595.71: 591.3:574.2

ADAPTIVE STRATEGIES OF THE COLLEMBOLANS' ONTHOGENESIS UNDER THE POLLUTION AS THE MANIFESTATIONS OF A HETEROCHRONY

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Influence of pollution on the development of laboratory cultures of Orthonychiurus stachianus, Folsomia candida and Heteromurus nitidus (Collembola) was studied. For regular moisturizing the increasing concentrations $Pb(N0_{3)2}$ were used. Experiments were carried out with different fixed temperature and two levels of relative humidity. Comparative analysis of the results showed significant acceleration of development velocity and reduce the amount of degree days (effective temperatures sum) in O. stachianus and F. candida under impact of increasing pollutant concentration. Otherwise, the life cycle duration and degree days sum of Heteromurus nitidus encreased at the such conditions. The representatives of different families demonstrated the different ontogenetic strategies that may be considered as variants of heterohrony process. The adaptive response of the investigated speces development differs accordingly to differences of their ecological strategies.

Analysis of the overall population density changes caused by pollution should take into account the possible acceleration of development velosity and increasing egg lying frequency, observed in some species, in addition to reducing the amount of egg lying and increase of mortality. This fact makes it difficult to assess population response to pollution.

K e y w o r d s: Collembola, pollution, development, ontogenesis, life cycle, embryogenesis, intermoulting period, adaptive strategies, degree days, effective temperatures sum, lower temperature threshold.

Адаптивні стратегії онтогенезу колембол під дією забруднення як прояви гетерохронії

Таращук М.В.

Вивчено вплив забруднення на розвиток лабораторних культур *Orthonychiurus stachianus, Folsomia candida* і *Heteromurus nitidus* ((Collembola)). Для регулярного зволоження використовано водний розчин Pb(N03)2 зростаючихмконцентрацій. Експерименти проводилися при різних фіксованих температурах і двох рівнях відносної вологості. Порівняльний аналіз результатів показав значне прискорення швидкості розвитку і зменшення кількості градусо-днів (сума ефективних температур) для видів *O. stachianus* і *F. candida* під впливом підвищення концентрації забруднювача. Натомість, тривалість життєвого циклу і сума градусо-днів *Heteromurus nitidus* зростали в таких умовах. Представники різних родин продемонстрували різні онтогенетичні стратегії, які можуть розглядатися як варіанти процесу гетерохронії. Адаптивна відповідь досліджуваних видів розвитку відрізняється відповідно до відмінностей їх екологічних стратегій.

Аналізуючи зміни загальної щільністі населення, викликані забрудненням, слід враховувати можливі прискорення швидкості розвитку і збільшення частоти яйцекладіння, що спостерігається у деяких видів, на додаток до зниження кількості яєць і збільшення смертності. Цей факт ускладнює оцінку популяційної відповіді на забруднення.

К л ю ч о в і с л о в а: колемболи, забруднення, розвиток, онтогенез, життєвий цикл, ембріогенез, міжлиньковий період, адаптивні стратегії, градусо-дні, сума ефективних температур, нижій температурний поріг.

Адаптивные стратегии онтогенеза коллембол под воздействием загрязнения как проявления гетерохронии
Таращук М.В.
Изучено влияние загрязнения на развитие лабораторных культур *Folsomia candida, Orthonychiurus, stachianus* и *Heteromurus nitidus* (Collembola). Для регулярного увлажнения использовались нарастающие концентрации $Pb(N0_3)_2$. Были проведены эксперименты при различных фиксированных температурах и двух уровнях относительной влажности. Сравнительный анализ результатов показал значительное ускорение развития скорости и уменьшение количества градусо-дней (сумма эффективных температур) в случае *O. stachianus* и *F. candida* под воздействием возрастания концентрации загрязнителя. Напротив, продолжительность жизненного цикла и сумма градусо-дней *Heteromurus nitidus* в таких условиях возрастает. Представители различных семейств продемонстрировали различные стратегии онтогенеза, которые могут рассматриваться как варианты процесса гетерохронии. Адаптивный ответ развития исследуемых видов различается соответственно различиям их экологических стратегий.
При анализе вызванных загрязнением изменений общей плотности населения следует учитывать возможное ускорение развития и учащение яйцекладок, наблюдаемое у некоторых видов, помимо уменьшения объема яйцекладок и увеличения смертности. Это обстоятельство усложняет оценку популяционного ответа на загрязнение.
Ключевые слова: ногохвостки, загрязнение, развитие, онтогенез, жизненный цикл, эмбриогенез, межлиночный период, адаптивные стратегии, градусо-дни, сумма эффективных температур, нижний температурный порог.

INTRODUCTION

The features of soil animals development, the velocity and other parameters of development under abiotic factors define the structure of the communities, how are the causal mechanisms of environmental niches division, alongside with trophic preferences. The duration of development under the temperature, the temperature regulation of the ektoterm organisms ontogenesis have attracted the interest of researchers during about 100 years (Blunck, 1914; Kozhanchikov, 1946, 1961 (in russian); Mednikov, 1977 (in russian); Campbell et al., 1974; Ratte, 1985; Kolodochka, 1987 (in russian), 1988; Cannon, Block, 1988; Lamb, 1992; Honěk, 1996; Lopatina, Kipjatkov, 1998; Trudgill et al., 2005; Balashov, Kipjatkov, 2008 (in russian); Kipjatkov, Lopatina, 2010 (in russian) etc.)

For most species of springtails (Collembola) thermal constants of ontogenesis (the sum of effective temperatures, low temperature threshold, development velocity etc.) are unknown. However, for some identified species of different families the upper lethal temperatures and temperature optimum also upper temperature limits as well as duration of the intermoulting period under different temperatures were defined (Thibaud, 1977 a, b). A number of works devoted to the research of resistance to low temperatures and dehydration, the impact on the viability of populations of different concentrations of pollutants under different levels of temperature, humidity, etc. (Vannier, 1994; Van Straalen, 1994; Van Straalen et al., 1986; Sandifer, Hopkin, 1997; Fountain, Hopkin, 2004, 2005).

