

# Changes in the life-history strategy of *Gammarus lacustris* (Crustacea, Amphipoda) in water bodies with different environmental conditions

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**Abstract.** Life history features, such as duration of juvenile period, size, and fecundity of individuals, were studied in some *Gammarus lacustris* populations from water-bodies with different temperature regimes. There are two opposite trends in variations of life-history parameters in populations of *G. lacustris*, namely "gigantism" and "dwarfism". The first trend takes place mainly in warm plain and plateau lakes. The second, in other types of water-bodies such as cold alpine lakes, cold springs, and warm geothermal streams. The "gigantic" populations are characterized by a large size of adult females, high fecundity, and a short juvenile period. The "dwarfish" ones are distinguished by small sizes, low fecundity, and a prolonged juvenile period. Such changes in life-history parameters do not correspond with the classical concept of r/K-selection. The decrease of the juvenile periods (r-selection) in the "gigantic" populations is accompanied by an increase of the adult size (K-selection). On the contrary, an increase of the juvenile period (K-selection) in the "dwarf" populations is accompanied by diminished adult size (r-selection). The life-history characteristics of *G. lacustris* populations from water bodies with rather constant temperatures (cold spring, geothermal stream) are in rather good agreement with the so called "A-selection" which occurs in some severe but predictable habitats.

**Key words:** Life-history strategy, r/K-selection, growth and reproduction variability, distribution area, plain and alpine water bodies

## Introduction

The theory of the life history strategy is one of the central concepts in the present-day ecology. However, at present there is no general consensus as to what this term means and how it would be defined (Romanovsky 1984, Williams 1991). Therefore, in most cases this problem is examined within the much more robust "r/K-selection" concept. The several quantitative growth and reproduction param-

eters of the organism and population levels are generally recognized as the determinant factors of opposite r- or K-directions of such selection. Among them there are longevity of the life span stages (especially of the juvenile period), size of organisms in successive stages, fecundity, an intrinsic rate of the population growth, etc (MacArthur and Wilson 1967, Pianka 1970, Begon *et al.* 1986).

These parameters may be very different not only between but within the species, especially if different populations are inhabiting habitats with different ecological conditions. Plasticity of the life-history parameters is one of the most important prerequisites for species adaptation to a wide range of environmental factors (Williams *et al.*, 1995). Unfortunately, trends in changes of these parameters at the subspecies level are poorly known.

This paper aimed at such a study of populations of the amphipod *Gammarus lacustris* Sars. This species has a large distribution area including a greater part of the Arctoboreal zone of continental Eurasia and North America (Dedyu 1980). It may live in almost all types of fresh water bodies, from oligotrophic arctic and mountain lakes to eutrophic plain ponds and from cold springs to geothermal streams. Comparative estimation of the life history parameters in the various *G. lacustris* populations may reveal some trends in species adaptation to a wide range of ecological conditions.

This will allow to clear up the controversial problem of existence of different life-history strategies at the intraspecific level (Brown 1983).

## Material and methods

On the basis of results our own investigations (Golubev and Rosthchin 1990) and available literature data (Table 1) the general trends of the life history changes in populations of *G. lacustris* from water bodies with different environmental conditions have been examined. These water bodies can be divided in this respect into four separate groups.

The first group is composed by lakes and rivers (Lyatskiye, Drisvjaty, Ladoga, Neva estuary) in temperate zone of East European Plain. They are characterized by substantial seasonal temperature changes, from 1-2°C in winter to 22-25°C in midsummer. Such ranges are close to the borders of temperature tolerance for this species within the distribution area.

The second group consists of lakes Ivan, Staroe, Baklanje, Arakhlei, Glubokoe, Uglovoe. They are

located in the southern part of the Middle Siberian plateau (alt. up to 1,000 m) in a zone with extremely continental climate characterized by short but rather hot summers (water temperature up to 23°C) and long severe winters.

The third group is represented by two cold oligotrophic alpine lakes in the Caucasus, namely Sevan (altitude 1,900 m), and Sev-Lich (altitude 2,675 m) with a maximal summer temperature at almost 18°C and Khubsugul (1,645 m) in Mongolia where this temperature reaches only 10-11°C.

