

Factors determining the average body size of geographically separated *Arctodiaptomus salinus* (Daday, 1885) populations

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Abstract: *Arctodiaptomus salinus* inhabits water bodies across Eurasia and North Africa. Based on our own data and that from the literature, we analyzed the influences of several factors on the intra- and inter-population variability of this species. A strong negative linear correlation between temperature and average body size in the Crimean and African populations was found, in which the parameters might be influenced by salinity. Meanwhile, a significant negative correlation between female body size and the altitude of habitats was found by comparing body size in populations from different regions. Individuals from environments with highly varying abiotic parameters, e.g. temporary reservoirs, had a larger body size than individuals from permanent water bodies. The changes in average body mass in populations were at 11.4 times, whereas, those in individual metabolic activities were at 6.2 times. Moreover, two size groups of *A. salinus* in the Crimean and the Siberian lakes were observed. The ratio of female length to male length fluctuated between 1.02 and 1.30. The average size of *A. salinus* in populations and its variations were determined by both genetic and environmental factors. However, the parities of these factors were unequal in either spatial or temporal scales.

Keywords: Copepoda; *Arctodiaptomus salinus*; Body size; Sexual dimorphism; Variability

As a fundamental biological parameter, body size largely determines species' functional and environmental characteristics, growth, life duration, population density, and species' place in food webs (Peters, 1983; Schmidt-Nielsen, 1984; Yodzis & Innes, 1992). Mean animal size in populations and communities can be, to some extent, an indicator of water quality in water bodies (Havens & Beaver, 2011).

The average size of copepods in populations is determined by several factors (Deevey, 1964; Marcus, 1979; Prusova & Shadrin, 1983; Shadrin & Solokhina, 1992). In most species of freshwater and marine copepods, males and females are characterized with different body size (Bayly, 1978; Geddes & Cole, 1981; Shadrin & Solokhina, 1991). Meanwhile, the manifestation level of sexual size dimorphism in populations may vary (Rodriguez & Jimenez, 1989; Shadrin & Solokhina, 1991), which is likely to be applied in evaluating the population's status and in monitoring aquatic ecosystems. However, correlations

between factors determining average body sizes of copepods are not yet well understood.

The highly eurythermal and euryhaline species *Arctodiaptomus salinus* (Daday, 1885) inhabits different water bodies across Eurasia (from Spain to China) and North Africa, including deep lakes as well as different kinds of wetlands (Comín et al, 1983; Folijan, 1966; Krupa et al, 2008; Samraoui, 2002). Its most southern localities are in India and Algeria (N20-21°) (Samraoui, 2002); the most northern localities are in the lower reaches of the River Ob (Russia) (N65°) (Seminoma et al, 2000); the most western localities are in Spain and Morocco (E24°) (Alonso, 1990; Rokneddine & Chentoufi, 2004); and the most eastern localities are in China (E110°) (Zhao et al, 2005). *A. salinus* plays a dominant role in plankton in different types of water bodies (Folijan, 1966; Krupa et al, 2008; Marrone, 2006).

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Understanding the effects of various factors on its size and level of sexual dimorphism are necessary in assessing its dynamics and functional roles in aquatic ecosystems. *A. salinus* populations in different types of water bodies have different average sizes (Folijan, 1966; Rokneddine, 2004), and their sexual dimorphism has long been known (Folijan, 1966; Mohammed & Salman, 2009), but the influences from various factors are yet to be elucidated.

There are three objectives of this: (1) to assess the effects of various factors on the average adult size of *A. salinus* and its variability in different populations; (2) to analyze the manifestation level of sexual dimorphism in *A. salinus* from different regions; (3) to discuss the role and maintenance of intra-population diversity. This study mainly focuses on *A. salinus* from water bodies of the Crimea, the largest peninsula in the Black Sea. Among the more than 50 shallow saline lakes in the Crimea, ones of marine origins are characterized by a similar ion ratio as that of seawater, while ones of continental origins are sulfate lakes (Shadrin, 2008, 2009). *A. salinus* was found in the saline/hyper-saline water bodies of both marine and continental origins (Anufrieva & Shadrin, 2014; Balushkina et al, 2009; Belmonte et al, 2012). Our years of integrated research of the Crimean lakes have been presented in a number of the publications (Balushkina et al, 2009; Belmonte et al, 2012; Shadrin, 2008, 2009; etc.).