The ability of survival at temperatures below the water freezing temperature point of many species of collembolas were studied in the last decades of the previous century (Block, 1982, 1991; Sшmme, 1982; Zettel, 1984; Zettel, et al., 1989; Meier et al., 1988). The lower lethal temperatures lie in the area of -10 to -15°C, but some, for example, *Cryptopygus antarcticus*, survive in -27°C. The resistance of the springtails to temperatures significantly below 0°C is achieved by the accumulation of cryoprotectants in hemolymph, such as sugar or poligidridnye alcohols (glycerol, glucose, fructose). For example, for *Orchesella villosa* are known (average): the lower threshold of -9,4°C, the upper thermal stupor +44,9°C and thermal limit +54,3°C (Vannier, 1994).

For most taxonomic groups, biomonitoring sites, including springtails, a significant number of autekologic parameters (gigropreferency, thermopreferency, etc.) are obtained by field observations, and often corrected in further studies. The results of these adjustments may conflict with primary data from different authors, may be even diametrically opposed (e.g. *Folsomides marchicus* is described as gigromezophylous (Kuznetsova, 2005) and kserophylous (Kaprus′ et al., 2006). These options can be refined in the laboratory, by methods of research of the impact of progressive gradation of factor on the population of living cultures.

Duration of collembolans' ontogenesis predominantly small, less than 1 year, 4—5 months frequently. Some species of collembola live 1—2 years, while regular moult (Hopkin, 1997). Development cycle *Cryptopygus antarcticus* from egg to egg in Antarctic conditions lasts for about 2 years, and the complete ontogenesis can last for about 7 years (Burn, 1981; Convey, 1994; cited by: Hopkin, 1997). In our experiments ontogenesis of 5 specimens of *Orthonychiurus stachianus* at a temperature of 20—22°C and relative humidity of 75% lasts for 10.5 months, during this time was 32—33 molting. The comparative analysis of the development cycles of collembola with different adaptive strategies, shows that most short life cycle is characterized by species-explerents and violents (especially members of the family Isotomidae) (Greenslade, 1981).

The life cycle of the most primitive Poduromorpha consists of the embryonic and 6 to 8 larval stages. The exeption shown by the development cycle of euedaphic Tullbergiidae (*Mesaphorura krausbaueri*) that rich the sexual maturity after third moulting (Hale, 1965). *Orchesella cincta* (Entomobryidae) pass 10 to 12 juvenil stages before maturing (Janssen, Joosse, 1987). According to our information the sexual organs of the females Symphypleona representatives (*Sphaeridia pumilis*) can ripen after 4—5 moulting, and in males even after third one. The developmental cycle of *Megalothorax incertus* (Neelipleona) prolongates during 30 to 32 days on the 21°C, with embryogenesis durated 20 days, as well as sexual maturing come after first moulting, on the second larval stage (Tarashchuk, 2000). These examples demonstrate the probably occurring the facts of the heterochrony processes in the onthogeny of different representatives of a class Collembola, that means the shift of developmental time of the several organs in compare to another (according to Ernst Haeckel, cited to: "Biological Encyclopedic Vocabulary...", 1986).

THE OBJECTS AND METHODS

We studied the duration of development cycles *Orthonychiurus stachianus*[1] (Onychiuridae), *Folsomia candida*[2] (Isotomidae) and *Heteromurus nitidus*[3] (Entomobryidae) at different temperature levels, and two levels of relative humidity of air (table 1). To achieve the humidity of 80 ± 5% in the respective thermostats TB-80 we apply a bowl with water and humidity of 40 ± 5% was achieved with no using of the water bowl. Humidity was measured by M-68 gigrometers. In laboratory containers with gypsy-carbonic (7:1 respectively) substrate were placed on 10 mature specimens, which were extracted from container after the deposition portions of 20—30 eggs. The cultures investigated have been supply by dry yeasts and wetted by filtered boiled water. Statistical reliability of the data provided by three replies of each option and standard methods of processing results. Cycles of development from egg to egg of *F. candida* and also *H. nitidus* in the similar conditions are about 1.5 times shorter than that of *O. stachianus.*

Besides the described experiences used as control, influence of the gradual concentrations of lead nitrate Pb $(No_3)_2$ on the duration of the life cycle of *O. sta-*

[1] Matrix population got from Val′kovskij island, the Dnieper River near Kyiv; meadow, September, 2006.

[2] Matrix population contained from Roslavskij island, the Dnieper River in Kyiv region, Obukhovsky region; coastal biotopes, September, 2006.

[3] Matrix population is from Holosiiv oak forest in Kyiv, Holosiivsky region

chianus, F. candida and *H. nitidus* were studied: 10 mg/l (0.5 maximum allowable concentration MAC), 20 mg/l (the maximum allowable concentration for Kyiv), 40 mg/l (2 × MAC). The laboratory cultures are wetted by these concentrations of lead nitrate water solution (1 ml/container) through the day in the three repeat of each of the variants.

Amount of degree days (effective temperatures sum, ETS) is calculated according to the formula: (Kozhanchikov, 1946):

ETS = $\sum$ №$^{-D}$(T^D -T°) * (D),

where T^D is the temperature fixed; T° is the lower temperature threshold of development, C; D is the duration of the total development in days.

At constant temperature T of the laboratory experiment: ETS = (T — T°) D [1]. Given into account the relative constancy of ETS (at constant values of factors other than temperature) for the two versions of the experience at temperatures T1 and T2 we get equality:

(T1-T°) D1 = (T2-T°) D2, of which the lower threshold of development is:

T° = (T1D1 — T2D2)/D1-D2 [2].

Another way to determine the threshold of development is a graphical (Kozhanchikov, 1961; Mednikov, 1977; Kipjatkov, Lopatina, 2010) By a curve based on the duration of the development cycle on temperature with linear regression equation (y = bx + a) of this dependence, we get the linear function of the speed of ontogeny (V = y = bT+a), as the backward regresion of the duration of development. (The approximation coefficient rİ predominantly 0.9 and higher). The intersection of the ontogeny speed regresion line with temperature axis (V = 0) specifies the lower threshold of development. Computation of the formulas of thermal constants on the graphs are obtained by coherent algebraic permutations, substituting the coefficients values into the formula of linear regression of ontogeny speed:

T° =-*a*/*b* [3] and

ETS = 1/(*b*) [4]. The coefficients *a* and *b* (from the regression formula of the ontogeny speed of y = *b*x + *a* = *b*T + *a*) characterize the dependence of the developmental speed on temperature: *a* identifies a point of intersection with the axis of ordinates; *b* — slope of the regression line to the abscissa, characterizes the degree of dependence of the speed of development on temperature, or thermolability (Kozhanchikov, 1961; Mednikov, 1977, cited in: Kipjatkov, Lopatina, 2010).

