

Variation Structure of the Reproductive Characteristics in *Rana temporaria* and Their Relationship with Size and Age of the Frog

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Abstract—Based of the long-term studies of breeding *Rana temporaria* females, the components of intrapopulation variation of body size and reproductive characteristics were described, and the structure of relationship between them was estimated. The relegation of individuals to a certain generation was determined by skeletochronology. Within each generation female body length, fecundity, and egg size, but not reproductive effort and the relative clutch mass increased with aging. Both the increase and decrease of annual average values of body length, fecundity and egg size in females of different generations in the same years were revealed. Both body size and age of the frogs correlated positively and significantly with their fecundity and egg size. As shown by principal component analysis, each character (except for reproductive effort strongly influenced by fecundity) varied independently. Relationship between separate pairs of characters demonstrated the same relative independence. The weaker relationship of the relative clutch mass with age (compared to the other characters), intergeneration and annual variation is stipulated by the maximum investment of females in each reproduction, the latter characteristic correlating poorly with age and size of females.

Only long-term stationary studies of population dynamics allow us to estimate the range of intrapopulation variation of reproductive characteristics in temperate zone anurans. The fact is that formation of reproductive characteristics of the species with perennial reproduction is strongly influenced by conditions of warm season prior to a given breeding season (Jorgensen, 1981; Cherdantsev *et al.*, 1997). Thus, the long-term study of dynamics of several *Rana arvalis* generations allow us to reveal similar yearly changes of reproductive characteristics in females of different ages (Lyapkov *et al.*, 2001a). The reproductive characteristics in *R. arvalis* females, along with survivorship, determine their reproductive value as well as net rate of reproduction (R_0) of a given generation (Lyapkov *et al.*, 2001b), one of estimates of general fitness most often applied in population biology.

The common frog (*Rana temporaria* L.) is a species, in many ways similar to *R. arvalis* in ecology and reproductive biology characteristics, but at the same time it has a set of differences. The growth rate of *R. temporaria* until maturity is higher (Lyapkov, 1997), and the mature frogs are significantly larger. The larger female size of this species corresponds to higher fecundity. Moreover, female size can affect egg size and reproductive effort or relative clutch mass (see

review Gibbons and McCarthy, 1986; Cherdantsev *et al.*, 1997). Therefore, the study of reproductive characteristics of sympatric (and often syntopic) population of these close species, but with some peculiarities, is of great interest.

With reference to the above data, in our study we set the following aims: (1) to make a general portrait of variability of reproductive characteristics of *R. temporaria* females within the population studied for many years; (2) to determine the character of dependence of reproductive characteristics on female body size and age; (3) to estimate the age dynamics of these reproductive characteristics and to separate the influence of these dynamics from the effect of difference between seasons (i.e. years); (4) to characterize the general structure of relationships between the body size of females, their age, and reproductive characteristics.

MATERIALS AND METHODS

The mature *R. temporaria* females were collected during the breeding period in 1993–1997, in several ponds near Zvenigorod Biological Station of Moscow State University. The females were caught in those ponds that present the breeding site of major fraction of adult *R. temporaria*. Body length, fecundity, and

egg diameter (with eyepiece micrometer of binocular) were measured in each female. In 1993 clutches were obtained in aquaria in laboratory from females collected *in amplexus*. Further, fecundity was determined in each female by measured clutch volume and volume of clutch portion (for more detail, see Cherdantsev *et al.*, 1997). In 1994–1997 fecundity was estimated by the mass of the whole clutch taken out of dissected females (previously weighted) and by the mass of the portion containing the known egg number. With the help of these measures the relative clutch mass, i.e. clutch mass relative to gravid female mass was also estimated. Since previously in our study of *R. arvalis* for the estimation of reproductive output of a given female we used only the index of reproductive effort (Cherdantsev *et al.*, 1997; Lyapkov *et al.*, 2001a), for comparison of these two species in this study we also calculated this index. Index of reproductive effort was calculated according to formula $E = FD^3/L^3$, where F is fecundity; D , egg diameter; L , body length. The age was determined in all females by standard skeletochronological method (cross-sections of shin-bone stained by Ehrlich hematoxyline) in the sample of 1996 and by longitudinal slides of the fourth phalange of the fourth toe (Kornilova *et al.*, 1996), in samples of all other years. Attribution of females to a certain generation was determined by their age.

In material processing, Excel 7.0 and a statistical software package STATISTICA 5.0 were employed.

RESULTS

Reproductive Characteristics of Females in the R. temporaria Population Studied

Body size (Fig. 1A, Table 1). Body size of females collected at breeding sites demonstrates rather high variability: minimum recorded body length was 56 mm; maximum, 97 mm. The distribution of the combined sample did not differ from normal. Moreover, the mean of this sample pooled from all years and all means of different years of study fall within modal size class (75–80 mm).

Age structure (Fig. 1B, Table 1). Most females reproduce firstly after the 3rd wintering. Only one 2-year-old female (with body length 69 mm) was collected at the breeding site. The maximum recorded age was 9 years. In general, the age distribution differs significantly from normal by positive skewness. All average ages of each year of study fall within modal age class (less than 5 years). Moreover, since the

number of 3-year-old females was slightly smaller than that of 4-year-olds, we can conclude that part of the females bred firstly only after 4th wintering.

Fecundity (Fig. 1C, Table 1). Minimum recorded value of fecundity amounts to 388 eggs, whereas maximum, to 2963. In general, the distribution of this trait does not differ significantly from normal. Nevertheless, among all traits studied (except age), fecundity and reproductive effort are distinguished by the maximum variability, estimated as the value of coefficient of variation (see Table 1).

Egg diameter (Fig. 1D, Table 1). The values of egg diameter can vary within a wide range: from 1.4 to 2.3 mm. At the same time, the variation of this trait estimated by the coefficient of variation is the same as in body length and lower than in fecundity, relative clutch mass and reproductive effort (see Table 1). In general, the distribution of egg diameter does not differ significantly from normal. In addition, this trait is distinguished by higher variation among years: 3 of the 5 annual average values fall out of modal age class (1.7–1.8 mm).

Relative clutch mass and reproductive effort (Fig. 1F, Table 1). Relative clutch mass representing the direct estimation of current reproductive output, varied from 12.4 to 36.0%. In general, the distribution of this trait differed significantly from normal by negative skewness, and its variation was sufficiently lower than in fecundity. Another index of reproductive output, reproductive effort (E), was also distinguished by non-normal distribution (positive skewness) and by high (as in fecundity) variability level (Fig. 1E, Table 1). Note that the correlation between these two indexes was rather high ($r = +0.528$) and significant. The exception of body length effect, i.e. the calculation of partial correlation coefficient ($r = +0.558$), indicates that the relationship of these indexes was not affected by general size.