MATERIALS AND METHODS

Zooplankton samples collected from salt water bodies of the Crimea (Ukraine) (2009–2012) were served as our study materials. One additional sample (11/07/2012) was taken from the Tambukan salt lake, located in the North Caucasus (Russia). All the Crimean lakes are very shallow, as usually, less than 1 m in depth. Due to the difficulties in directly using plankton net we took a bucket of 5 L volume to take water. Meanwhile, zooplankton samples were collected quantitatively by filtering only 50–100 L of water through an Epstein net (mesh size 110 μm) because of its high density, and were then fixed by 4% formalin. Salinity, temperature, and pH of water were measured during sampling. Animal numbers were determined by direct counting under Olympus SZ-ST stereo microscope (2 \times) with subsequent recalculation on the volume of filtered water. Zooplankton samples from water bodies in Italy, Spain,

and Tunisia, together with their accompanying information were kindly provided by F. Marrone. Total length of 30 (or less) individuals of each gender from each sample (total 634 specimens) were measured under Olympus SZ-ST stereo microscope (4 \times) using an ocular micrometer.

Length variability in the samples was qualified by the coefficient of variability (CV) and the level of sexual dimorphism was evaluated by the ratio of female length to male length. Data were subjected to standard statistical processing. Significance of differences in average values was evaluated by Student's *t*-test, and confidence level of correlation coefficients was determined by comparison with parameter critical values from the table (Müller et al, 1979). To evaluate homogeneity and the normality of lengths in the Crimean sets in males and females, the probability paper method (Cassie, 1954) was applied to analyze size frequency distributions. Moreover, published data on the size of *A. salinus* from different habitats (Table 1) were included in the main analysis. Samples included in our analysis were presented in Table 2.

RESULTS

Mean length of males and females

The average size of females and males were 1.65 mm (varying from 1.24 mm (Lake Tambukan) to 2.29 mm (Lake Takilskoye)) and 1.53 mm (varying from 1.15 mm (Lake Tambukan) to 2.02 mm (Lake Takilskoye and Sebkha El Ariana)), respectively. In the Lake Issyk-Kul population, the average size of females and males were 1.00 mm and 0.77 mm (Folijan, 1966), respectively. The largest females (2.38 mm) were found in Sebkha Zima (Rokneddine, 2004) population. Thus, among different populations, the differences in average size of females and males were up to 1.38 mm and 1.25 mm (Table 2), respectively. Copepods with the largest average size were from temporal and ephemeral ponds with highly variable abiotic parameters. Among the sampled lakes in the Crimea, Lake Takilskoye, in which the biggest copepods were found, is the most variable one, characterized with frequent and long dry periods. While, the smallest copepods were found in both Lake Issyk-Kul, the deepest lake with a maximum depth of 702 m, and Lake Shira, which is 24 m in depth. These results are consistent with previous research (Geddes & Cole, 1981).