THE EXPERIMENTAL PART

Results of the control tests are presented in table 1. Graphical representation and conversion of these data in the full development cycle *O. stachianus* shown in figure 1[4].

Thresholds and amounts of degree days sum, received by the graphical method (table 2) are conditional parameters. However, in the view of a number of the researchers, they are convenient for comparing species. These meanings are closely related to the values of real physiological thresholds (Lamb, 1992). If one species threshold equation calculated by regression in a few degrees lower than the other, then the real physiological thresholds of these species differ in much the same way. This creates the opportunity for an objective comparison of the species (Kipjatkov, Lopatina, 2010).

Orthonychiurus stachianus

The reprodactive ability of *O. stachianus* begins after 6th moulting, on the 7th stage. On the basis of indicators of the lower threshold of full life cycle development one can note a remarkable low temperature resistance or boreophility of this species (table 2), that is the sign of patient adaptive strategy. In dry conditions as the temperature threshold values, and the sum of effective temperatures are lower than in high humidity conditions.

ETS for this species at high humidity of 80 ± 5% is 941,6 degree-days; when at low

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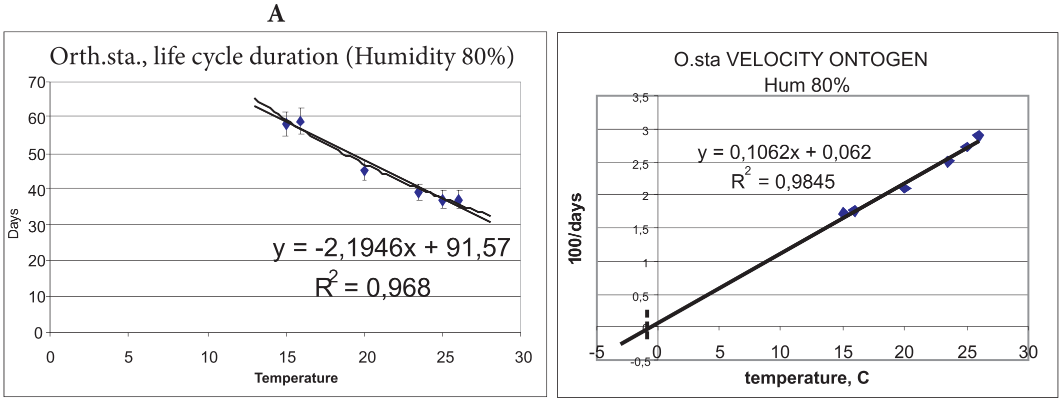
[4] Table of duration of development cycles under the impact of increasing concentrations of Pb $(N0_3)_2$, as well as most intermediate graphic representations are omitted due to the limitation of the article.

Table 1.

The duration of development cycle of the three species of Collembola under different temperatures and two levels of relative humidity of air (experimental data).

	Humidity 80 ± 5%						Humidity 40 ± 5%					
	Orthonychiurus stachianus		*Folsomia candida*		*Heteromurus nitidus*		*Orthonychiurus stachianus*		*Folsomia candida*		*Heteromurus nitidus*	
T, Grad.	Life cycle, days (M+m)	Embr. period in days (M+m)	Life cycle, days (M+m)	Embr. period in days (M+m)	Life cycle, days (M+m)	Embr. period in days (M+m)	Life cycle, days (M+m)	Embr. period in days (M+m)	Life cycle, days (M+m)	Embr. period in days (M+m)	Life cycle, days (M+m)	Embr. period in days (M+m)
26°	37±0,2	12±0,1	24±0,1	7±0,1	22±0,1	4±0,1	36±0,1	15±0,3	25±0,2	9±0,4	21±0,1	5±0,1
25°	37±0,1	14±0,3	25±0,3	8±0,2	24±0,1	5±0,1	34±0,2	14±0,1	26±0,1	7±0,1	23±0,1	6±0,1
23.5°	39±0,1	14±0,1	28±0,1	9±0,1	27±0,2	6±0,1	37±0,1	16±0,4	28±0,1	10±0,2	25±0,3	7±0,1
21°	40±0,2	17±0,1	30±0,2	10±0,2	33±0,1	8±0,1	39±0,2	16±0,1	29±0,3	9±0,1	28±0,1	9±0,1
20°	45±0,1	16±0,1	33±0,1	11±0,1	35±0,4	9±0,1	41±0,1	18±0,2	34±0,1	12±0,2	29±0,1	9±0,1
16°	56±0,1	20±0,1	46±0,4	15±0,1	46±0,1	11±0,1	53±0,1	22±0,2	45±0,1	15±0,1	39±0,1	12±0,1
15°	58±0,2	20±0,1	48±0,2	16±0,2	49±0,3	14±0,2	51±0,2	22±0,1	49±0,4	17±0,1	44±0,1	13±0,1

A



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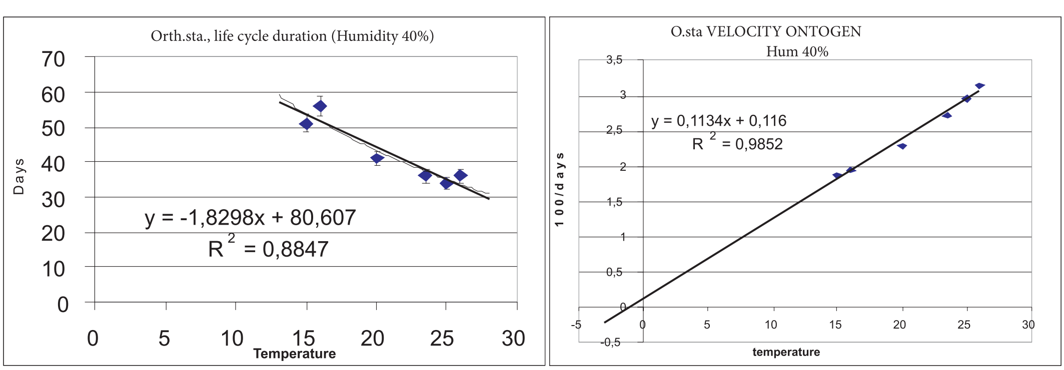

Fig. 1. Graphs of dependency of cycle development *O. stachianus* on temperature in 2 levels of humidity (A — humidity 80%; B — 40% respectively) and received graphics of velocity of ontogeny by the applying of the inverse functions.