The Dependence of Reproductive Characteristics on Female Size and Age

We used the sample combined across generations to reveal the general picture of dependence of reproductive characteristics on female body length and age. Body length correlates positively and significantly not only with fecundity and egg diameter (Table 2), but with relative clutch mass (Table 2), although the latter correlation was much lower. Non-significant (close to null) correlation was revealed between body length

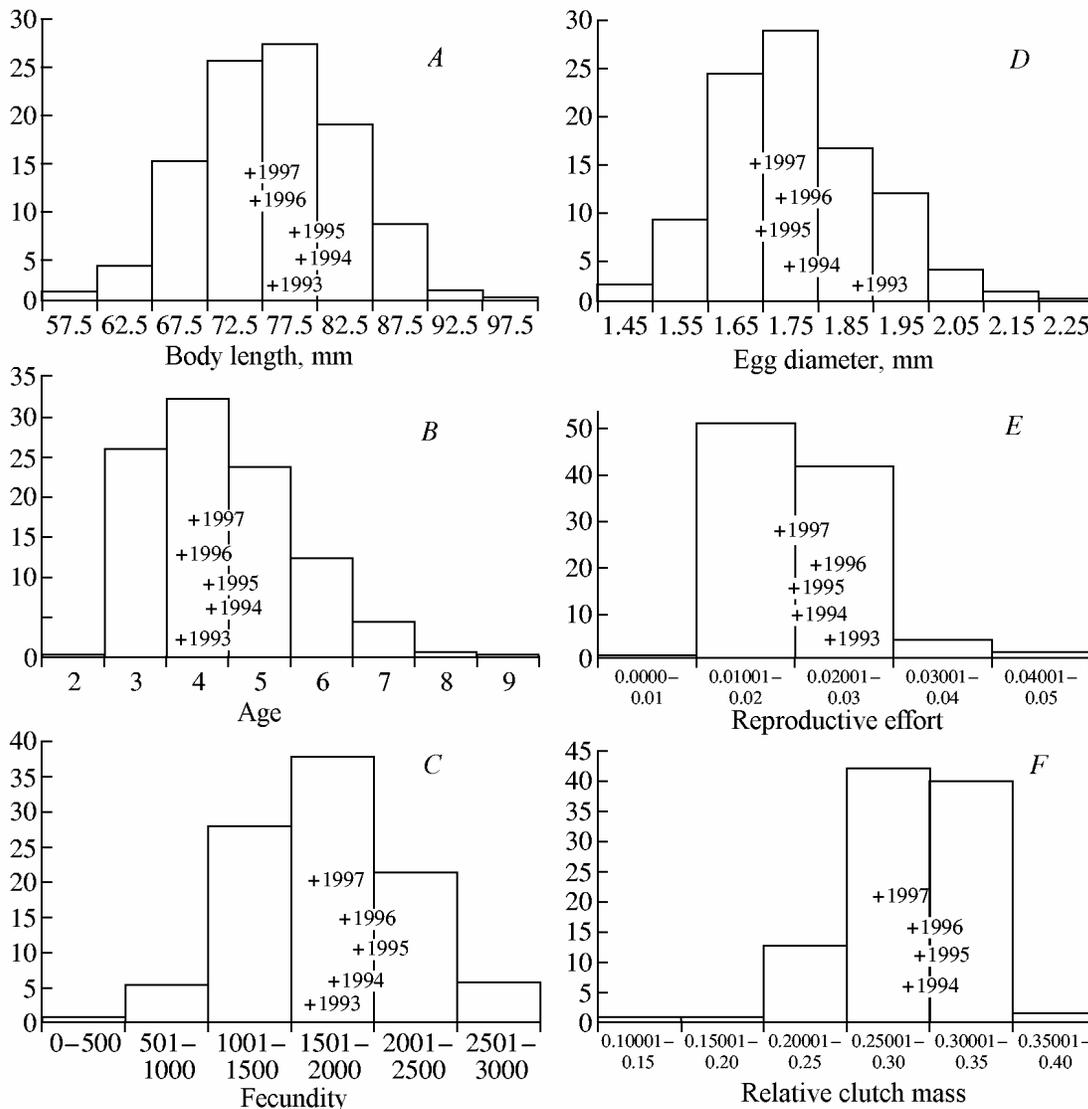


Fig. 1. Distribution (frequency, %) of characteristics of reproductive *Rana temporaria* female: body length (A), age (B), fecundity (C), egg diameter (D), reproductive effort (E), and relative clutch mass (F). The combined yearly data are presented, annual averages are indicated by crosses.

and reproductive effort: as body length increased, this trait remained practically constant (Table 2). The dependence of reproductive characteristics on female size is significantly non-linear. Fecundity is related to body length by positive allometry, both egg diameter and relative clutch mass, by negative allometry (Table 2). Moreover, the shape of relationship varied weakly from year to year (Table 1), which confirms the specificity of relationship of each trait with body length (for details, see below).

Only female body length correlated highly positively (and significantly) with age (Table 2). In addition, average values of each age (Table 1) differed among themselves (except for 6- and 7-year-olds),

which was demonstrated by results of one-way ANOVA and post hoc multiple comparisons. The correlations of age with fecundity, egg diameter and relative clutch mass were much weaker although they remained significant (Table 2). The same result was revealed by comparison of average values of each age. Fecundity of 7-year-old females does not differ from fecundity of all other ages, fecundity of 4-year-old females does not differ from fecundity of 5-year-olds, which in turn does not differ from 6-year-olds. Correlation between age and egg size was somewhat higher (Table 2). The average egg diameter of 3-year-old females was significantly smaller than in all other ages, in 4-year-old females, smaller than in 6- and 7-year-olds, and in 5-year-old females, smaller than in

Table 1. Body size, age, and reproductive characteristics of females

Sample	Body length (mm)			Egg diameter (mm)		Fecundity		Reproductive effort		Relative clutch mass			Age	
	<i>n</i>	<i>x</i>	<i>CV</i>	<i>x</i>	<i>CV</i>	<i>x</i>	<i>CV</i>	<i>x</i>	<i>CV</i>	<i>n</i>	<i>x</i>	<i>CV</i>	<i>x</i>	<i>CV</i>
Total	290	76.53	8.989	1.758	8.048	1714	28.49	0.021	28.59	201	0.287	13.58	4.39	27.38
1993	89	76.25	8.662	1.879	6.793	1605	32.82	0.024	32.05	–			4.15	26.11
1994	60	77.92	9.620	1.739	5.467	1756	27.62	0.019	17.83	60	0.290	10.44	4.55	26.08
1995	41	78.66	7.318	1.683	5.137	1890	23.70	0.018	18.85	41	0.297	10.68	4.68	28.02
1996	40	75.14	8.932	1.724	7.201	1775	26.51	0.021	24.78	40	0.298	13.34	4.38	30.49
1997	60	75.08	9.390	1.674	7.357	1672	26.11	0.018	22.16	60	0.270	16.73	4.42	26.79
3-year-olds	74	70.01	6.899	1.676	7.214	1494	28.28	0.020	29.56	45	0.272	15.41		
4-year-olds	91	75.37	6.219	1.760	6.982	1711	28.34	0.022	32.04	63	0.290	13.00		
5-year-olds	67	80.24	5.846	1.784	8.191	1829	24.46	0.020	20.22	48	0.294	11.64		
6-year-olds	35	82.77	7.775	1.848	7.846	1946	28.33	0.021	28.70	24	0.294	10.37		
7-year-olds	12	84.83	6.512	1.845	7.326	1692	30.24	0.017	24.65	11	0.277	19.01		
8-year-olds	2	83.50	9.315	1.733	2.653	2214	16.82	0.021	28.84	2	0.334	9.083		

n is sample size; *x*, mean value; *CV*, coefficient of variation, %.