Table 1 Characteristics of *A. salinus* habitats included in this study

Water body	Country, region	Coordinate	Type of the habitat	Altitude	Area (km ²)	Max depth (m)
Lake Banyoles	Spain	N42°07'–E02°45'	Lake, permanent	172	1.18	62.4
Pantano Grande di Vendicari	Italy, Sicily	N40°44'–E33°30'	Swamp, temporary	0	–	–
Sebkha El Ariana	Tunisia	N40°53'–E32°37'	Sebkha, temporary	1	–	–
Stagno 4 di Isola Longa	Italy, Sicily	N41°57'–E33°17'	Pond, temporary	2	–	–
Lago di Pergusa	Italy, Sicily	N41°31'–E33°20'	Lake, unstable	667	1.83	12
Lake Tambukan,	Russia, Kabardino-Balkaria	N43°58'–E43°10'	Lake, unstable	548	1.87	10
Lake Takilskoye	Ukraine, Crimea	N45°07'–E36°24'	Lake, unstable	0	0.25	1
Lake Yanyshskoye	Ukraine, Crimea	N45°07'–E36°24'	Lake, unstable	0	0.2	1
Aktashskoye	Ukraine, Crimea	N45°22'–E35°49'	Lake, unstable	0.5	26.8	2
Tobechik	Ukraine, Crimea	N45°10'–E36°21'	Lake, unstable, temporary	0.3	18.7	1.2
Shagan	Kazakhstan	N50°25'–E80°09'	Man-made reservoir on river	340	–	–
Issyk Kul	Kyrgyzstan	N42°26'–E77°11'	Big Lake, permanent, stable	1609	6236	702
Lake Shira	Russia, Siberia (Khakassia)	N54°31'–E90°12'	Lake, permanent	353	35	24
Lake Shunet	Russia, Siberia (Khakassia)	N54°25'–E90°14'	Lake, permanent	319	0.47	3
Sawa Lake	Southern Iraq	N31°18'–E45°10'	Lake, unstable	30	10	5
La Sebkha Zima	Morocco	N32°05'–W08°40'	Salt Marsh, temporary	365	7	–

Table 2 Average body length and sexual dimorphism of *A. salinus* in different water bodies

Water body	Study date	Salinity (‰)	Temperature (°C)	Length ♀ (CV)	Length ♂/(CV)	Length♀/L♂	Reference source
Lake Banyoles	17/06/05	0.7–2	–	1.42 (3.32)	1.26 (5.00)	1.13	6
Pantano Grande di Vendicari	21/04/05	19.6	15.4	1.55 (17.96)	1.48\ (6.68)	1.04	6
Sebkha El Ariana	15/02/06	2.2	19.2	2.08 (7.26)	2.02 (3.42)	1.03	6
Stagno 4 di Isola Longa	25/02/05	3.0	13.7	1.45 (7.52)	1.41 (5.18)	1.03	6
Lago di Pergusa	30/07/02	5.0	25.6	1.72 (8.44)	1.65 (4.04)	1.05	6
Lake Tambukan	11/07/12	21	22	1.24 (5.19)	1.15 (7.24)	1.07	6
Lake Yanyshskoye	02/06/12	25	24	1.44 (10.22)	1.44 (12.23)	1.00	6
Lake Takilskoye	01/05/09	16	13	2.29 (5.58)	2.02 (3.83)	1.13	6
Lake Yanyshskoye	01/05/09	16	13	2.08 (11.46)	1.94 (8.69)	1.07	6
Lake Yanyshskoye	13/08/09	74	24.5	1.62 (6.57)	1.45 (5.58)	1.12	6
Aktashskoye	06/08/12	60	32	1.41 (5.45)	1.26 (5.58)	1.12	6
Tobechik	17/08/10	35	26	1.49 (6.26)	1.32 (4.95)	1.13	6
Shagan	–	28	24	1.66	1.51	1.10	5
Issyk Kul	–	5.9	3–23	1.00	0.77	1.30	2
Lake Shira	–	17.5	–	1.02	–	–	1
Lake Shunet	–	22.6	–	1.18	–	–	1
Sawa Lake	–	14–19	9.38	1.38	1.11	1.24	3
La Sebkha Zima	–	0.6–171	12.3–28	1.24–2.36	–	–	4

References: 1: Anufrieva (2006); 2: Folijan (1966); 3: Mohammed & Salman (2009); 4: Rokneddine (2004); 5: Stuge (2001); 6: own data.

Probabilistic analysis was used to analyze occurrence frequencies of individuals with different size in the Crimean lakes, by which bimodal distributions were found. Among the two size groups of females and males (Figure 1), the average length of a “small” and a “large” female were 1.51 mm (CV=9.89) and 2.25 mm

(CV= 6.27), respectively, whereas, those in males were 1.38 mm (CV=10.22) and 2.00 mm (CV=5.62), respectively. In general, 71%–74% of the Crimean *A. salinus* specimens were “small” sized individuals. Typically, populations mainly consisted with one sized individuals were sharply dominated at any given moment in a lake.