Table 2.

Thermal constants of three species of collembola under the influence of increasing concentrations of Pb $(N0_3)_2$ and two levels of the relative humidity.

Species	The concentration of the pollutant, MAC	Humidity 80 ± 5%			Humidity of 40 ± 5%		
		Lower thermal threshold t°		The degree days (effective temperatu-res sum) ETS	Lower thermal threshold t°		The degree days (effective temperatu-res sum) ETS
		Development cycle	Èmbr. period	Development cycle	Development cycle	Èmbr. period	Development cycle
O. stachianus	Testing control	-0.6	0.8	941.6	-1	0.4	881.8
	0.5 Pb	-1.8	-4.1	872.6	-3.4	-4.1	896.9$^{\pm}$
	1 Pb	-1.8	-2.5$^{\pm}$	709.7	-4.4	-4.1	746.8
	2 Pb	-1.4$^{\pm}$	-2.7	632.9	-3.8$^{\pm}$	-2.2$^{\pm}$	661.4
F. candida	Testing	6.2	6.6	462.3	4.4	4.1	529.9
	0.5 Pb	5.95$^{\pm}$	7.57	433.1	4.9	6.61	442.3
	1 Pb	5.87	7.03	336.8	4.77$^{\pm}$	5.25$^{\pm}$	336.8
	2 Pb	5.39	7.18	327.3	4.57$^{\pm}$	4.46$^{\pm}$	334
H. nitidus	Testing	4.9	7.04	505.1	5.0	6.37	454.5
	0.5 Pb	5.65	9.57	476.2	4.9	6.4	416.7
	1 Pb	5.28	9.56	555.6	4.87	6.08	512.8
	2 Pb	4.72	10.25	653.6	4.72	7.21	561.8

humidity 40 ± 5% is 881,8 degree-days. Hence, in dry conditions for the development of this species it is necessary of less amount of heat energy. Under the influence of sequentially increasing concentrations of $Pb(N0_3)_2$ the heating degree day value consistently declining, both in wet and dry conditions. The exception is in case of 0.5 MAC pollutant impacts in dry conditions (noted in table 2 by the sign $^{\pm}$).

The lower temperature threshold of *O. stachianus* also tends to decline under the impact of increasing concentrations of Pb $(N0_3)_2$, except for the dual-MAC in wet and dry conditions, as well as single MAC during embryogenesis (noted $^{\pm}$).

A comparison of regression lines, angular speed of development depending on the temperature, as well as regression coefficients *b* (fig. 2, 3) showed an increase of the speed of development and thermolability of *O. stachianus* under the effect of increasing concentrations of Pb $(N0_3)_2$. This increase is a trend, the validity of which is partially confirmed (table 3).

$^{\pm}$Exception to the general trend

Folsomia candida

The sexual maturity of this species come after 6th to 7th moulting, on the 7th or 8th stage. The thermal threshold of *F. candida* development has positive value indicating thermophily. In dry conditions it is lower than the threshold values in moist, like the previous species. The sum of effective temperatures of *F. candida* in wet conditions 462.3 degree-days, in dry cases — increases to 529.9 degree-days (table 2). In dry conditions for the development this violent species requires a greater amount of heat than in humid conditions, unlike *O. stachianus*. These differences probably explain the different adaptive strategies.

Due to the increasing amount of pollutant concentration degree days successively reduced as in wet and dry conditions (table 2). Changing the temperature threshold *F. candida* under the influence of lead nitrate does not identify stable trends, but mainly tends to the ascending order; the steady decline observed only in a case of the full development cycle at high humidity (see table 2).

The dependency graphs of *F. candida* development speed under the growing concentration of $Pb(N0_3)_2$ (fig. 4, 5) show a trend of increasing angles of the regres-

Table 3.

Value and development velocity of regression coefficients of two types of collembola under the influence of the concentration of$Pb(NO_3)_2$ and reliability of the differences.

Species	The concentration of the pollutant, MPC	Humidity 80 ± 5%			Humidity of 40 ± 5%		
		Coeff. of regression and error		Reliability of distinction	Coeff. of regression and error		Reliability of distinction
		(b)	STD. err. (b)	$\frac{b_1-b_2}{S_{d\,(b1-b2)}}$	(b)	STD. err. (b)	$\frac{b_1-b_2}{S_{d\,(b1-b2)}}$
O. stachianus	Testing	0,10699	0,00596	2,2	0,11932	0,01004	1,9
	0,5 Pb	0,11565	0,0071		0,11245	0,00643	
	1 Pb	0,14227	0,00874	2,0	0,13493	0,00742	2,2
	2 Pb	0,15956	0,00997	2,0	0,15236	0,00856	2,0
F. candida	Testing	0,22027	0,0185	1,97	0,19133	0,0141	2,0
	0,5 Pb	0,23618	0,02224		0,23058	0,02025	
	1 Pb	0,30259	0,02832	2,0	0,29237	0,02547	1,97
	2 Pb	0,31198	0,02829	0,25**	0,30509	0,0262	0,5**
H. nitidus	Testing	0,198	0,0164	1,97	0,2234	0,0202	2,0
	0,5 Pb	0,2145	0,0235		0,2389	0,0193	
	1 Pb	0,1807	0,0132	2,0	0,1952	0,0272	1,97
	2 Pb	0,1533	0,0314	1,66	0,1776	0,0311	0,5**