The last group includes water bodies with a rather constant temperatures, a geothermal stream in Kamchatka and a cold spring near Baikal shore. In these water bodies, the annual temperatures are varying in the ranges of 14-21°C and 6-8°C, respectively.

For the females released from the first spring brood (the first spring cohort, FSC) of several *G.lacustris* populations, the average values of the following life cycle parameters have been compared. Among them there are duration of the juvenile period ( $D_j$ ); weight of newborn individuals ( $W_o$ ); weight of females at reaching maturity ( $W_g$ ); weight of females at the end of the first growing season ( $W_1$ ); definitive weight of females ( $W_d$ ); the number of offsprings in the first brood of females ( $E_1$ ) and their maximal fecundity ( $E_{max}$ ).

On the basis of the annual temperature dynamics in water bodies the average temperatures for the juvenile period ( $t_{dj}$ ) of the FSC-females have been calculated for each *G.lacustris* population.

The matrix of Spearman's coefficients of correlations for the life-history parameters studied and some characteristics (GS duration,  $t_{dj}$ ) of the water bodies have been calculated.

On the basis of the correlation matrix (except for the data for  $t_{dj}$  and GS), clusterization of *G.lacustris* groups studied was carried out by Ward's method (Sokal and Rohlf 1995).

## Results

Average life history parameters for FSC-females in several *G.lacustris* populations and some characteristics of water-bodies inhabited by them are presented in Table 1. The variability of parameters studied is very different. The values of  $W_o$  are the most stable. On the contrary, the size parameters of adult females ( $W_g$  and  $W_d$ ) differ 5 - 8 times. The fecundity indices ( $E_1$ ,  $E_{max}$ ) have a mean variability of up to 2 - 5 times.

Obviously, since each *G.lacustris* population is adapted to the ecological situation in their habitat, corresponding values of life-history parameters are optimal for such environmental conditions. So far as the temperature and biologic characteristics of the investigated water bodies embrace almost the entire tolerance zone for *G.lacustris*, the ranges of these variations in populations studies almost correspond to their species ranges.

In all the lakes, reproduction of *G.lacustris* (copulation and egg-bearing) begins when the water temperature in the spring season reaches 5 - 6°C. Newborns of the first spring cohort (FSC) emerge at the temperature of about 9-10°C. The reproduction of *G.lacustris* ceases in autumn, when the tem-

perature drops below 9-10 °C. However, the individuals continue growing at the temperatures above 5-6 °C.

The period of a year with water temperatures above 4°C may be defined as the "growing season" (GS) for the species. It lasts 4-5 months in cold alpine lakes and to 7-8 months in rather warm plain water bodies. In geothermal stream and cold spring with relatively narrow changes this season continues all year round.

In general *G.lacustris* has a rather long juvenile period. In populations from warm water bodies ( $t_{dj} > 13$  °C) FSC-females reach sexual maturity by autumn of the same year but start to reproduce in the beginning of the following growing season (Kuzmenko 1964, Shapovalova 1972, Panov 1988, Golubev and Rostchin 1990). This may be explained by the fact that the autumn reproduction does not give any advantages for the *G.lacustris* populations as their newborns do not survive at temperatures below 4-5 °C (Safronov 1993).

In populations that live in cooler Middle Siberian plateau (Arakhlei, Glubokoe, Uglovoe) and alpine (Sevan, Khubsugul) lakes with  $t_{gs} < 13$ °C, FSC-females reach sexual maturity and start reproduction in the middle of the following growing season (Markosjan 1948, Bekman 1954, Shapovalova 1972, Safronov 1993). In the Caucassian lake Sev-Lich such females mature by the end of the second growing season and start to reproduce in the third one (Ostrovskij 1990).

The growth rate of the FSC-juveniles depends on the average temperature in growing season and its duration. Due to the substantial differences of particular *G.lacustris* populations in  $W_g$  (from 4.5 to 35 mg), the growth rates of juveniles from different water bodies have been compared in terms of the relative daily weight increment (Q). It may be calculated as:  $Q = (W_t / W_g \cdot t) \cdot 100\%$ . Where  $W_t$  is the average weight of individuals (mg) at the age  $t$  (days);  $W_g$  is the average weight at reaching sexual maturity. The  $W_g$  value was determined for the age of 90 - 100 days.