Table 2. Dependence of reproductive characteristics of *Rana temporaria* females on their body length and age (data combined through all years)

Character	Body length (X)			Age (X)		
	<i>r</i>	<i>a</i>	<i>b</i>	<i>r</i>	<i>a</i>	<i>b</i>
Body length	–	–	–	<u>0.672</u>	54.740	0.231
Fecundity	<u>0.496</u>	2.133	1.541	<u>0.280</u>	1101.000	0.305
Egg diameter	<u>0.439</u>	0.324	0.390	<u>0.380</u>	1.480	0.119
Relative clutch mass	<u>0.233</u>	0.063	0.349	<u>0.175</u>	0.251	0.094
Reproductive effort	–0.058	0.043	–0.169	–0.040	0.022	–0.032

r is correlation coefficient; *a*, *b*, allometric coefficients in equation $Y = aX^b$. Values of *r* significantly differed from 0 are underlined.

6-year-olds. The average value of relative clutch mass of 3-year-old females was significantly smaller than in 4-, 5-, and 6-year-olds. Only a significant correlation between age and reproductive effort was not revealed (Table 2): as age increased the average values of this characteristic both increased and decreased. Thus, the average reproductive effort in 4-year-olds was larger than in 5- and 7-year-olds, whereas in 6-year-olds it was larger than in 7-year-olds.

All the above characteristics were related with age by negative allometry, with values of power coefficient *b* not exceeding 0.305 (Table 2). As in the case of relationship with body length, this dependence of each trait on age changes from year to year weakly. The exception was a strong increase of egg sizes with age in the sample of 1993 (Table 1).

Relationship of Age and Season Dynamics of Reproductive Characteristics

Together with general tendency to increase average values (for each age) of most characters, strong differences between generations were revealed among generations (within each age) (Figs. 2–6). The 4-year-old females born in 1989 and 1993, born in 1990 and 1991, born in 1990 and 1992 (Fig. 2A) differed significantly in average body length (according to results of one-way ANOVA and post hoc multiple comparisons). The 5-year-old females born in 1988 and 1990, born in 1988 and 1992 differed significantly in average fecundity (Fig. 3A). The differences among generations in average egg size were revealed within each age except for 7-year-olds (Fig. 4A), with the earlier generations (born in 1986–1989) characterized

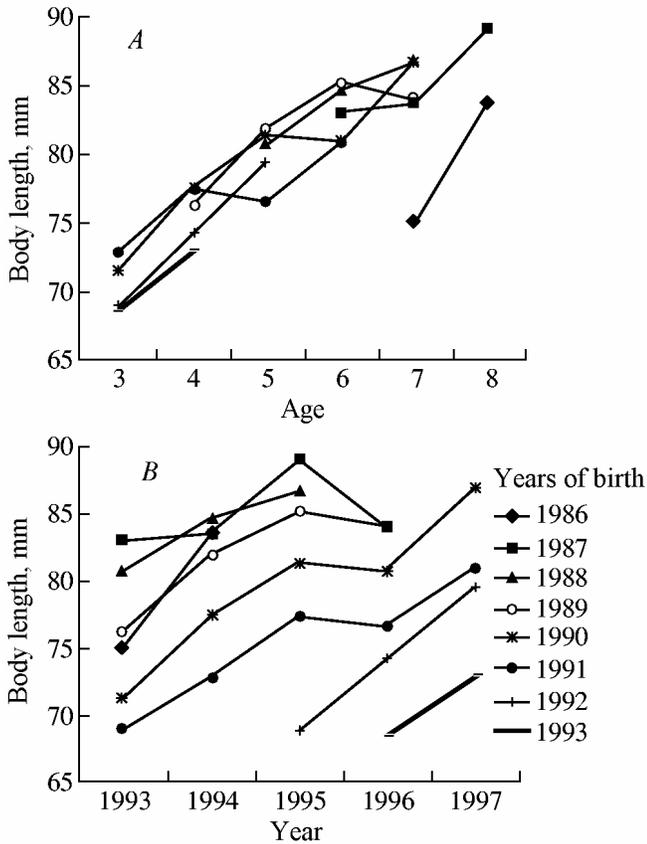


Fig. 2. Changes in average (for each generation) values of body length: (A) age dynamics, (B) yearly dynamics.

by larger average egg diameters at each given age. A similar tendency was revealed for average (for each generation) values of reproductive effort (Fig. 5A) among 3-, 4- and 5-year-old females. Significant differences between generations were not revealed only in average relative clutch mass (Fig. 6A).

At the same time, yearly changes were revealed that cannot be explained only by aging within a given generation. Thus, from 1993 to 1994 and from 1994 to 1995 an increase in average body length (Fig. 2B) occurred in all generations (except for the latest generations born in 1992 and 1993), in spite of the fact that each year the generations were represented by individuals of different ages. This increase from 1993 to 1994 was significant in generations of 1989 and 1990, the increase from 1994 to 1995 was significant in generation of 1991. Hereafter, i.e. from 1995 to 1996, a decrease in mean body length was recorded, regardless of increase of age of each generation by one year! The exception was the increase in late generation of 1992 (mean body length was larger in 4-year-olds than in 3-year-olds). A similar tendency was also re-

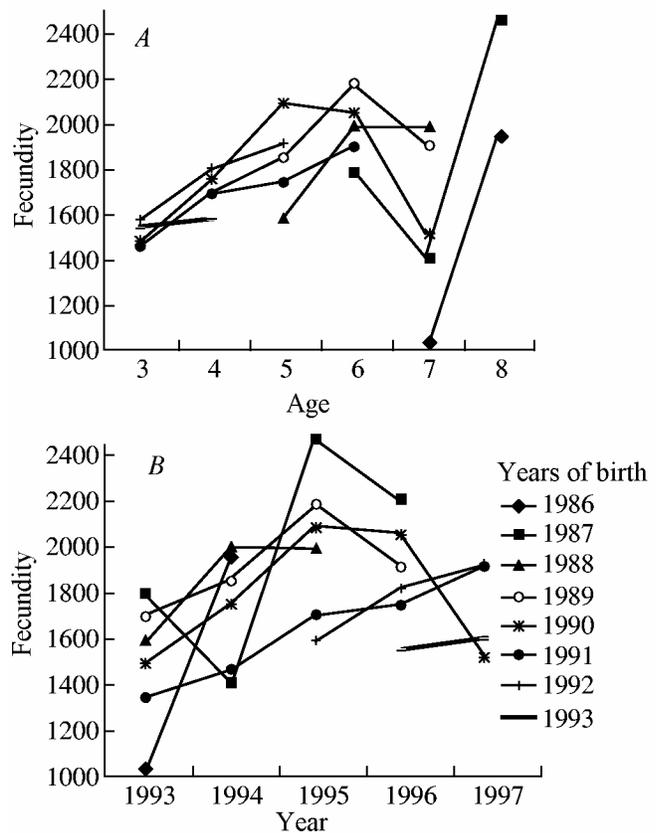


Fig. 3. Changes in average (for each generation) values of fecundity: (A) age dynamics, (B) yearly dynamics.

vealed in the case of fecundity (Fig. 3B) which (as already mentioned) was connected with body length by high positive correlation. The increase of mean fecundity from 1993 to 1994 was significant in generations of 1988 and 1990, those from 1994 to 1995, in generation of 1990.