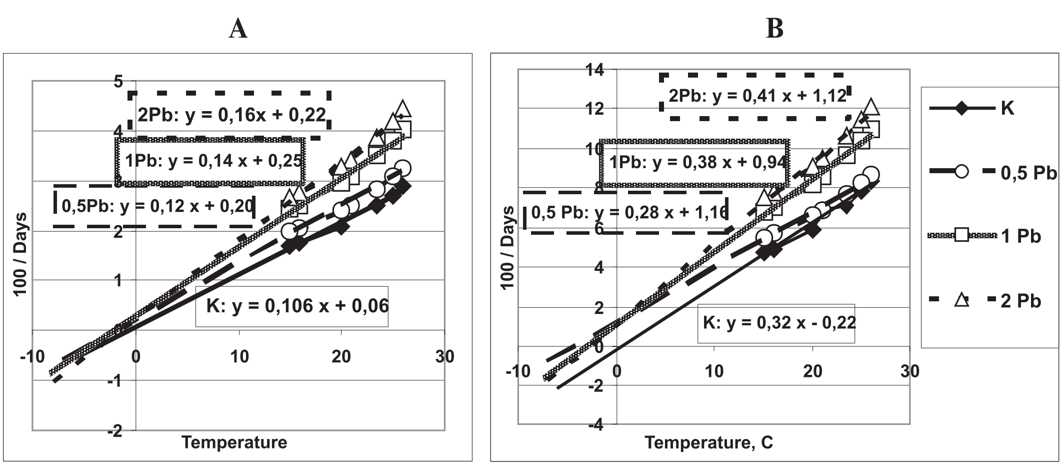

Fig. 2.The impact of the concentration of Pb $(N0_3)_2$ on the development velocity of the *O. stachianus* at humidity 80% (A — general the cycle from egg to egg; B — period of embryogenesis).

**The distinction is not reliable

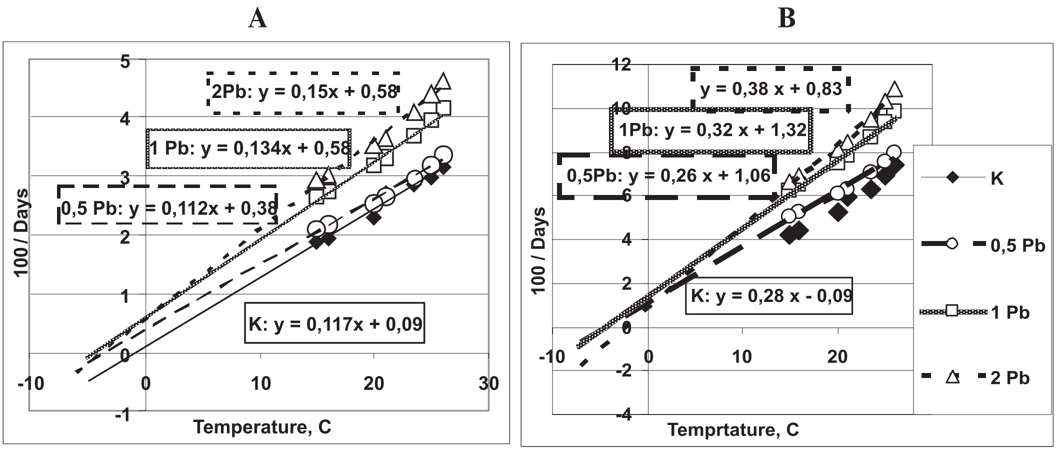

Fig. 3. The impact of the concentration of Pb $(N0_3)_2$ on the speed of development of the *O. stachianus* at humidity **40%** (A — general the cycle from egg to egg; B — period of embryogenesis).

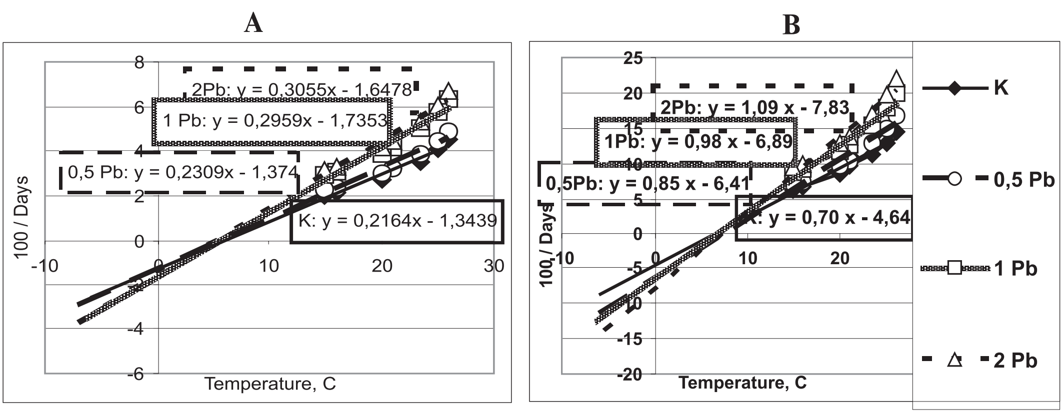

Fig. 4. The impact of the concentration of Pb $(N0_3)_2$ on the development velocity of *Folsomia candida* at humidity 80% (A — the general life cycle from egg to egg; B — period of embryogenesis).

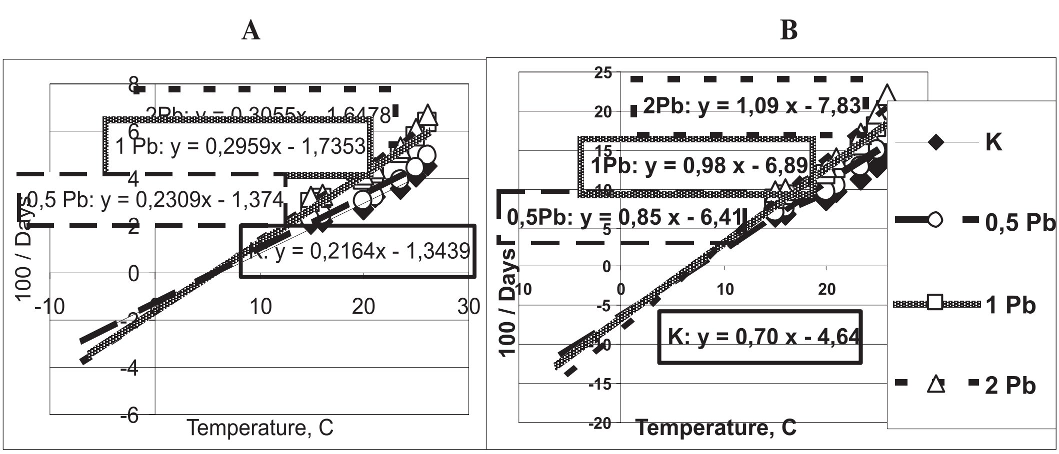

Fig. 5. The impact of the concentration of Pb $(N0_3)_2$ on the development velocity of *Folsomia candida* in the humidity of 40% (A — the general cycle from egg to egg; B — period of embryogenesis).

sion lines and the consistent increase of the rate of the coefficient *b* in regression formulas, enhancement of development speed and termolability.