Since the growth rate in poikilothermic organisms greatly depends on temperature, the relations between Q and GS was estimated for a group of *G.lacustris* populations from rather warm water bodies with  $t_{gs} > 13$ °C.

A clear significant ( $P < 0.01$ ) negative correlation between Q and GS was established (Fig. 1). Thus, shortening of GS in rather warm water bodies leads to the increase of the relative growth rate of

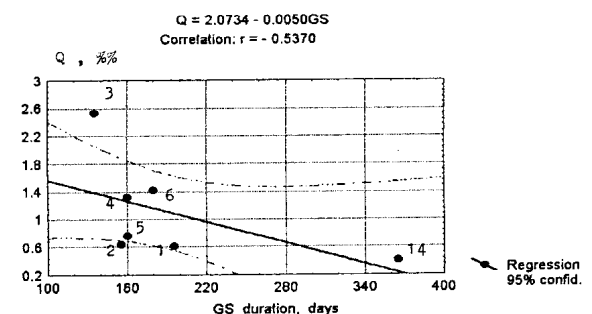


Fig.1. Relationship between duration of growing season (GS, days) and relative weight growth increment (Q, %) in different populations of *G.lacustris*. The numbers of dots correspond to those in Table 1.

Population	Limits of GS	GS	ADB	$D_j$	$W_0$	$W_g$	$W_1$	$W_d$	$E_1$	$E_{max}$	Q	$t_{dj}$	References
	days	days	days	days	mg	mg	mg	mg			%%	°C	
1.Lyatskiye	1Apr-2Oct	195	1\5	125	0.24	35	57	96	18	70	0.61	18.6	Golubev and Rostchin(1990)
2.Drivvjaty	1May-1Oct	155	1\6	120	0.21	25	25	75	20	40	0.64	17.0	Golubev and Rostchin(1990)
3.Ivan	2May-1Oct	140	2\6	73	0.16	9	27	40	10	50	2.53	17.1	Shapovalova (1972)
4.Staroje	1May-2Oct	175	3\5	92	0.37	20	55	80	—	—	1.32	18.0	Bekman (1954)
5.Baklanje	1May-2Oct	160	2\6	115	0.37	20	25	—	—	—	0.76	16.0	Bekman (1954)
6.Neva estu.	1May-1Nov	180	3\5	70	0.25	15	52	55	16	64	1.43	19.2	Panov (1988)
7.Sevan	2Jun-2Dec	240	2\5	195	—	7	9	30	7	19	0.31	13.5	Markosjan (1948)
8.Ladoga L.	3May-2Oct	145	1\7	90	—	15	15	100	—	—	1.11	13.8	Kuzmenko (1964)
9.Arakhlei	1Apr-2Oct	175	1\7	225	0.16	9	5	53	5	44	0.53	10.7	Shapovalova (1973)
10.Glubokoe	2May-2Oct	150	2\6	175	0.37	20	15	40	—	—	0.63	11.5	Bekman (1954)
11.Uglovoe	2May-1Oct	135	1\7	270	0.37	20	4	30	—	—	0.19	10.5	Bekman (1954)
12.Sev-Lich	1Jun-3Oct	150	1\6	300	—	30	9	70	—	—	0.25	13.0	Ostrovskij (1990)
13.Khubsugul	1Jul-3Oct	135	1\6	225	—	4.5	2	30	7	23	0.26	8.0	Erbaeva <i>et al.</i> (1990)
14.Geotherm.	absent	365 all y		120	0.185	10	20	20	5	22	0.41	19.0	Golubev and Rostchin (1990)
15.Cold spring	absent	365 all y		520	—	7	30	30	4	15	0.15	6.5	Golubev and Rostchin (1990), Nesterovich (1990)

**Table 1.** Average values of life-history characters for the first spring cohort in some *Gammarus lacustris* populations. 1-8 = populations where newborns from the first spring cohort reach sexual maturity at the first growing season, and 9-13 = at the second growing season. 14-15 = populations inhabiting waters of relatively constant temperatures, values in italics - the duration of a juvenile stage when the period of a year with the temperatures below 4°C was excluded, underlined - definitive body weight. For abbreviations see Material and methods, and Results. ADB - average date of birth (decade/month).