The dynamics of yearly changes in egg sizes (Fig. 4B) was different: a decrease in annual mean values of this trait occurred in most generations from 1993 to 1994; lack of such tendency, from 1994 to 1995, and increase (contrary to body length), from 1995 to 1996. The increase from 1993 to 1994 was significant in generations of 1988 and 1989. The increase from 1995 to 1996 was significant in generations of 1989, 1990, and 1991. Similar dynamics occurred in the case of reproductive effort (Fig. 5B), but only decrease in average values from 1993 to 1994 in generation of 1989 was significant.

Annual averages of relative clutch mass (Fig. 6B) remained virtually constant in all generations (except for increase of this index in 7-year-old females born in 1990). In other words, the yearly change of the charac-

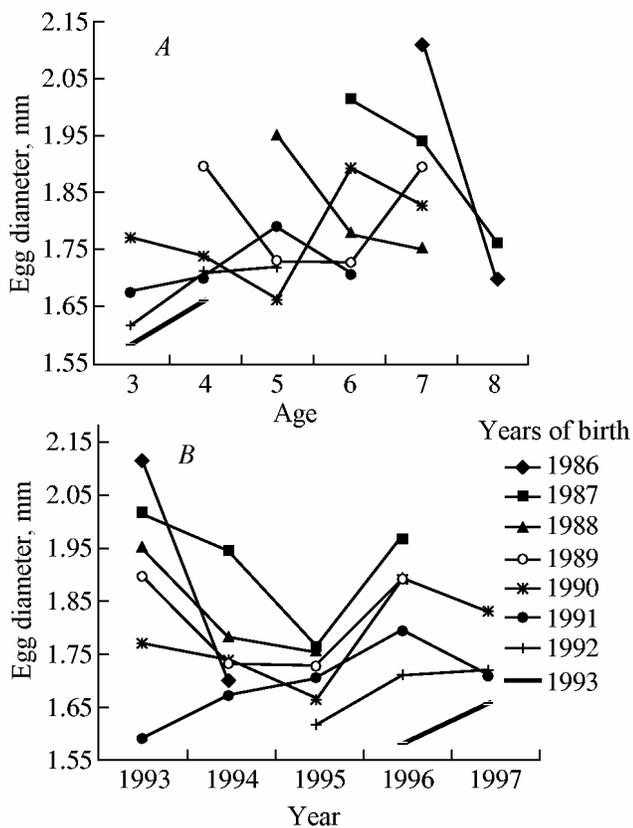


Fig. 4. Changes in average (for each generation) values of egg diameter: (A) age dynamics, (B) yearly dynamics.

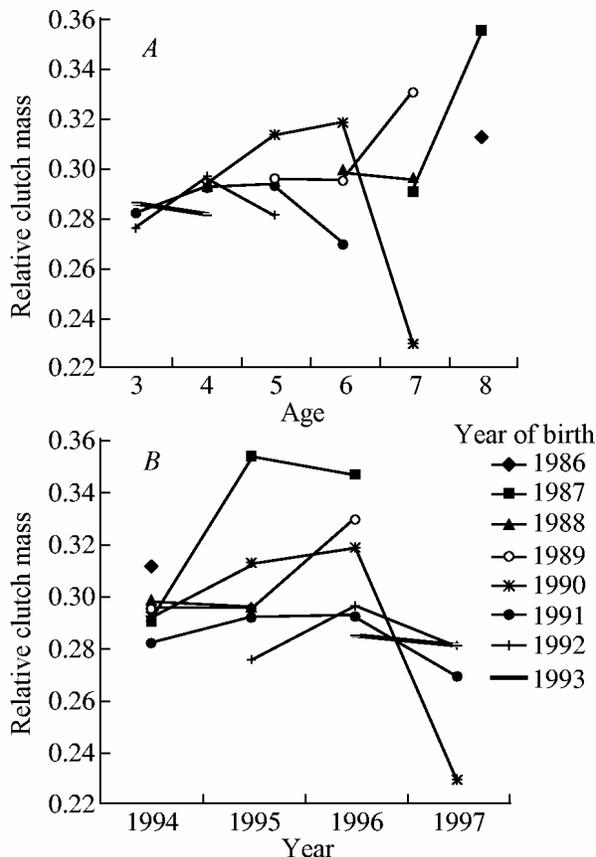


Fig. 6. Changes in average (for each generation) values of relative clutch mass: (A) age dynamics, (B) yearly dynamics.

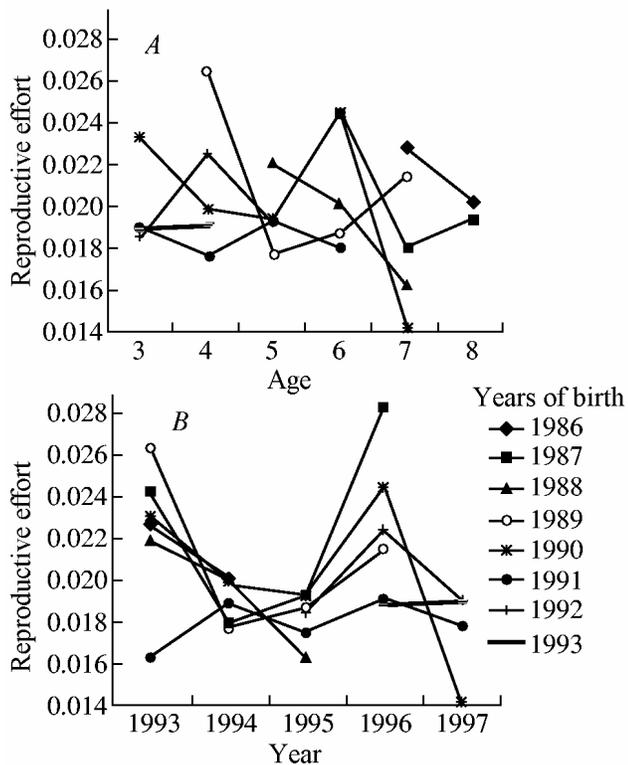


Fig. 5. Changes in average (for each generation) values of reproductive effort: (A) age dynamics, (B) yearly dynamics.

teristic also differed from dynamics of the above characteristics. Unlike dynamics of reproductive effort, this characteristic was more independent of yearly changes of conditions. Thus, the character of differences between generations within a given age was specific for each of the traits examined. By themselves, these differences are affected by yearly changes similar for a number of successive generations, independent on age or weakly dependent on it.