Heteromurus nitidus

At the first wiew, the development parameters and thermal constants of *H. nitidus* are similar to those of *F. candida* (see tables 1, 2). Thus, the duration of the life cycle is very near in the same conditions while duration of the *H. nitidus* embryogenesis is shorter, especially at the high temperature (about 1,5 to 2 times at 26°C). Also the lower threshold indexes as well as the amounts of degree days sum of *H. nitidus* are in the same level of those of *F. candida*. Really this entomobryid species demonstrates the violent strategy of development parameters that confirmed by very active behaviour of most of individuals (high speed of moving, active searching for food, frequent grooming etc.)

Therefore we can note the trends of adaptive response of development on the increasing concentration of pollutant absolutely differ from trends of two previous species. Actually the duration of whole life cycle of *H. nitidus* accelerates with increasing concentration of lead nitrate (table 1). As a result, the amount of effective temperature sum of *H. nitidus* is extended with increasing concentration of $Pb(N0_3)_2$ in both wet and dry conditions: consequently from 505,1 and 454,5 in control to 653,6 and 561,8 in a case of 2 MAC (table 2).

The comparison of graphs of the developmental speed for the whole life cycle of *H. nitidus* depending on the rising pollutant concentration shows tendency of diminution angles slope of regression lines as well as the thermolability consequently (fig. 6 A, 7 A). Otherwise the duration of the embryonic stage reducted under increasing the contamination and as a result the velocity of embryonic development grows in that condition (table 2, fig 6 B, 7 B). Those phenomena explained by rising of larval studies number corresponding to the pollution level. Thus, in control testing case the females of *H. nitidus* usually oviposit on the 8—9th stage, after 7—8 moulting. Under the enlargement concentration of lead nitrate the egg lying may begins at more late stages: at 0,5 MAC sometimes sexual maturity begins at 9th to 11th stages, at 1 MAC it may come at 10th to 13th and in case of 2 MAC we noted the first oviposition at 18 and 20 stages at the temperature of 21°C (probably optimal).

With this peculiarities it is essentially to analise the duration of intermoulting period of *H. nitidus* development under our experimental conditions using the previous

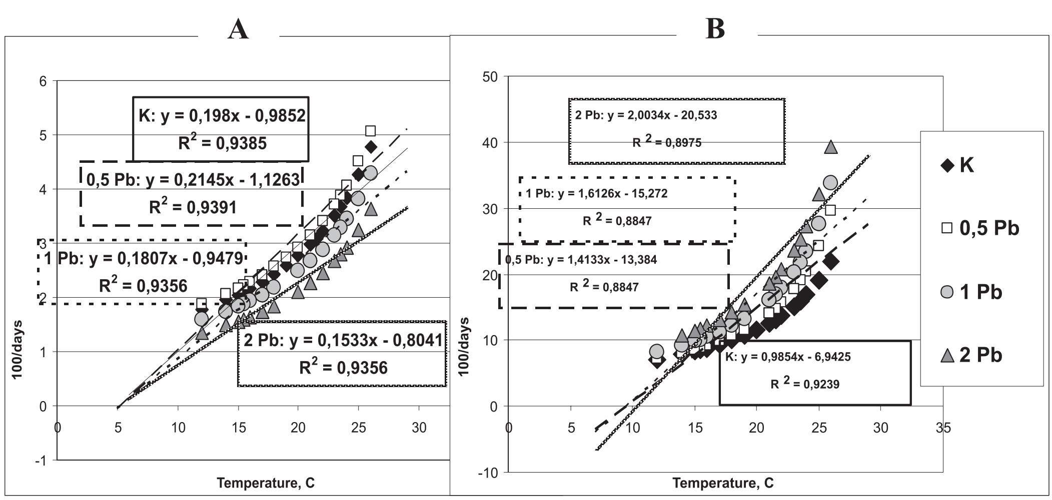

Fig. 6. The impact of the concentration of $Pb(N0_3)_2$ on the development velocity of *H. nitidus candida* at humidity 80% (A — the general life cycle from egg to egg; B — period of embryogenesis).

methods. As it been expected, the speed and frequency of moulting of this species mainly rises accordingly to increasing of contamination (with exceptions of 0,5 MAC in wet conditions and of 2 MAC in dry). It is possible to compare that meaning by comparing of coefficients *b* of regression lines (fig. 8).

DISCUSSION OF RESULTS

When one compares the lower threshold and the sum of effective temperatures produced by formulas (Kozhanchikov, 1946 [1], [2] and the graphical method [3] and [4]), the results differ by a few degrees, but there are similar trends. The so called “thermal constants” vary significantly at different levels of humidity as the embry-