Variables	GS	$D_j$	$W_0$	$W_g$	$W_1$	$W_d$	$E_1$	$E_{max}$	Q	$t_{dj}$
GS	1.00	0.42	-0.33	-0.35	0.14	-0.32	-0.43	-0.50	-0.24	-0.04
$D_j$		1.00	-0.06	-0.20	-0.35	-0.44	-0.19	<b>-0.52</b>	<b>-0.64</b>	<b>-0.81</b>
$W_0$			1.00	0.48	0.17	0.07	0.16	0.05	-0.15	0.04
$W_g$				1.00	0.39	<b>0.53</b>	<b>0.80</b>	<b>0.61</b>	-0.09	0.41
$W_1$					1.00	<b>0.64</b>	<b>0.23</b>	<b>0.52</b>	0.44	<b>0.65</b>
$W_d$						1.00	<b>0.62</b>	<b>0.85</b>	0.32	<b>0.52</b>
$E_1$							1.00	<b>0.62</b>	0.00	0.37
$E_{max}$								1.00	<b>0.47</b>	<b>0.53</b>
Q									1.00	<b>0.57</b>
$t_{dj}$										0.13

**Table 2.** Spearman correlation coefficients among life-history parameters in *G. lacustris* populations and some characteristics of water bodies. Bold - significant correlation at  $P < 0.05$ ; for abbreviations see Material and methods.

juveniles.

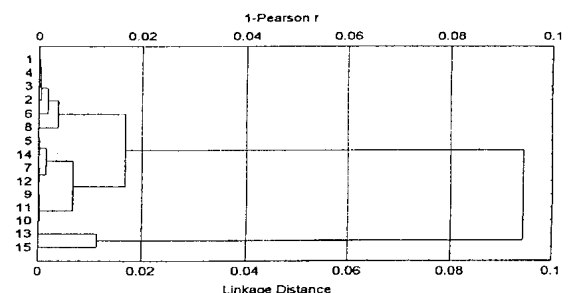
The life cycle of each species represents a certain compromise between the energies spent on growth and reproduction. Therefore, acceleration of one process can have a certain effect on the others. It is interesting to evaluate the effect of accelerated maturation in some *G. lacustris* populations on the other life-history parameters. The values of the Spearman correlation coefficients between the various pairs of life-history parameters such as between these parameters, GS, and  $t_{gs}$  is quite different (Table 2). No distinct correlations between  $D_j$  and size parameters of adult females are revealed, but  $D_j$  is found to have a significant negative correlation with the  $E_{max}$  values.

The results of clusterization of the investigated *G. lacustris* populations on the base of correlation matrix of their life-history parameters are presented in Fig.2.

By the cluster analysis, the populations were distinctly divided into three main groups. The first group is composed by the populations (nos. 1 -

4, 6, 8) from plain warm water bodies. Females from these populations have minimal  $D_j$ , maximal sizes, and fecundity. This trend in life-history parameters can be conventionally determined as "gigantism".

The majority of the populations in the second main group (nos. 5, 7, 9-12, 14) inhabit Middle Siberian plateau and apline lakes with shortened growing seasons and lower temperatures in the gro-



**Fig. 2.** Tree diagram of distribution of different populations of *G. lacustris* according to life-history characters. The numbers of populations correspond to those in Table 1. Explanations are in the text.

wing season. The FSC-females have a prolonged juvenile period, much smaller sizes and lower fecundity. This trend can be called "dwarfism".

The third group consists of two "dwarfed" populations from alpine lake Khubsugul and a cold spring.

## Discussion

It can be concluded that two opposite trends of life-history changes various populations of *G.lacustris* have been established, namely "gigantism" and "dwarfism". The first one takes place mainly in warm plain and plateau lakes, the second, in the other types of water bodies such as alpine lakes, cold springs and warm geothermal streams.

Both trends are not consistent with the general characteristics of r- and K-selection concept. For example, decrease of  $D_j$  (r-selection) in the populations from warm lakes is accompanied by increase of  $W_g$  and  $W_d$  (K-selection). On the contrary, increase of  $D_j$  in the populations from most of the cold water bodies (K-selection) leads to diminished size of adults (r-selection).

