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МОДЕЛИРОВАНИЕ РОСТА ИНВАЗИВНОГО ВИДА РЕЧНЫХ РАКОВ *PROCAMBARUS VIRGINALIS* (DECAPODA, ASTACIDEA) В РАЗЛИЧНЫХ ТЕМПЕРАТУРНЫХ УСЛОВИЯХ

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У мраморного рака *Procambarus virginalis* определена зависимость длительности межлиночных интервалов от массы тела и величины приростов массы тела за отдельные межлиночные интервалы в диапазонах температуры 15,3–17,9 °С; 7,5–18,9; 19,1–20,8; 21,0–22,8; 22,9–25,2 и 25,3–28,9 °С. По этим данным рассчитаны кривые роста их в указанных диапазонах температур и суммы эффективных температур ($S_{ef)}$ у особей за периоды ювенильного роста и размножения. Среднее значение S_{ef} за ювенильный период *P. virginalis* (до достижения новорожденными особями массы тела 1,4 г) в исследованных температурных интервалах составляет 4316 градусо-дней при температуре биологического нуля, равном 7,6 °С. Для периода размножения (до достижения массы тела от 1,4 г до предельной массы 15 г) 10630 градусо-дней и 3,0 °С соответственно. По годовой динамике среднемесячных температур в шести континентальных водоемах в пределах инвазивного ареала *P. virginalis* (Швеция, Беларусь, Германия, Словакия, Северная Македония и Малави) рассчитаны значения S_{ef} для периодов года, в течение которых возможен рост ювенильных и размножение половозрелых особей. В водоемах умеренных широт, расположенных в Швеции, Беларуси, Германии и Словакии, значения S_{ef} в период роста ювенильных особей изменяются в пределах 1083–2099 градусо-дней. В более южном водоеме Северной Македонии этот показатель достигает 2990, а в тропическом африканском водоеме в Малави – 7076 градусо-дней. Следовательно, новорожденные особи *P. virginalis*, которые в водоемах умеренной зоны Европы отрождаются в первой половине лета, способны достичь половой зрелости лишь в третье лето жизни, а в тропическом водоеме – уже в первое лето жизни. Значения S_{ef} для периодов года, благоприятных для роста половозрелых особей, в исследованных водоемах Европы возрастают от 2031 (водоем в Швеции) до 4657 градусо-дней (водоем в Северной Македонии). В тропическом водоеме Малави этот показатель достигает 8058 градусо-дней, то есть максимальная продолжительность жизни *P. virginalis* в нем не превышает двух лет. Тем не менее, во всем ареале половозрелые особи *P. virginalis* способны произвести не более 2–5 кладок яиц за жизненный цикл.

Ключевые слова: биологические инвазии; температурный режим; речные раки; мраморный рак *Procambarus virginalis*; скорость роста; инвазивный потенциал.

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MODELING THE GROWTH OF THE INVASIVE RIVER CRAYFISH SPECIES *PROCAMBARUS VIRGINALIS* (DECAPODA, ASTACIDEA) UNDER DIFFERENT TEMPERATURE CONDITIONS