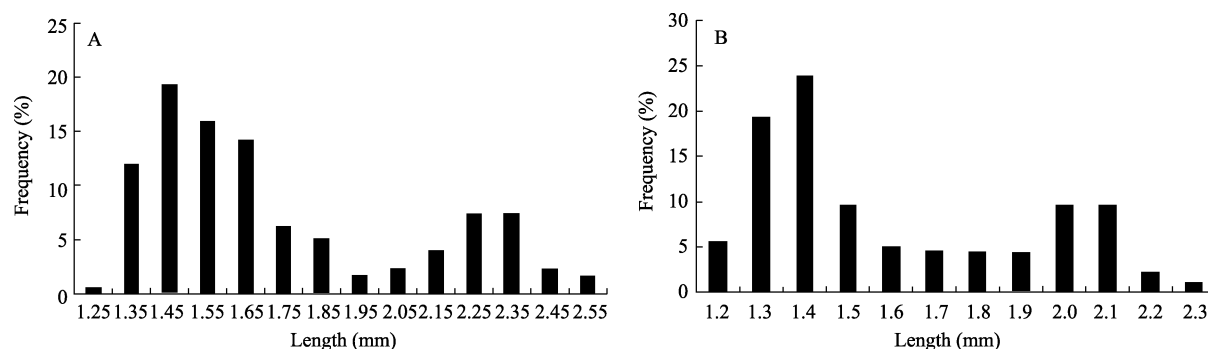


Figure 1 Occurrence frequencies of size groups in female (A) and male (B) *A. salinus* from the Crimean lakes samples

Index of sexual dimorphism

The average index of sexual dimorphism of *A. salinus* populations in the Crimean water bodies was 1.11 (1.00–1.3, CV=7.51), whereas, those of “small” and “large” sized populations were 1.10 and 1.13, respectively. Data obtained from different periods of a single lake (Lake Yanyshskoye) showed that this index could vary widely within a population.

Factors influencing length

No linear relationship between size and salinity in the entire sets of samples was demonstrated (Figure 2A).

In *A. salinus* from the Crimean lakes, a dramatic decrease in body size of both males and females with increase of salinity from 13‰–15‰ up to 30‰–40‰ were noted, and their average sizes were not affected by more salinity increase (up to 80‰) (Figure 2B).

A significant correlation between average size of females and temperature in the entire set of samples is shown in Figure 3A ($P < 0.05$, correlation coefficient=0.53), whereas, the analogous correlation coefficient in males was 0.577 ($P < 0.05$). Thus, the geographic variations in females (28%) and males (33%) could be explained by temperature differences. This

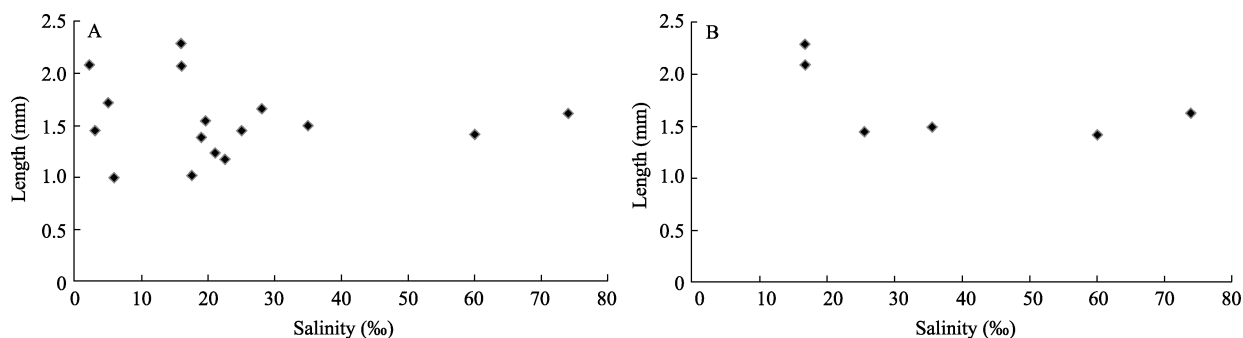


Figure 2 Influence of salinity on average body length of *A. salinus* females

A: Inter-population comparison; B: The Crimean population.