Relationship of Reproductive Characteristics, Body Size, and Age

Together with calculation of correlations and regression of single pairs of traits, the analysis of the principal components (PCA) was employed for estimation of the general picture of relationship of body length of females, their age, fecundity, relative clutch mass, reproductive effort and egg diameter. By application of PCA the factor rotation (by method "varimax normalized") was used that enables us to distinguish the set of correlated traits more successfully (Okun, 1974; for more detailed description of application of

PCA for analysis of ontogenesis processes, see Scobeyeva and Cherdantsev, 1999). As different generations in different years were represented by differing frequencies of ages, we first examined the structure of relationship between reproductive characteristics within each of the ages. Note that although the 5 principal components (PC) were extracted, all traits demonstrated relatively low loading to 5th PC. The relationship of traits, i.e. their collective investment into each of the three PC (their factor loadings, Table 3), was very similar at different ages. Slight differences were revealed in 5-year-olds and 7-year-olds only. Reproductive effort correlated significantly with fecundity, contributing the maximum loading to 1st PC (in 5-year-olds, to 3rd PC); body length, egg diameter and relative clutch mass did not correlate between themselves and with other traits and contributed the maximum loading to other (different) PCs.

Such similarity allowed us to combine all ages by which each generation in different years was represented, i.e. to introduce age to the set of examined traits, thereby expanding the number of extracted PCs to 5 (since the loading of each trait to 6th PC was small). PCA was performed separately for each generation, except for the earliest and the latest, represented by low number of individuals (Table 4, left part). Fecundity usually strongly correlated either with body length (in generations of 1988, 1989 and 1991), or with reproductive effort (in generations of 1990 and 1992). However, these traits as well as each of the 4 other traits had maximum factor loading to different (1st, 2nd, 3rd, 4th, or 5th) PC, with the proportion of each of these PC relatively to total variation being approximately equal and constituting not less than 15% (confirming the necessity of extraction of the four PCs). In some generations (of 1990, 1991, and 1992) a strong correlation between age and body length was revealed.

Besides the effect of age and generation, an additional source of variation of structure of relationship between traits can be differences between years of study. For revealing of these potential differences, the samples of each year were examined (Table 4, right part). By such combining, fecundity as before, gave maximum loading to one of PCs together with reproductive effort, and occasionally (1994), to other PCs together with body length. As in the case of different generations, the maximum loading of egg diameter (to the 3rd PC) was not connected with loadings of other traits. The exception was a relatively strong connection of this trait with age and with body length

Table 3. Structure of relationship (factor loadings, the maximum values are underlined) between characters in *R. temporaria* females of different age

Character	Principal component			
	1	2	3	4
3-year-olds				
Body length	0.01	0.18	<u>0.97</u>	0.17
Relative clutch mass	0.33	0.07	0.22	<u>0.91</u>
Reproductive effort	<u>0.95</u>	0.15	-0.07	0.28
Fecundity	<u>0.72</u>	-0.31	0.56	0.26
Egg diameter	0.04	<u>0.99</u>	0.12	0.07
4-year-olds				
Body length	0.03	<u>0.97</u>	0.24	0.08
Relative clutch mass	0.30	0.09	0.07	<u>0.95</u>
Reproductive effort	<u>0.93</u>	-0.21	0.16	0.23
Fecundity	<u>0.89</u>	0.34	-0.17	0.24
Egg diameter	0.01	0.22	<u>0.97</u>	0.07
5-year-olds				
Body length	<u>0.96</u>	0.24	-0.06	0.10
Relative clutch mass	0.14	-0.18	0.19	<u>0.95</u>
Reproductive effort	-0.03	0.13	<u>0.98</u>	0.17
Fecundity	<u>0.62</u>	-0.47	0.54	0.28
Egg diameter	0.18	<u>0.96</u>	0.12	-0.17
6-year-olds				
Body length	-0.09	<u>0.85</u>	0.42	-0.31
Relative clutch mass	<u>0.94</u>	0.09	0.08	0.32
Reproductive effort	0.43	0.03	0.20	<u>0.88</u>
Fecundity	0.19	<u>0.94</u>	-0.14	0.24
Egg diameter	0.10	0.06	<u>0.98</u>	0.16
7-year-olds				
Body length	-0.01	-0.17	<u>0.99</u>	0
Relative clutch mass	<u>0.96</u>	0.04	-0.02	-0.28
Reproductive effort	<u>0.96</u>	-0.17	-0.13	0.19
Fecundity	<u>0.82</u>	0.46	0.29	0.17
Egg diameter	0	<u>-0.98</u>	0.19	0.01

(1st PC) in 1996. Note also that in 1993, 1994, and 1994 age did not correlate with any other trait. It means that fecundity, egg diameter and relative clutch mass had such variance component that is affected neither by general size, nor by age. In all appearance, this component is to be interpreted as environment variation. It should be noted that the relationship between fecundity and egg diameter has also two com-

Table 4. Structure of relationship (factor loadings, the maximum values are underlined) between characters in *R. temporaria* females of different generations (years of birth are indicated, left part of the table) and different years of study (years of sampling are indicated, right part of the table)