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In the marbled crayfish P*rocambarus virginalis*, the dependence of the duration of inter-larval intervals on body weight and the magnitude of body weight gains for individual inter-larval intervals in the temperature ranges 15.3–17.9 °C, 7.5–18.9, 19.1–20.8, 21.0–22.8, 22.9–25.2 and 25.3–28.9 °C was determined. The growth curves of individuals in these temperature ranges and the sum of effective temperatures (S_{ef}) of individuals during juvenile growth and breeding periods were calculated from these data. The average S_{ef} value for the juvenile period of *P. virginalis* (until newborn individuals reach a body weight of 1.4 g) in the studied temperature ranges is 4316 degree·days at the biological zero temperature of 7.6 °C. For the breeding period (until reaching the body weight from 1.4 g to the limit weight of 15 g) – respectively 10630 degree·days and 3.0 °C. Based on the annual dynamics of mean monthly temperatures in six continental water bodies within the invasive range of *P. virginalis* (Sweden, Belarus, Germany, Slovakia, North Macedonia and Malawi), S_{ef} values were calculated for the periods of the year during which juvenile growth and reproduction of sexually mature individuals are possible. In temperate water bodies located in Sweden, Belarus, Germany and Slovakia, S_{ef} values during the juvenile growth period vary between 1083 and 2099 degree·days. In the more southern body of water in Northern Macedonia, this value reaches 2990 degree·days, and in the tropical African body of water in Malawi it reaches 7076 degree·days. Consequently, newborn individuals of *P. virginalis*, which in water bodies of the temperate zone of Europe hatch in the first half of summer, can reach sexual maturity only in the third summer of life, and in a tropical water body – already in the first summer of life. S_{ef} values for periods of the year favorable for the growth of sexually mature individuals in the studied water bodies of Europe increase from 2031 degree·days (water body in Sweden) to 4657 degree·days (water body in Northern Macedonia). In the tropical water body of Malawi, this figure reaches 8058 degree·days, i.e. the maximum life span of *P. virginalis* in this water body does not exceed two years. Nevertheless, throughout the entire range, sexually mature individuals of *P. virginalis* are capable of producing no more than 2–5 clutches of eggs per life cycle.

Keywords: biological invasions; river crayfish; marbled crayfish *Procambarus virginalis*; growth rate; invasive potential.

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Introduction

Invasion of animal and plant species into new geographic regions as a result of the influence of numerous natural (geological, climatic and biological) factors with the displacement of native species has always existed. With the advent of man and the anthropogenic factors he created, the process of invasion began to accelerate more and more and in the second half of the twentieth century it became a serious environmental problem in almost all regions of the planet.

One of the striking examples among aquatic organisms is the massive penetration of alien species of crayfish (order Decapoda, infraorder Astacidea) of North American and Australian origin into water bodies of Europe, Asia and Africa, caused almost exclusively by anthropogenic factors. It leads not only to a decrease in the number and even complete displacement of native crayfish species and the destruction of established biotic complexes of inland water bodies, but also causes significant material damage. For the period 2000–2020 economic losses from invasion of various crayfish species worldwide exceed 120 million dollars [1].

By the beginning of the 21st century, in many European countries, the number of invasive crayfish species reached and even exceeded the number of their native relatives [2]. In the current situation, a number of methods and measures have been proposed for the conservation of native species of crayfish, but their effectiveness raises reasonable doubts [3; 4]. In the foreseeable future, it is possible to expect that invasive crayfish in European water bodies will become dominant not only in the number of species, but also in the number and biomass of populations. In this case, they will inevitably enter into intense competition with each other, the outcome of which is currently impossible to predict.

However, this question is of significant scientific interest, since it will expand the understanding of the patterns of transformation processes of the fauna of continental water bodies in the modern era under the influence of global natural (climate changes, biological invasions) and anthropogenic (pollution of water bodies, changes in their abiotic and biotic characteristics, etc.) factors.

One of the most aggressive species of invasive decapod crayfish, rapidly spreading throughout the planet, is the marbled crayfish, *Procambarus virginalis* (family Cambaridae), popular among aquarists around the world [5]. Its distinctive feature is obligate parthenogenetic reproduction, which is a unique case in the infraorder Astacidea.

Special molecular genetic studies have established that all aquarium parthenogenetic individuals of marbled crayfish are triploid females, which originated from a single individual of the subtropical North American species *Procambarus fallax* (Hagen, 1870) as a result of a genomic mutation [6]. Two sex X chromosomes in the chromosome set of *Procambarus virginalis* are genetically completely identical, and the third has quite significant differences from them [7]. Most likely, in one female *P. fallax*, as a result of a violation of meiosis, an egg cell with two X chromosomes was formed, which was successfully fertilized by spermatozoon with an X-chromosome.

After the experimental establishment of reproductive isolation between *P. fallax* males and females of marbled crayfish, the latter was recognized as an independent species, *Procambarus virginalis sp. nov.* Lyko, 2017 [5]. Its occurrence is a striking example of saltation, or quantum speciation [8].