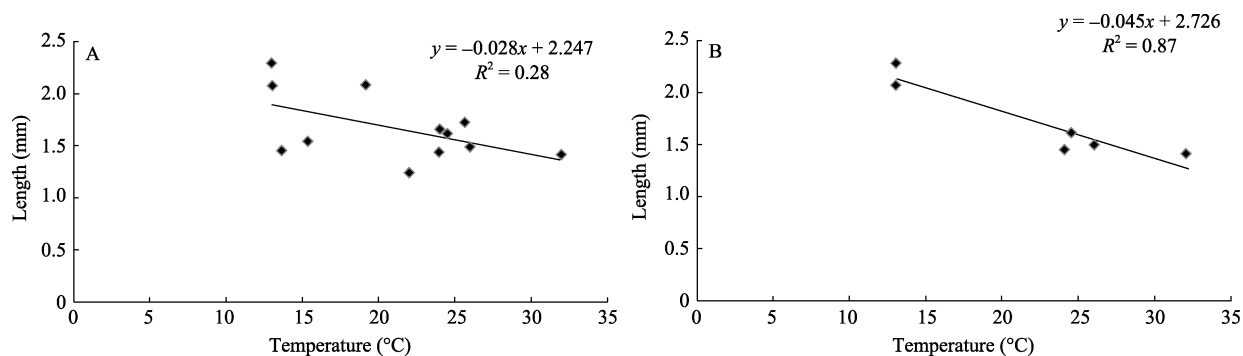


Figure 3 Influence of temperature on average length of *A. salinus* females

A: Inter-population comparison; B: The Crimean population.

relationship was even stronger when considering only the Crimean samples into account (Figure 3B) ($P < 0.005$, correlation coefficient = 0.987). In a certain temperature range (13–32 °C), the dependence could be inferred by a linear equation:

$$L_{\text{♀}} = 2.73 - 0.045 t \quad (1)$$

Where, $L_{\text{♀}}$: size of females (mm), t : temperature (°C).

A similar relationship was also observed in males ($P = 0.0005$, correlation coefficient = 0.999), and the dependence could be deduced by the equation:

$$L_{\text{♂}} = 2.49 - 0.042 t \quad (2)$$

Where, $L_{\text{♂}}$: size of males (mm), t : temperature (°C).

No pH effects on average body sizes of males and females in the Crimea lakes were found.

To evaluate the dependence of average size of males and females on population density, we exclusively adopted our Crimean data, which are the only ones with population density values, but no significant relationship was found.

Using data from Table 2, a negative linear correlation between female body size and altitudes of the habitats were found ($P < 0.05$, correlation coefficient = 0.466). Thus, 22% of total body size variability might be explained by the altitude differences in water bodies. However, no significant correlation between the depth of water bodies and female size was found.

Although the Crimean lakes and Lake Tambukan are quite close in population density, salinity, and temperature, the average size of individuals in the

Crimean lakes populations was twice as large as those in Lake Tambukan.

Intra-population variation of body length

Comparisons of CVs showed that in the general data set, the variations in size of males and females were 20.40 and 20.89, respectively. CVs of average intra-population size in total samples were 19.85 (males, 3.42–12.23) and 19.93 (females, 3.32–17.96), whereas, those in the Crimean population were fluctuated from 5.45 to 11.46 in females and from 3.83 to 12.23 in males. These data indicated that inter-population variation was higher than that of intra-population. Meanwhile, certain non-linear dependence between intra-population CV and salinity was presented. The highest CVs in females and males were both observed in a narrow range of salinity (15‰–25‰).

CVs of average size in males and females in the Crimean sample sets were not significantly dependent on temperature. Variations of body size in females (CV) in the Crimean lakes demonstrated a significant positive linear dependence on population density ($P < 0.025$, correlation coefficient = 0.82) (Figure 4), whereas this correlation in males was more close to a dome-shaped dependence (Figure 4) ($P < 0.05$, correlation coefficient = 0.76). A positive but not significant trend was found between the average body length in population and coefficient of its variation due to the small number of analyzed samples.