Nevertheless, the life-history characteristics of *G.lacustris* populations from water bodies with rather constant temperatures (cold spring, geothermal stream) are in rather good agreement with the so called "A-selection" which occurs in some severe but predictable habitats in conditions of weak interspecific competition. This form of selection leads to maturity, prolonged life cycle, and low fecundity (Greenlade 1983, Williams 1991).

It is important to note acceleration of the growth rate of *G.lacustris* juveniles with shortening the duration of the growing season (Fig. 1.). This tendency is displayed most clearly in the population of South Siberian lake Ivan with a short growing season (4 months) but with a high (up to 22.5 °C) summer temperature.

Similar data were obtained from comparison of the growth rates of *G.lacustris* newborns in arctic Lake Chayachiye on the shore of the Barents sea and in Belarussian Lake Lyatskiye (Golubev *et al.* 1984). Shallow (up to 0.3 - 0.5 m in depth) Lake Chayachiye is located on a granite which is warmed very well due to permanent solar radiation during the polar day. Therefore, in July the temperature in this lake reaches 22-25 °C. This corresponds to summer temperature in Lake Lyatskie. However, the growing season for *G.lacustris* in the arctic lake lasts only 2.5 months (mid-June - September) and in the Belarussian Lake it can be 7 months (April - October). At equal temperatures the specific growth rate of newborns was significantly higher ( $P < 0.01$ ) as compared with the Belarussian one.

In contrast, juveniles in the geothermal stream in Kamtchatka have much lower Q values when compared with the same from the lakes with comparable summer temperatures.

Undoubtedly, the acceleration of juvenile growth in water-bodies with shortened growing seasons may be considered as an adaptation that ensures the most rapid maturation in conditions of reduced period of optimal environmental conditions.

The same trends were observed for North

American amphipod *Hyalella azteca* (Strong, 1972). Three populations of this species have been investigated: from a mountain lakes (alt. 1,050 - 1,640 m), a coastal lake and a hot spring. The water temperature in the mountain lake varied from 1-3°C in winter to 15-25°C in summer; in the coastal lake, from 8-10°C to 15-25°C. In the hot spring it varied irregularly within the range 20 - 40°C but the highest abundance of *H.azteca* was found in zones with 20 - 25°C.

In the mountain and coastal lakes *H.azteca* grow and reproduce at temperatures above 12°C, which approximately corresponds to the summer season. In the hot spring these processes occur throughout the year. At equal temperatures the average duration of the juvenile period in individuals from the hot spring was significantly higher as compared with the other water bodies.

The body length of adults from the hot spring population that exists at relatively stable temperatures (20-25°C) was significantly lower ( $P < 0.05$ ) than in populations from alpine lakes with sharp fluctuations of the annual temperatures (1 - 25°C). On the contrary, there are no significant differences in adult size between the populations in hot spring and shore lakes locations where the annual temperature range is 8 - 25°C.

While results are mostly explicable as a function of annual temperature regime, there are two apparent exceptions. Firstly, the "dwarfed" population with a prolonged juvenile period from a geothermal spring is much more similar in these respects to the populations from colder plateau lakes than to the populations from plain warm water bodies.

It should be noted that the *G.lacustris* population in Khubsugul has the lowest size of females. The temperature range in this lake during the growing season (4 - 11°C) is much more similar to the temperature ranges in cold spring than to those in the other alpine lakes.

Similar results were obtained when comparing two *Gammarus fossarum* populations which were living in two habitats with annual temperatures ranging from 8.8 to 9.9°C and from 3 to 19°C. The size of adults in the second population was higher than it was in the first population (Brzezinska-Blaszczyk and Jazdzewski, 1980).

Probably, the relatively narrow annual limits of temperature changes in water bodies (both cold and warm) may be one of the reasons of the diminished body size of *G.lacustris*, *G.fossarum* and *H.azteca*.

The "gigantic" *G.lacustris* population from cold alpine lake Sev-Lich is the second evident exception. It is very similar in size and fecundity respects to the populations from warm plain lakes and very different from the other alpine populations in Sevan and Khubsugul. I think this can be explained by peculiarities of reproductive cycles of *G.lacustris*.