The natural range of *P. fallax* covers only the basin of the small Satilla River in the states of Georgia and Florida (USA). This species, like other Astacidea, is bisexual. However, recent molecular genetic studies have revealed the presence of parthenogenetic females of *P. virginalis* in its natural populations. Therefore, along with the offspring from the bisexual reproduction of *P. fallax*, they also contain clones originating from parthenogenetic individuals of *P. virginalis* [9].

In North America, *P. fallax* is one of the most important objects of the aquarium animal trade [10; 11]. Obviously, some batches of *P. fallax*, caught from natural reservoirs for sale in the USA and then in Europe, also contained parthenogenetic individuals, which quickly spread among aquarists.

Since the beginning of the 21st century *P. virginalis* from aquaria, as a result of accidental or deliberate introduction, has widely spread throughout the water bodies of many countries of the world with significantly different temperature conditions. In Europe, it is distributed from Belgium to Romania and from Sweden to Ukraine and Croatia [12–15]. Beyond its borders, the marbled crayfish has widely settled in numerous reservoirs of the lowland part of the island of Madagascar [16]. It was also found in one of the lakes on the Japanese island of Hokkaido [17], reservoirs in Taiwan [18], Israel [19], and an ornamental pond in Macau (China) [20].

One of the most important parameters determining the invasive potential of a particular species is the rate of growth of their populations in comparison with that of closely related native species [21]. In turn, it is determined by three important parameters: the survival rate of juveniles, the total fecundity of females during the life cycle, and generation time [22]. The total fecundity of female crayfish is quite easy to determine based on the results of field population studies.

It is much more difficult to determine the generation time in natural populations of crayfish. For rough estimates, it can be equated to the duration of the juvenile period in females, i. e. the age at which they laid their first clutch. However, most species of crustaceans have a long-life cycle (from 2–3 to 10 or more years), which does not always allow for appropriate laboratory experiments.

However, the growth rate of all crayfish species is determined by the frequency of their molts, which in turn is largely determined by the temperature of the environment [23]. Using the noble crayfish *Astacus astacus* as an example, we developed a model for reconstructing the somatic growth of individuals based on the duration of intermolt intervals in individuals with different body weights and body weight increments during separate intermolt intervals [24]. The results of calculations of *A. astacus* growth curves using this model showed good agreement with the corresponding empirical data. Therefore, we used this method to simulate the growth processes of marbled crayfish over their life cycle.

The modern extensive invasive area of marbled crayfish covers regions with different natural and climatic, primarily temperature, conditions. One of the most important limiting environmental factors for crayfish is the temperature regime of water bodies, which has a significant impact not only on their survival and seasonality of reproduction, but also on the duration of embryogenesis and intermolt intervals [25]. Therefore, studying the effect of temperature on the growth of marbled crayfish individuals allows us to make predictive estimates of the invasive potential of their populations in new habitat conditions.

Materials and methods

The studies were conducted in 2015–2022 on individuals from a laboratory culture of *P. virginalis* kept at the International Sakharov Environmental Institute of Belarusian State University. The culture obtained from a single maternal individual was, of necessity, located in a laboratory room that was poorly heated in winter and strongly heated in summer. During the year, the temperature in it varied from 13–16 °C in December–February and to 28–32 °C in July–August. However, this same circumstance made it possible to estimate the effect of the temperature factor on the frequency of molting.

Newborns at the age of 2–3 weeks were seated individually in vessels with a volume of 1 liter. Then, as they grew, they were transferred to larger aquariums with a water volume of up to 5 liters. All containers with animals were checked at least 1–2 days to record the dates of individual molts and the laying of eggs on pleopods. All individuals were weighed after each molt. For further analysis, we used only the duration of time intervals between two successive molts, during which females did not lay eggs or bear young.

The water temperature in the vessels was determined daily. These data were used to calculate average temperatures for individual intermolt intervals. The animals in the experiment were fed live larvae of the chironomid *Chirinomus sp.* and Cladocera species *Daphnia magna*, supplied in abundance. At least twice a week, a complete change of water was carried out in all containers.