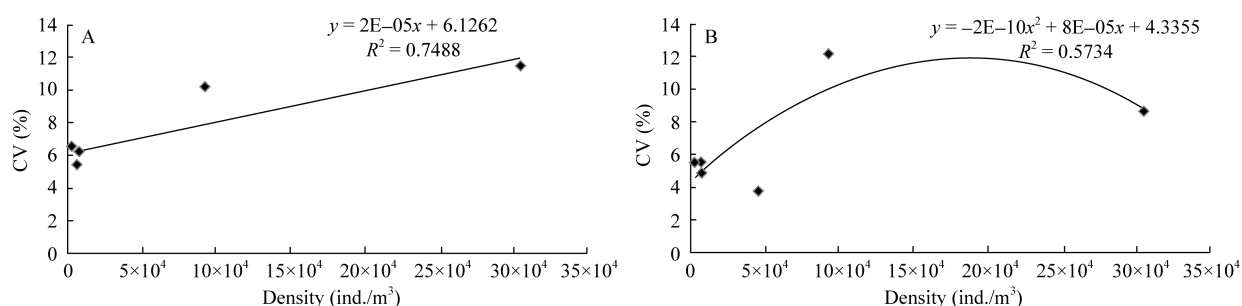


Figure 4 Influence of population density on variability of average body length of *Arctodiaptomus salinus* in the Crimean population
A: female; B: male.

DISCUSSION

Inter-population differences in mean length: a functional aspect

The average length of females in *A. salinus* populations varies from 1.00 mm to 2.38 mm. According to the correlation between body weight and length in calanoids (Balushkina & Winberg, 1979), the variation of body

mass in different populations of *A. salinus* would be 11.4 times, which indicates a significantly different functional role this species plays in specific habitats. Moreover, based on a parabolic equation describing the correlation of respiration rate and weights in copepods (Edmondson & Winberg, 1971), changes in an individual's metabolic activities would also be high (6.2 times).

Length determined factors

While the variation of body size in Copepoda (geographic, inter- and intra-water body, seasonal) has long been known (Deevey, 1964; Gaudy & Verriopoulos, 2004; Marcus, 1979; Prusova & Shadrin, 1983), temperature is one of the main factors causing this variation in ectotherms (Partridge & French, 1996; Winberg, 1937). In Copepoda, body length generally is inversely proportional correlated with temperature and can be inferred by a linear regression equation (Marcus, 1979; Prusova & Shadrin, 1983). By referring Rokneddine (2004), which described the effects of temperature (10–28°C) and salinity (10‰–40‰) on *A. salinus* female size (the Morocco population), we calculated the correlations coefficients and parameters of approximating equations. The linear regressions revealed a significant dependence of female size on temperature with good approximations ($P=0.05$ – 0.01 , correlation coefficient= 0.99 – 0.98). This dependence could be inferred by an equation:

$$L_{\text{♀}} = a - b \cdot t \quad (3)$$

Where, $L_{\text{♀}}$: female body size (mm); t : temperature (°C); a and b : parameters.

Parameters “ a ” and “ b ” vary with salinity; “ a ” decrease from 2.95 to 2.20 and “ b ” - from 0.061 to 0.021, respectively, when salinity increases from 10‰ to 40‰. Parameter “ b ” indicates the effect of temperature on body size, which decreases when salinity increases. Parameter “ b ” in the Crimean population is roughly the fair value of parameters in Rokneddine’s (2004) study. Therefore, we conclude that parameter “ b ” (0.04–0.05) can be applied in *A. salinus* populations, whereas, parameter “ a ” varies in different populations. Values of parameter “ b ” in other calanoids are various, for example, it is 0.016 in *Acartia clausi* Giesbrecht, 1889 (Prusova & Shadrin, 1983).

No effects, but an insignificant negative correlation between body size and salinity in total samples were found in Rokneddine (2004)’s study. In general, salinity effects could be significantly altered by an increased temperature, which may explain why no correlation between body size and salinity in the Crimean population was found in hot summer (Figure 2B).