The life span of this species varies from two years in warm plain water bodies to three - four years in cold ones. Due to a prolonged juvenile stage, the reproductive period of females in warm lakes lasts only one growing season (in the year following the year of birth) and in colder water bodies it lasts 1.5 growing seasons.

At 20°C the embryonic development in *G.lacustris* lasts 15 days, at 12°C, 30 days, at 5 - 7°C, 58

days. Therefore, females in warm lakes are potentially able to produce up to ten egg broods per growing season. But in reality females from Lyatskie Lake produced not more than four broods per life cycle due to long time intervals between newborn release and the next copulation (Khmeleva and Golubev 1986).

It is likely that a similar number of broods per female life time is typical of the majority of *G.lacustris* populations. Even in population from a geothermal spring with all-year-around reproduction, percentage of egg-bearing females in winter is as low as about 5% of the mature ones. In summer this value reaches 90 - 95%. In contrast, in the population from a cold spring, percentage of egg-bearing females practically is almost the same in all seasons, amounting to about 40 - 50% (Nesterovich 1990). Undoubtedly, a rather stable reproduction level in this population throughout a year compensates to some extent for the negative effect of low temperatures on the rate of embryonic development and low individual fecundity.

Since the population density and biomass of *G.lacustris* populations in all water bodies studied is very high, it is evident that four broods per life cycle is sufficient to maintain the recruitment at a necessary level to ensure stability of the populations.

Because of short growing seasons and low summer temperatures, females from the population in Sev-Lich Lake produce only one brood per year (Ostrovskij 1990). Therefore, the maximal number of broods per female lifetime is two. Since fecundity increases with the size of animal the number of eggs in two broods of large females in Sev-Lich is comparable to the number in four broods of small females in other cold water bodies.

It is important to stress that *G.lacustris* is capable of reproducing even in cold springs with a temperature of about 6-8°C. In such conditions the average  $D_1$  value can be 520 days. At these temperatures the total length of the life cycle of *G.lacustris* lasts at least 3-4 years.

The existence of *G.lacustris* population in cold springs disproves the traditional explanation of the absence of this ubiquitous and eurybionthic species in Baikal Lake by low summer temperatures (Bekman 1954). To my opinion, it is caused by competition with numerous endemic Baikal amphipods which occupied all ecological niches potentially suitable for *G.lacustris*.

It is confirmed by the fact that *G.lacustris* is rather abundant in the alpine lake Khubsugul whose water is cooler than in Baikal. Only two amphipod species, namely endemics *Gammarus kozhovi* and *G.hanhi* live there together with *G.lacustris*, but each of these congenial species occupies a separate ecological niche (Safronov 1993).

#### Conclusion

The characteristics of the life-history of *G.lacustris* females within the area distribution are first of all the duration of juvenile period and sizes of adults which are very variable. This factor stipulates the existence of several opposite trends of the life-history changes in different local *G.lacustris* populations within the area distribution of this species.

High plasticity of life history parameters at the species level is a necessary prerequisite for existence of different life-history strategies at the intraspecific level (Hornbach *et al.* 1991). However, this possibility can be realized if separate populations of the same species exist in very different environmental conditions, as it does in the case of *G.lacustris*.

The absence of a close correlations between most of the life-history parameters causes plasticity of *G.lacustris* life cycle. It is especially important for adaptation to exist in the unstable or unpredictable environment. So far as this species lives in water bodies with different longevity of growing seasons, maximization of Q values is not optimal for all populations. The strategy of Q values optimization is the reaching of sexual maturity by the necessary term, mostly by the end of the first or second growing season.

It may be preliminarily concluded that several species such as *G.lacustris* with high degree of plasticity in their life cycle variables within their distribution area may have different life-history strategies at subspecies level.

Obviously, the problem of the life-history strategy changes in eurybionthic species requires further study. In their course it is necessary to take into account not only the growth and reproduction parameters at an individual level but some populational characteristics. Among them, we can mention survival, mortality, and fecundity of various size and age groups, intrinsic rate of population growth, seasonal dynamics of the abundance, biomass and size structure of populations, ability to competition, etc.

#### Acknowledgements

I am grateful to Dr. M. Janiga for reading and criticism of my manuscript.

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Received 20 August 1996; revised 28 July 1997,  
accepted 15 September 1997