Character	Principal component									
	1	2	3	4	5	1	2	3	4	5
	1988					1993				
Age	0	0.05	<u>-0.97</u>	0.07	-0.22	0.40	-0.01	0.35	<u>0.85</u>	
Body length	0.14	<u>0.78</u>	-0.12	-0.46	-0.38	0.22	0.08	<u>0.92</u>	0.31	
Relative clutch mass	<u>-0.95</u>	0.07	0	0.18	0.26	On 1993 data absent				
Reproductive effort	-0.30	0.06	0.28	0.03	<u>0.91</u>	0.27	<u>0.94</u>	-0.18	-0.03	
Fecundity	-0.16	<u>0.95</u>	0.01	0.13	0.22	-0.14	<u>0.90</u>	0.41	0.05	
Egg diameter	0.16	0.03	0.08	<u>-0.98</u>	-0.02	<u>0.91</u>	0.11	0.20	0.34	
	1989					1994				
Age	0.17	0.24	0.06	<u>0.95</u>	0.08	0.19	-0.01	0.18	<u>0.96</u>	0.08
Body length	-0.01	0.34	<u>0.92</u>	0.07	0.16	<u>0.85</u>	-0.26	0.39	0.21	0.09
Relative clutch mass	0.44	0.09	0.30	0.10	<u>0.83</u>	0.18	0.22	0.02	0.08	<u>0.95</u>
Reproductive effort	<u>0.91</u>	0.03	0.14	0.20	0.32	0.06	<u>0.97</u>	0.04	-0.02	0.22
Fecundity	0.48	-0.24	<u>0.80</u>	0.05	0.24	<u>0.89</u>	0.34	-0.16	0.13	0.20
Egg diameter	0.01	<u>0.96</u>	0.11	0.24	0.06	0.06	0.04	<u>0.98</u>	0.17	0.01
	1990					1995				
Age	0.03	0.25	0.14	<u>0.95</u>	-0.13	<u>0.95</u>	0	0.20	0.14	0.19
Body length	0.01	<u>0.93</u>	0.21	0.29	-0.02	0.62	-0.04	0.31	0.23	<u>0.69</u>
Relative clutch mass	-0.35	-0.03	-0.08	-0.14	<u>0.92</u>	0.18	0.34	0.03	<u>0.91</u>	0.15
Reproductive effort	<u>-0.83</u>	-0.35	0.32	-0.08	0.27	-0.09	<u>0.95</u>	0.13	0.25	-0.04
Fecundity	<u>-0.84</u>	0.30	-0.33	0.03	0.31	0.38	<u>0.62</u>	-0.25	0.41	0.48
Egg diameter	0.01	0.19	<u>0.97</u>	0.15	-0.08	0.20	0.06	<u>0.97</u>	0.01	0.08
	1991					1996				
Age	0.36	-0.01	0.15	-0.09	<u>0.92</u>	<u>0.89</u>	0.13	0.17	0.01	-0.41
Body length	<u>0.87</u>	-0.18	0.22	0.10	0.38	<u>0.82</u>	0.13	0.06	0.56	0.01
Relative clutch mass	0.18	0.34	0.11	<u>0.91</u>	-0.09	0.14	0.31	<u>0.94</u>	0.04	-0.03
Reproductive effort	-0.02	<u>0.92</u>	0.19	0.33	-0.04	0.12	<u>0.95</u>	0.24	-0.17	0.02
Fecundity	<u>0.74</u>	0.45	-0.33	0.31	0.23	0.13	<u>0.88</u>	0.20	0.39	-0.07
Egg diameter	0.04	0.15	<u>0.97</u>	0.10	0.15	<u>0.98</u>	0.11	0.09	0.01	0.15
	1992					1997				
Age	0.03	<u>0.94</u>	0.14	0.01	0.30	<u>0.95</u>	-0.05	0.27	-0.03	0.15
Body length	0.06	0.39	0.25	-0.04	<u>0.88</u>	<u>0.59</u>	-0.16	0.54	0.14	0.56
Relative clutch mass	0.27	0.01	-0.14	<u>0.95</u>	-0.02	-0.01	0.31	0	<u>0.93</u>	0.18
Reproductive effort	<u>0.95</u>	-0.05	0.18	0.20	-0.15	-0.12	<u>0.94</u>	0.07	0.29	0.11
Fecundity	<u>0.85</u>	0.13	-0.24	0.21	0.39	0.26	0.53	-0.10	0.35	<u>0.72</u>
Egg diameter	0.01	0.14	<u>0.96</u>	-0.14	0.18	0.26	0.08	<u>0.96</u>	-0.03	-0.02
						All years				
Age						0.25	-0.01	0.27	0.06	<u>0.93</u>
Body length						<u>0.76</u>	-0.19	0.47	0.12	0.38
Relative clutch mass						0.19	0.28	0.04	<u>0.94</u>	0.06
Reproductive effort						0.07	<u>0.96</u>	0.09	0.26	-0.04
Fecundity						<u>0.79</u>	0.50	-0.13	0.29	0.17
Egg diameter						0.07	0.09	<u>0.96</u>	0.03	0.24

Table 5. Minimum, maximum, and average values (\bar{x}) of body length (mm) of mature *Rana temporaria* females, literature data

Locality of study	Min	\bar{x}	Max	Source
Northern Sub-Ural	72.5	78.6	89.0	Anufriev and Bobretsov, 1996
Belarus	39.0	60.8	70.0	Ishchenko, 1978
Leningrad Province	47.0	64.1	80.0	Ishchenko, 1978
Polar Ural	54.0	70.3	82.0	Ishchenko, 1978
Northern Ural	52.0	67.2	85.0	Ishchenko, 1978
Sverdlovsk Province	51.0	62.3	77.0	Ishchenko, 1978
Belarus	51.0		67.2 ¹	Pikulik, 1985
Leningrad Province	55.0	–	85.0	Terentjev, 1945, 1950
Polar Ural	53.4	–	83.0	Toporkova and Zubareva, 1965
Eastern France, population 1	50.0	63.7 ... 67.1	85.0	Augert and Joly, 1993
Eastern France, population 2	43.0	52.6 ... 61.8	80.0	Augert and Joly, 1993
England, Lincolnshire		58.3 ... 61.8		Cummins, 1986
England, Norfolk		63.1 ... 69.6		Cummins, 1986
England, Cambridgeshire		77.5 ... 81.2		Cummins, 1986
England, Devon		66.3 ... 68.2		Cummins, 1986
Central Sweden, 50 m above sea level	–	76.5	–	Elmberg, 1991
Northern Sweden, 430 m above sea level	–	79.3	–	Elmberg, 1991
Northern Sweden, 820 m above sea level	–	73.3	–	Elmberg, 1991
Southern Sweden	–	57.0	70.0	Loman, 1978
Western Germany	55.0	68.8	85.0	Geisselmann <i>et al.</i> , 1971
Western Germany	70.0	89.3	107.0	Schluepmann, 1981
Western Ireland	54.0	66.6	82.0	Gibbons and McCarthy, 1984
Western Ireland	50.4	67.5	80.7	Gibbons and McCarthy, 1986
Swiss Alps, 655 m above sea level	63.0	79.0	96.0	Heusser, 1970
North-eastern Slovakia	58.0	82.2	100.0	Kminiak, 1971
Northern Finland	–	79.6	90.0	Koskela and Pasanen, 1974
Poland, 200 m above sea level	67.0	80.5	103.0	Kozłowska, 1971
Poland, 700 m above sea level	69.0	89.0	100.0	Kozłowska, 1971
Poland, 1000 m above sea level	78.0	87.4	100.0	Kozłowska, 1971
Poland, upward of 1000 m above sea level	65.0	78.0	94.0	Kozłowska, 1971
Spain, Barcelona	65.0	–	–	Montori and Pascual, 1987
Switzerland, 600 m above sea level	62.0	80.2 ... 81.6	98.0	Ryser, 1988
Switzerland, 1930 m above sea level	65.0	80.6	94.0	Ryser, 1996

The minimum and maximum average values are cited, if in given study data of several populations of one locality or of several years are presented.

¹In all likelihood, original study contains erratum and the correct value is 87.2 mm.

ponents: along the 1st PC (with maximum loading of body length) the correlation between them is slightly positive, along the 3rd PC (with low loading of body length but maximum loading of egg diameter) the correlation is negative. This ambiguousness is confirmed by values of correlation coefficients between fecundity

and egg diameter: the simple correlation (Pearson coefficient) being virtually equal to zero (–0.058), whereas the partial correlation that remains after accepting body length effect (i.e. analogous to component that did not depend on general size) is weakly negative but significant (–0.353).

DISCUSSION

Variation of Reproductive Characteristics

The maximum body length in females of most other localities of *R. temporaria* range does not exceed the corresponding value in population under our study (literature data are summarized in Table 5). Therefore, the scale of revealed intrapopulation variation of size is quite comparable with size variation in other localities of species range. The higher values of maximum body size of *R. temporaria* females were recorded only in southern parts of the range (Poland, Slovakia, Germany, Switzerland). We also noted a similar tendency when comparing *R. arvalis* in Moscow Province with southern population of Kiev Province (Lyapkov, 1999). However, the comparison of average sizes does not allow us to reveal directional changes: females of both southern and northern populations are characterized by larger body size (as compared with our data). It will be also noted that certain literature data may be somewhat underestimated, since females were collected after breeding season and part of them (according to external characters belonging to mature frogs) had not yet bred. In addition, in some instances preserved frogs were measured, whose size decreases by preservation (Lee, 1982). According to our data, after preservation in 5-% formaldehyde solution their body length decreased on the average by 2.8 %.