The specific growth rate of individuals (r, time^{-1}) for certain periods of time ($\tau_1 - \tau_2$) was calculated according to (1):

$$r = \frac{\ln W_2 - \ln W_1}{\tau_2 - \tau_1}, \tag{1}$$

where W_2 and W_1 are the weight of individuals at ages τ_2 and τ_1.

The Van't Hoff coefficient values (Q_{10}) for molting frequency ($V = 1/D_m$, day^{-1}, where D_m is the duration of the intermolt interval) for individual temperature ranges were calculated according to (2):

$$Q_{10} = \left(\frac{V_2}{V_1}\right)^{\frac{10}{(t_2 - t_1)}}, \tag{2}$$

where V_1 and V_2 are the frequency of molts at temperatures t_1 and t_2.

All calculations are performed in the *STATISTICA 8* software package.

The present-day wide invasive area of marble crayfish covers various natural zones – from the tropics to the subarctic regions. The temperature regime of reservoirs in these regions varies sharply, which has a significant impact on the processes of growth and reproduction of this species. We conducted a comparative analysis of the features of changes in average monthly temperatures in six model reservoirs in different zones of the range of this species and the features of the impact of their temperature regime on the growth of marbled crayfish. The model reservoirs were:

1. A reservoir near the city of Jönköping in Southern Sweden, where the northern border of the invasive area of *P. virginalis* currently lies [26].
2. Zaslavskaye reservoir near Minsk (Belarus). As of 2024, this species has not been found in natural reservoirs of Belarus. However, in our country it is also a popular aquarium species and sold in specialized stores [27], which, unfortunately, does not exclude its penetration into the natural environment. In addition, Zaslavskaye Reservoir is located in the central part of Belarus, so its thermal regime is quite typical for reservoirs throughout the country.
3. A reservoir in Frankfurt am Main (Germany), since the marbled crayfish was first discovered in natural water bodies exactly in Germany [28].
4. A reservoir in Bratislava (Slovakia), since a stable population of this species was found near this city [29].
5. Plain Dojran Lake (North Macedonia), since currently the marbled crayfish actively populates the water bodies of the Balkan Peninsula [30].
6. Coastal zone of Monkey Bay on the extreme southwestern section of the shore of Nyasa Lake (Malawi, East Africa). We took it for rough estimation of the temperature regime in freshwater bodies of the island of Madagascar, which is the southern border of the modern invasive range of the marbled crayfish [16]. Unfortunately, we were unable to find the necessary data on the thermal regime of freshwater bodies on this island in publicly available sources of information. However, since Madagascar and Malawi are located in the geographic region of Southeast Africa there is every reason to believe that the temperature regimes of freshwater bodies of Madagascar and Lake. Nyasa Lake are very similar.

Data on the temperature regime of the listed reservoirs are taken from the publicly available Internet resource https://seatemperature.info/. Calculations of the sums of temperatures for separate periods of the year were carried out in the computer program «Integral Calculator» https://www.integral-calculator.ru/.

Results and discussion

In all species of crustaceans the duration of intermolt intervals increases with increasing mass of individuals and decreases with increasing temperature [31]. In our experiments, individuals grew and molted over a wide temperature range. Therefore, to eliminate the influence of the temperature factor on the dependence of the duration of intermolt intervals (D_m) on the mass of individuals (W), all available D_m values were distributed over six temperature intervals in which the average temperatures during intermolt intervals changed by no more than 3 °C.

Despite the rather significant scatter of empirical data in all temperature intervals, the relationship between these parameters in *P. virginalis*, as well as in other species of crustaceans, is well approximated by the power equation:

$$D_m = pW^q, \tag{3}$$

where p and q are empirical coefficients, the parameters of which are presented in table 1.

In double logarithmic coordinates, equation (3) is transformed into a linear regression equation:

$$\lg D_m = \lg p + q\lg W. \tag{4}$$

In graphical form, the dependence of D_m on W in different temperature intervals is presented in Fig. 1, and the parameters of equation (1) for different temperatures are in table 1.

Due to the large range of variation in individual weights, both scales are presented in logarithmic coordinates. The straight lines are the regression lines of equation (2), whose parameters are given in Table 1; the dashed line is the 95 % significance level.