Data from Table 2 show that the smallest average size in *A. salinus* was observed in the deepest oligotrophic lake, the Lake Issyk-Kul. But is the oligotrophy the only reason why *A. salinus* there is so small? Brooks (1968) claimed that the intensive

development of predators might lead to the size decrease of planktonic copepods in a water body. Therefore, the several planktivorous fish species mainly feed on *A. salinus* in the Lake Issyk-Kul may explain the small average size of *A. salinus* (Folijan, 1966; Savvaitova & Petr, 1992). However, in the Lake Shira, a mesotrophic lake without fish, *A. salinus* is also very small. The largest average size of crustaceans was recorded in the Crimean lakes and in La Sebkha Zima, which are all hypereutrophic, very shallow, with highly variable salinity, and seasonally or periodically dried when salinity exceeds 350‰ (Belmonte et al, 2012; Rokneddine, 2004; Shadrin, 2009). Energy budget approach indicates that food quantity only limits definitive size of copepods in low concentration (Shadrin, 2011), which may explain why high values of correlation coefficients of average size with temperature were observed in our highly productive lakes.

Because all the lakes are located relatively close to each other in this study (<100 km), and *A. salinus* has rested eggs that can be dispersed between lakes by birds or wind, all the Crimean *A. salinus* has been regarded as a single population and their variations as an intra-population variation. The comparison of intra- and inter-population differences in body size leads to the general conclusion that the intra-population variation of body size is primarily determined by ecology-physiological mechanisms and is lower than that of inter-population, which is determined by other factors, such as gene pool differences and biotic and abiotic characteristics of water bodies. This may explain the high level of correlation between average size and temperature in the Crimean population and the low level of correlation in total samples from different regions. But, more data are necessary to further discuss this matter.

Sexual dimorphism

In most Calanoida species, other than very few exceptions, females are always bigger than males (Bayly, 1978; Gilbert & Williamson, 1983; Belmonte & Cavallo, 1997). The smaller size of calanoid males is generally attributed to their shorter developmental span of copepodite stage (Corkett & McLaren, 1979), which enables males to fertilize females as soon as molting (Landry, 1978). In zooplankters, the smaller size and the reduced feeding activity of males could maximize female fecundity by decreasing intraspecific competition for food (Gilbert & Williamson, 1983). In unpredictable

environments, where generalism is favored, the sexual size-dimorphism may represent a way to widen the ecological niche of the species (Roughgarden, 1979). Thus, in *A. salinus*, their sexual dimorphism in populations is profitable. We assume that high levels of sexual dimorphism may present in stable habitats. Among the habitats shown in Table 1, the Lake Issyk-Kul is the most stable (with the modest fluctuations of salinity and water levels) one and therefore, the highest level of sexual dimorphism (1.3) was observed there.

The identified range of variability of sexual dimorphism index in *A. salinus* (1.0–1.3) is very close to those in 42 diaptomids species of North America (1.02–1.23) (Geddes & Cole, 1981). However, in our study, no correlation between the length of female and the index of sexual dimorphism was found.

Size bimodality

As in the Crimean lakes, in the lakes of Siberia (Shira and Shunet), two size groups of *A. salinus* females (0.95 mm and 1.35 mm, respectively) were observed earlier. In the deeper lake, the Lake Shira, 3%–23% females were large sized ones, whereas, in the Lake Shunet, that was 60% (Anufrieva, 2006). In Shagan, a reservoir in Kazakhstan, two size groups of *A. salinus* were also presented (Stuge et al, 2001). Meanwhile, size polymorphism was identified in several species of Copepoda, particularly, *Paracalanus parvus* (Claus, 1863) (Kovalev, 1969), *Pseudocalanus minutus* (Boeck, 1865) (Shadrin & Solokhina, 1991), *Nannocalanus minor* (Claus, 1863) and *Euchaeta marina* (Prestandrea, 1833) (Gruzov & Alekseeva, 1971), *Neocalanus flemingeri* Miller, 1988 and *N. plumchrus* (Marukawa, 1921) (Tsuda et al, 1999), *Oncaea venusta* Philippi, 1843 (Böttger-Schnack & Huys, 2004).