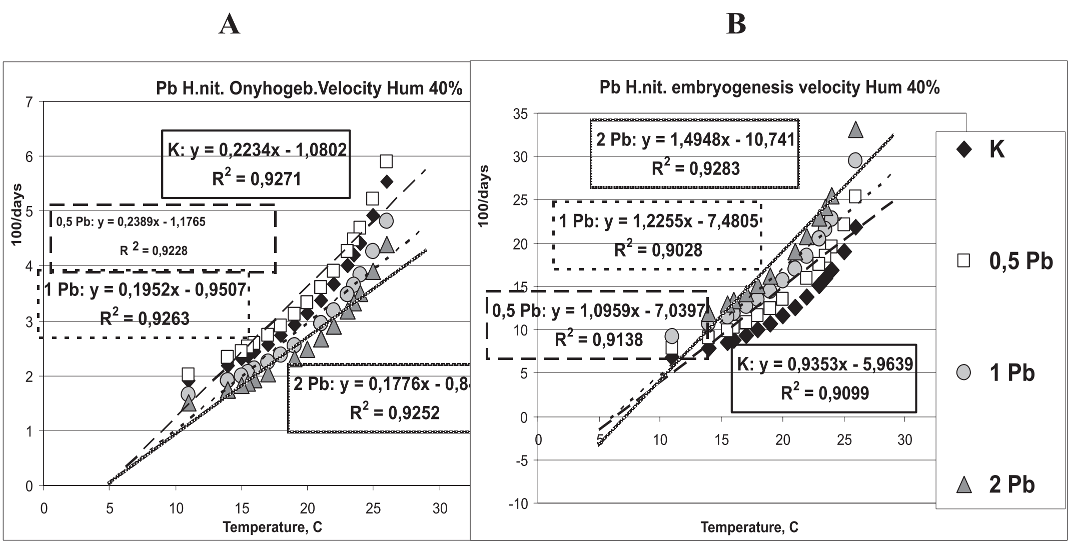

Fig. 7. The impact of the concentration of Pb $(N0_3)_2$ on the development velocity of *H. nitidus* in the humidity of 40% (A — the general cycle from egg to egg; B — period of embryogenesis).

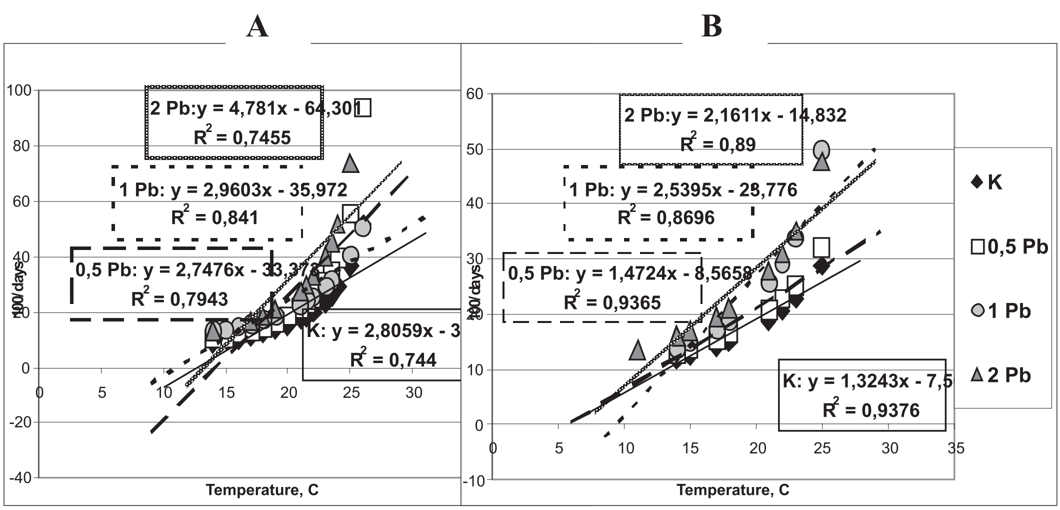

Fig. 8. The impact of the concentration of Pb $(N0_3)_2$ on the development velocity in the intermoulting stages of *H. nitidus* (A — in the humidity of 80%; B — in the humidity of 40%).

onic stage and at the stage of completed cycle (table 1, fig. 1). Our observations are consistent with the data provided for in other groups of arthropods: ticks-fitoseid (Kolodochka, 1988), ants (Kipjatkov, Lopatina, 2010), bedbugs-soldiers (Balashov, Kipjatkov, 2008).

Study of the influence of increasing concentrations of Pb $(No_3)_2$ on population *Orthonychiurus stachianus* and *Folsomia candida* showed a reduction of up to a total loss of populations[1], reducing cycle time and increasing the temperature dependence of the cycle development (ontogenesis termolability) compared to controle conditions (table 2, 3).

Periodic shedding of epidermis in collembolas occur regularly during ontogeny, in addition to the adaptive effect of growth, performing the function of the excretion (Joosse, Verhoef, 1983; cited by: Hopkin, 1997). Effects of pollutant, sedimented in the intestines epidermis and other animal tissues, causing the need to intensify the excretory functions, including growth the frequency of moulting. Development cycle of *Orthonychiurus stachianus* and *Folsomia candida* decreased in proportion to the reduction in intermoulting period. Otherwise, the the life cycle duration of *Heteromurus nitidus* encreased at the such conditions due to delay of sexual organs ripening, though the frequency of moulting is rised in the same time. One can define the fact of the different ontogenetic strategies of adaptive response on contamination. Note the above (see “Introduction”), accelerate the development of two species and slowing-down of maturing and reproduction of third species examined that belongs to different families as a reaction to extreme effect may be considered as variants of heterohrony process, common among the class Collembola.

In subsequent studies should extend the species composition of members of other families of collembola with different adaptive strategies, and increase the list of chemical contaminants and their concentrations.

CONCLUSION

Thermal constants (the sum of effective temperatures, thermal thresholds) of the collembolan species are different in the stages of ontogenesis and change under the influence of other factors (humidity).

Laboratory populations of the studied species *Orthonychiurus stachianus, Folsomia candida* under the influence of an increasing concentration of pollutant Pb $(No_3)_2$ tended to accelerate the velocity of the ontogeny, increase termolability development, decrease or increase the temperature threshold of development and decrease the amount of effective temperatures (degree days). Otherwise, the life cycle duration of *Heteromurus nitidus* as well as degree days sum encreased at the such conditions. The representatives of different familied demonstrated the different ontogenetic strategies that may be considered as a cases of heterohrony process.

Analysis of contamination changes the overall population density should take into account the possible acceleration of development velocity and increasing egg lying frequency, observed in some species, in addition to the expected decrease in egg lying amount and increased mortality. This fact makes it difficult to assess population response to pollution.

Study of thermal constants of different families and different adaptive strategies has bioindicative and theoretical value. Parameters of the collembolan species with different adaptive strategies determine the distribution of ecological niches in biocenosis.

[1]Population of *O. stachianus* was lost after the first molt of the second generation in two variants of experience when exposed to concentrations of pollutant 2 MAC

REFERENCES

Balashov S.V., Kipyatkov V.E. The first proof of the possibility of changing the temperature of insect development by artificial selection for rapid or slow development on the example of the Bedbug-soldier Pyrrhocoris apterus l. // Journ. Evoluts. Biochemistry and Phyiziol., 2008, vol. 44, issue 2. P. 162—167 (in russian).

