, since the growth proper requires high energy expenditure (see Jørgensen, 1989), it may obviously compete with the dispersal ability.

At the same time, for species or populations with numerous metamorphs, the process of dispersal acquires another, even more important meaning. According to our results, with higher mass leaving the pond in 1989 as compared with 1990, the juvenile survival in the near-shore zone was seen to decrease. However, the survival of juveniles that successfully passed the near-shore zone with the highest density is already independent of this density and the initial body sizes (or this dependence becomes much weaker).

Thus, it is conceivable that the subsequent increase in the survival rate may be due to the dispersal proper. And this is not only a question of density-independent survival, but may be associated with the fact that at higher initial density the migration rate steadily rises, thereby reducing the density pressure exerted on some more actively dispersing specimens near the pond.

As reported previously (Lyapkov, 1995), there are two main factors of crucial importance for the juvenile survival. One is the dispersal proper, intended to reduce the density pressure. The other is the juvenile growth proper rendering any individual more resistant to population density, predators, and other density-independent adverse effects (e. g., heavy shower). The obtained estimates make it possible to maintain that there exists a negative feedback between the juvenile mortality just after leaving the pond, and that after their further dispersal. For example, we observed in 1990 at higher juvenile survival rate near the pond, a sharper fall in their later survival. Metamorphs leaving ponds at lower density and thus having some advantage at the start, were commonly more sensitive to further adverse density-independent effects (including bad weather conditions). Such negative relations are enhanced by the fact that small-sized juveniles, emerging onto land at higher density near the pond (in 1989) and surviving there, grow faster, compared with individuals of formally the same size group, but emerging onto land at lower density (in 1990). On the whole, the relation between density-dependent and density-independent survival components is entirely consistent with the classic "Mathew–Kurmak multitude" (Semevsky and Semenov, 1982).

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