Such bimodality results from the interaction of several characteristics of the individuals composing a population with critical factors that influence those characteristics (Huston & DeAngelis, 1987). In our opinion, these critical factors can be classified into: (1) differences in growth rates among individuals, which results from intra-population communications; (2) the genetic polymorphism in a population; (3) epigenetic diversity of developmental creods in a genotype.

This bimodality might be explained by the high plasticity of species-specific developmental rates (Jiménez-Melero et al, 2007). Like in many other aquatic organisms (Shvarts et al, 1976; Zelikman & Geinrikh,

1959), two groups sharply differing in developmental rates were observed in *A. salinus* populations. Individuals developed rapidly were much smaller than the slowly developed ones. This is a population adaptation to live in poorly predictable environments (Shvarts et al, 1976). It has been previously shown in copepods, including *A. salinus*, variations in developmental rates increase when animals are being reared under limited conditions, such as with temperature or salinity far from the optimum settings (Jiménez-Melero et al, 2007). The increased population density, as shown in *Eucyclops serrulatus* (Fischer, 1851) (Zelikman & Geinrikh, 1959) and *Cyclops abyssorum* Sars G.O., 1863 (Whitehouse & Levis, 1973), also significantly affects the median duration of development, meanwhile, increases its variation in copepod generations.

Whether size polymorphism is caused by genetic polymorphism or phenotypic plasticity cannot be clarified in the present analyses. Currently, it is well known that a genotype may induce several discrete creods of development, resulting alternative discrete adaptive forms. C. Waddington (1940) wrote: “The phenotype can be represented as a branching system of trajectories in phase space spreading along the time axis”. Khlebovich (2009) showed that different external factors, e.g. predators, may affect prey “choice” of a creod of development, which leads, with an unchanged genotype, to the formation of morphologically different forms in the presence or absence of predators. Being an extremely plastic species, *A. salinus* lives under a wide range of both salinity (0.6‰–210‰) and temperature (1.5–35 °C) (Rokneddine, 2004; own unpublished data). It is hard to think that its existence in such broad habitat range is resulting from a single adaptive form. So far, it is tough to conclude if this bimodality is from different genotypes or is alternative discrete realizations of a single genotype.

Intra-population variability

CVs fluctuate widely in *A. salinus* populations (3.3–18.0), and likely are determined by the peculiarities of aquatic ecosystems and population genetic structures. Differences in average size variation/diversity in a population (CV) may depend on various factors affecting the genetic and epigenetic diversity in populations or on the destabilization of ontogenesis. In the Crimean populations, we found a significant positive correlation between population density and CV. Hence, we may conclude that the increase of genetic diversity in a

population correlates with the increase of its density (Aleschenko & Bukvareva, 1991; Coulson et al, 2001).

Intra-population diversity is an adaptive potential of a population, which means that greater intra-population diversity gives a higher probability for the population's survival in the unpredictable world. However, this greater diversity needs more energy to maintain (Aleschenko & Bukvareva, 1991). It is advantageous for a population to possess high levels of phenotypic diversity, but at the same time, there are only limited energy resources to sustain this diversity. The modeling studies show that for each population under certain conditions, there is an optimal diversity level, and any deviation of this level may increase the risks of becoming extinct (Aleschenko & Bukvareva, 1991). To achieve sufficient density in a less stable environment, a population is forced to produce more diversified offspring, and meanwhile, to optimize its maximum density based on the capability of the environment. Interactions of these two elements result in the level of intra-population diversity/variation. However, its quantification is to be determined.

In conclusion, the average body size of *A. salinus* in populations varies in a wide range and has caused significant differences in the functional roles of this species plays in different habitats. In general, inter-population differences are much higher than intra-population variations. In lakes with two size groups of

A. salinus, both the average size and variation in populations are regulated by different factors. Size structures can be affected by different mechanisms on intra- and inter- population levels. It is assumed that the levels of effects from genetic and environmental factors on size structures are different. But, more studies are necessary to evaluate the impacts of various factors on the average size of individuals and size diversity in copepods populations both in spatial and temporal scales. Meanwhile, more attention need to be devoted to study the phenotypic and genetic diversity in copepods populations to better understand the role of intra-population size diversity plays in population function and survival in the world full of changes.

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