The population of central temperate zone under our study is mostly similar to that of Leningrad Province

(Ishchenko, 1996) in modal value and limits of age distribution. On the one hand, females of the population studied bred firstly at a later age than females in southern populations (Table 6). On the other hand, in the population studied extremely old individuals (10-year-olds and older), which are distinctive for northern and mountain populations, are absent.

Average and limit values of fecundity recorded in our study coincide in general with those of other localities of temperate zone of similar latitude (Table 7). It remains unknown why early in the same population of Zvenigorod Biological Station (Surova and Cherdantsev, 1987) much higher average and maximum values of fecundity were recorded, by which (according to our data) the oldest females are characterized (see Table 1). Comparing our data with the literature does not enable us to reveal the directional trend of geographic variation. It may be only concluded that in the central part of the range fecundity is somewhat higher than in its northern and southern parts, and in addition decreases in mountain populations of the given latitude.

Average and limit values of egg size (see Table 1 and Fig. 1) are similar in general to ones recorded in populations of many other localities of the temperate zone (Table 8). Somewhat larger eggs were recorded in the northern location of the temperate zone (Koskela and Pasanen, 1975) as well as in mountain populations of Poland and Switzerland. The reasons

Table 6. Minimum, maximum, and average values (\bar{x}) of age (number of winterings) of mature *Rana temporaria* females, literature data

Locality of study	Min	\bar{x}	Max	Source
Eastern France, population 1	2	–	5	Augert and Joly, 1993
Eastern France, population 2	2	–	6	Augert and Joly, 1993
Central Sweden, 50 m above sea level	3	3.7	6	Elmberg, 1991
Northern Sweden, 430 m above sea level	3	4.8	7	Elmberg, 1991
Northern Sweden, 820 m above sea level	5	6.0	7	Elmberg, 1991
Southern Sweden	2	–	6	Loman, 1978
Western Ireland	2	3.3	6	Gibbons and McCarthy, 1986
Swiss Alps, 655 m above sea level	3	–	8	Heusser, 1970
Belarus	2	–	7	Ishchenko, 1996
Leningrad Province	2	–	6	Ishchenko, 1996
Polar Ural	2	–	13	Ishchenko, 1996
Sverdlovsk Province	2	–	7	Ishchenko, 1996
French Alps, 2000 m above sea level	4	–	8	Miaud and Guyetant, 1998
French Alps, 2300 m above sea level	5	–	12	Miaud and Guyetant, 1998
Switzerland, 600 m above sea level	2	4.6	8	Ryser, 1988
Switzerland, 1930 m above sea level	4	8.3	13	Ryser, 1996

Table 7. Minimum, maximum, and average values (\bar{x}) of fecundity of mature *Rana temporaria* females, literature review

Locality of study	Min	\bar{x}	Max	Source
Pechoro-Ilych Nature Reserve	547	1509	2501	Anufriev and Bobretsov, 1996
Suburb of Syktyvkar	632	1149	1768	Anufriev and Bobretsov, 1996
Karelia	920	1916	3126	Ivanter, 1980
Moscow Province	100	2023	3416	Terentjev, 1950
Polar Ural	840	–	2178	Toporkova and Zubareva, 1965
Moscow Province, Zvenigorod Biological Station	500	2394	5500	Surova and Cherdantsev, 1987
Southern England	1067	1329	1608	Cooke, 1975
Central Sweden, 50 m above sea level	–	1782	–	Elmberg, 1991
Northern Sweden, 430 m above sea level	–	1876	–	Elmberg, 1991
Northern Sweden, 820 m above sea level	–	1589	–	Elmberg, 1991
Western Ireland	131	1008	1897	Gibbons and McCarthy, 1986
Finland, 60–61° N	–	1040	–	Haapanen, 1982
Finland, 61–62° N	–	980	–	Haapanen, 1982
Finland, 65–66° N	–	1070	–	Haapanen, 1982
Finland, 68–70° N	–	910	–	Haapanen, 1982
Switzerland (Basel)	739	1431	2605	Hintermann, 1984
Germany (Baden-Wuerttemberg)	1578	1858	2679	Hoening, 1966
Eastern France	250	–	2900	Joly, 1991
North-eastern Slovakia	1002	1456	2489	Kminiak, 1975
North-eastern Slovakia	–	1568	3150	Kminiak, 1987
Northern Finland	652	107	1885	Koskela and Pasanen, 1975
Poland, 200 m above sea level	1119	2522	4390	Kozłowska, 1971
Poland, 700 m above sea level	1156	2340	3740	Kozłowska, 1971
Poland, 1000 m above sea level	897	1880	2670	Kozłowska, 1971
Poland, upward of 1000 m above sea level	1231	1662	2485	Kozłowska, 1971
Switzerland, 600 m above sea level	726	–	1901	Ryser, 1989
Switzerland, 1930 m above sea level	784	–	1616	Ryser, 1996

Table 8. Minimum, maximum, and average values (\bar{x}) of egg diameter (mm) of mature *Rana temporaria* females, literature data

Locality of study	Min	\bar{x}	Max	Source
Moscow Province, Zvenigorod Biological Station	1.50	1.77	2.05	Surova and Cherdantsev, 1987
Western Ireland	1.68	2.32	2.70	Gibbons and McCarthy, 1986
Switzerland (Basel)	2.19	2.41	2.84	Hintermann, 1984
Denmark	1.10	–	1.90	Jorgensen, 1981
Northern Finland	1.79	1.99	2.34	Koskela and Pasanen, 1975
Poland, 200 m above sea level	1.58	1.75	1.93	Kozłowska, 1971
Poland, 700 m above sea level	1.76	1.95	2.16	Kozłowska, 1971
Poland, 1000 m above sea level	1.76	1.98	2.24	Kozłowska, 1971
Poland, upward of 1000 m above sea level	1.67	1.96	2.21	Kozłowska, 1971
Switzerland, 600 m above sea level	–	1.83	2.38	Ryser, 1988a

Table 9. Minimum, maximum, and average values (\bar{x}) of relative clutch mass (%) of mature *Rana temporaria* females, literature data

Locality of study	Min	\bar{x}	Max	Source
Eastern France, population 1	–	31.5	–	Augert, 1992
Eastern France, population 2	–	38.5	–	Augert, 1992
Eastern France	–	26.5 ... 43.5	–	Joly, 1991
Western Ireland	21.0	37.0	46.0	Gibbons and McCarthy, 1986
Switzerland	–	31.4	–	Grossenbacher, 1980
Switzerland (Basel)	21.0	34.0	49.0	Hintermann, 1984
Switzerland, 600 m above sea level	14.8	33.2 ... 37.1	53.1	Ryser, 1989
Germany	–	30.6 ... 36.6	–	Hellbernd, 1987
Germany (Baden-Wuerttemberg)	23.0	–	44.0	Hoening, 1966
Denmark	25.0	–	31.0	Jorgensen <i>et al.</i> , 1979
Poland	–	17.2	–	Juszczyk, 1959
Northern Finland	–	27.4	–	Koskela and Pasanen, 1975

The minimum and maximum average values are cited, if in given study data of several populations of one locality or of several years are presented.

for relatively larger eggs existing in populations of west Ireland, in which females were characterized by relatively small sizes (Gibbons and McCarthy, 1986), remain unclear. The relatively large egg size in the population near Basel (Hintermann, 1984) can be explained by the fact that in this study preserved material was measured.