Biological encyclopedia/[CHS. ed. M.s. New]. — 2-nd ed., amendable. — Moscow: Sovetskaya entsiklopediya, 1986. — 864 p. (in russian).

Kaprus' I.J., Shrubovich Yu.Yu., Tarashchuk M.V. Catalogue kolembol (Collembola) i protur (Protura) of Ukraine — Lviv, 2006. — 164 p (In ukrainian).

Kipyatkov V.E., Lopatina E.B. Intra-specific variability of temperature standards development in insects: new approaches and perspectives // Entomological review, 2010, vol. 89, ISS 1, p. 33—61 (in russian).

Kozhanchikov V.E. To the question about the life thermal optimume. VIII. The lability of insect development processes on thermal effects // Zool. Neuropsychopharmacology. 1946 t. 25, ISS 1, p. 27—35 (in russian).

Kozhanchikov Research Methods in ecology of insects. Moscow: Vysshaya Shkola, 1961. — 286 p. (in russian).

Kolodochka L.A. Development of three species of predatory mites-fitosejid (Parasitiformes). Communication (III) // The Journal of Zoology, 1988, no. 1. C. 51—56 (in russian).

Kuznetsova N.A. Organization communities of soil-dwelling collembolas. — M.: SAP Prometheus, 2005. — 244 p. (in russian).

Mednikov B.M. Temperature as a factor of development//External environment and evolving organism. M., 1977. P. 7—52 (in russian).

Block, W. Cold hardiness in invertebrate poikilotherms. Comparative Biochemistry and Physiology, 1982, 73, p. 581—93.

Block, W. To freeze or not to freeze? Invertebrate survival of sub-zero temperatures. Functional Ecology, 1991, 5, p. 284—90.

Blunck H. Die Entwicklung von Dytiscus marginatus L. vom Ei bis zur Imago // Zeitschr. Wiss. Zool. 1914. Bd. 111, S. 76–151.

Campbell A., Fraser B.D., Gilbert N., Gutierrez A.P., Mackauer M. Temperature requirements of some aphids and their parasites // J. Appl. Ecol. 1974, Vol. 11, p. 431—438.

Cannon, R.J.C., Block, W. Cold tolerance of microarthropods // Biological Reviews, 1988, 63, p. 23—77.

Fountain M.T., Hopkin S.P. A comparative study of the effects of metal contamination in Collembola in the field and in the laboratory. Ecotoxicology, 2004, 13, p. 573—587.

Hale, W.G. (). Post-embryonic development in some species of Collembola. Pedobiologia, 1965, № 5, p. 228—43.

Honěk A. The relationship between thermal constants for insect development: a verification // Acta Soc. Zool. Bohem. 1996. Vol. 60, p. 115—152.

Hopkin S.P. Biology of the Springtails (Insecta : Collembola). Oxford University Press (ISBN 0-19-854084-1), 1997. — 330 p.

Janssen, G.M., Joosse, E.N.G. (). Reproduction and growth in Collembola under laboratory conditions. Pedobiologia, 198, 730, p. 1—8.

Lamb R.J. Developmental rate of Acyrthosiphon pisum (Homoptera: Aphididae) at low temperatures: implications for estimating rate parameters for insects // Environm. Entomol. 1992, Vol. 21, p. 10—19.

Lopatina E.B., Kipyatkov V.E. Comparative study of temperature dependance of development in ants // Book of Abstracts, Proc. VIth Eur. Congr. Entomol. Ceske Budejovice, August 23—29, 1998. Ceske Budejovice, 1998, p. 224—225.

Meier, P., Suter, E., Zettel, J. Cold hardiness strategies of two subalpine springtails. Cryo Letters, 1988, № 9, p. 436.

Ratte H.T. Temperature and insect development / Hoffmann K. H. (Ed.). Environmental Physiology and Biochemistry of Insects. Berlin, Heidelberg, New York, Tokyo: Springer Verlag, 1985, p. 33—66.

Sandifer R.D., Hopkin S.P. Effects of Temperature on the Relative Toxicities of Cd, Cu, Pb, and Zn to Folsomia candida (Collembola) // Ecotoxycology and environmental safety, 1997, № 37, p. 125—130.

Sømme, L. Supercooling and winter survival in terrestrial arthropods. Comparative Biochemistry and Physiology, 1982, 73A, 519—543.

Tarashchuk M.V. Unusual type of heterochrony in the onthogenesis of Megalothorax incertus Borner, 1903 (Collembola, Entognatha)/ XI Int.Colloq. on Apterygota, Ces. Budejovice, 2000, p. 32.

Thibaud, J.M. Intermue et températures léthales chez les Insectes Collemboles Arthropléones. I. Hypogastruridae et Onychiuridae. Revue d'Écologie et de Biologie du Sol, 1977a, № 14, p. 45—61.

Thibaud, J.M. Intermue et températures léthales chez les Insectes Collemboles Arthropléones. II. Isotomidae, Entomobryidae et Tomoceridae. Revue d'Écologie et de Biologie du Sol, 1977 b, № 14, p. 267—278.

Trudgill D.L., Honěk A., Li D., van Straalen N.M. Thermal time — concepts and utility // Ann. Appl. Biol. 2005, Vol. 146, p. 1—14.

Vannier, G. The thermobiological limits of some freezing intolerant insects: the supercooling and thermostupor points. Acta Oecologia, 1994, № 15, p. 31—42.

Van Straalen, N.M. Adaptive significance of temperature responses in Collembola. Acta Zoológica Fennica, 1994, № 195, p. 135—142.

Van Straalen, N.M., Groot, G.M., Zoomer, H.R. Adaptation of Collembola to heavy metal soil contamination. Proceedings of the International Conference on Environmental Contamination, Amsterdam, 1986, p. 16—20.

Zettel, J. Cold hardiness strategies and thermal hysteresis in Collembola. Revue d'Écologie et de Biologie du Sol, 1984, № 21, p. 189—203.

Zettel, J., Meier, P., Suter, E., Von Allmen, H. Difference in cold hardiness strategies and the presence of cryoprotectants in two subalpine springtails: Isotoma hiemalis and Entomobrya nivalis. In Third International Seminar on Apterygota (ed. R. Dallai), University of Siena, Siena, 1989, p. 429—36.