Average values of relative clutch mass in population under our study (see Table 1) were somewhat smaller than in most populations from other parts of the range (Table 9). Comparison of our and literature data indicate that higher values of this characteristic of reproductive output are usual in southern parts of the range. However, both southern (Poland) and northern (northern Finland) populations were characterized by somewhat lower values of relative clutch mass. In all appearance, this similarity is explained by possible lack of relationship between diversity of habitats of populations and latitudinal gradient.

At the same time, the revealed high stability of relative clutch mass (both with aging and in relation to intergeneration differences) enables us to suggest that the females of any age have the maximized reproductive output under given environmental conditions. The reason is that changes in these conditions do not exceed the tolerance limits of the species, and the unfavorable effects are damped by behavior (i.e. by diurnal and seasonal dynamics of activity). It is also confirmed by comparatively low variation of relative clutch mass (Fig. 1 and Table 1). In addition, the revealed stability

of this characteristics indicates that it most adequately describes the reproductive output of a given individual.

Another peculiarity is revealed by interspecies comparison. Despite *R. temporaria* females of the population studied differing substantially in larger body length and larger fecundity, as well as in somewhat larger egg size, than females of sympatric *R. arvalis* population (Cherdantsev *et al.*, 1997), the value of reproductive effort in *R. temporaria* is significantly lower. According to our unpublished data on relative clutch mass in Zvenigorod population of *R. arvalis* and to data on trans-Uralian population (from 15.9 to 47.9%, average 33.4 %, see Ishchenko, 1999), this characteristic in *R. temporaria* is also significantly lower than in *R. arvalis*.

Intrapopulation differences in body size of reproduced females of *R. temporaria* and in egg size from year to year were revealed in each of the four localities of England (Cummins, 1986) and in one locality of western Ireland (Gibbons, McCarthy, 1986). Similar differences in body size of females were revealed within one locality in eastern France (Augert and Joly, 1993). Yearly differences in relative clutch mass were revealed in Switzerland (Ryser, 1989) and in eastern France (Joly, 1991).

In addition, the effect of abiotic factors (temperature and precipitation, during warm season before reproduction) on body size and reproductive characteristic was also recorded in some other temperate spe-

cies: in *R. arvalis* (on body length and egg size, see Ishchenko, 1999a; Lyapkov *et al.*, 2001a), in *R. sylvatica* (on fecundity, egg size, age at first reproduction, see Berven, 1982, 1988) and in *Bufo bufo* (on fecundity, see Reading and Clarke, 1995).

The importance of ambient conditions for development of size and number of ovulated eggs was demonstrated in several common species of the temperate zone, including *R. temporaria* (Jorgensen *et al.*, 1979). It is known that during gonads development the reserve of fat body was of significant importance. In its turn, fat body mass depends on nutrient conditions during the warm season. In addition, in large females of *R. temporaria* the total number of mature oocytes may be restricted by the total number of immature oocytes (Jorgensen, 1981), i.e. there exists a physiological mechanism of fecundity limitation independent of the environment.

Note that our data yearly dynamics of sympatric populations enable us to reveal similar changes in size and reproductive characteristics in *R. temporaria* (Figs. 2, 4, and 5) and *R. arvalis* (see fig. 4 in Lyapkov *et al.*, 2001a). Thus, an increase in body length in all generations of both species was recorded from 1993 to 1995. From 1993 to 1994 in both species decrease (in most generations) or weak increase of egg size as well as decrease of reproductive effort (in all generations) also occurred. Such a similar reaction of two close brown frog species confirms the significant importance of environmental conditions for development of reproductive characteristics directly connected with fitness.

Our data and the literature reviewed enable us to conclude that: (1) the level of intrapopulation (among years and among generations) variation of reproductive characteristics is comparable with that of interpopulation (including geographical) variation; (2) reproductive characteristics are strongly affected by conditions of the warm season prior to reproduction; (3) different characters variously respond to yearly changes of these conditions; (4) most distinct independence both on these ambient conditions and changes with aging is revealed in relative clutch mass; (5) yearly changes in conditions of warm seasons may have a similar effect on different (at least, close) species living sympatrically or syntopically.

Relationship between Reproductive Characteristics, Body Size and Age

The record of strong positive correlation between body length and fecundity and of somewhat weak but

also significant correlation with egg size and with relative clutch mass, revealed in *R. temporaria* in western Ireland (Gibbons and McCarthy, 1986), coincide with the results of our study. A high positive correlation of age with clutch mass ($r = 0.548$, $p < 0.001$) and with egg size ($r = 0.488$, $p < 0.001$) in the Ireland population also coincides with our results ($r = 0.537$ and $r = 0.380$, respectively, $p < 0.01$ in both cases). However, unlike our results (see Table 2), a significant correlation between age and fecundity ($r = 0.093$) was not revealed, in spite of the fact that correlation between age and egg mass was also positive. The possible reason of this discordance is that in the Ireland population the egg size increases more abruptly with aging. In addition, the "fattening" of females may not be limited by a relatively short warm season as in Moscow Province. This condition also levels distinction in fecundity between individuals of different age.

Moreover, relatively fine distinctions in mode of dependence of reproductive characters on body size are possible. Therefore comparison of females of *R. temporaria* between two localities of southwestern England (Cummins, 1986) enables us to reveal interpopulation differences in slopes of linear regression of fecundity on body length: at each given length fecundity was higher in one population than in the other.

In all likelihood, this relative independence of fecundity from body size is a general principle since it was revealed as a result of studying interspecies differences in reproductive and demographic characteristics in lizards of genera *Iguana* and *Scleroglossa* (Clobert *et al.*, 1998). At the same time the revealed independence between changes in body length, fecundity (together with reproductive effort), and egg size enables us to explain the cases of discordance in data on populations from different parts of species range.

A stronger correlation of fecundity, egg size and relative clutch mass with body length than with age means eventually that these reproductive characteristics are affected rather by environmental factors (i.e. by conditions of warm season of the preceding year) than by fitness that determines the age structure of the mature part of population in each given breeding season.

Finally, the revealed relative independence between changes in body length, fecundity (together with reproductive effort), and egg size does not enable us to estimate unambiguously the contribution of each of these traits to general fitness. More specifically, one

more characteristic required for such fitness estimation must be survivability of generation up to the first and then to each successive reproduction. Our following article is devoted to this problem.

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