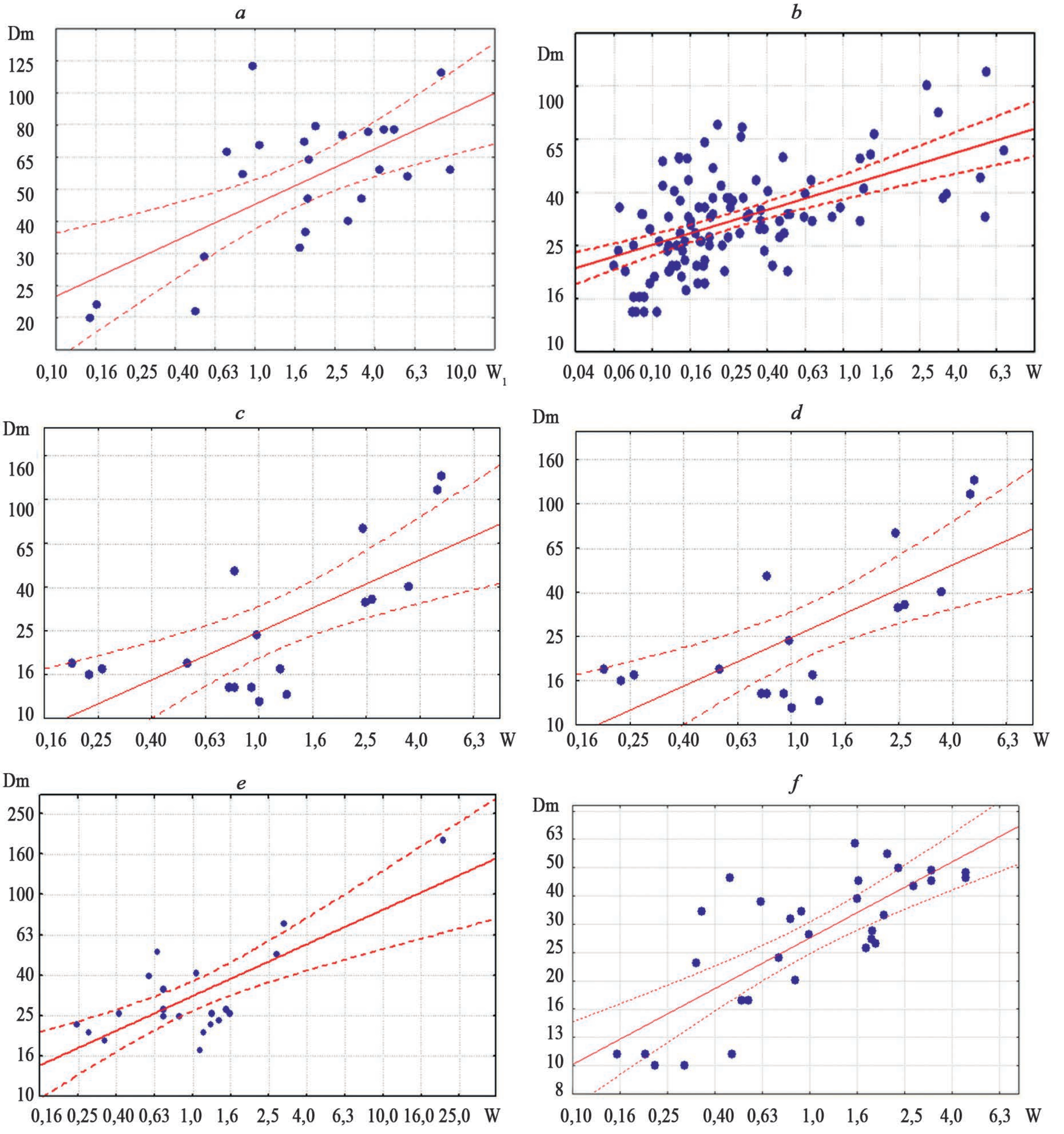

Fig. 1. Dependence between of the duration of intermolt periods (D_m, days)
and body weight (W, g) before the previous molt in marbled crayfish at different temperature intervals:
a) 15.3–17.1 °C; *b)* 17.5–18.9 °C; *c)* 19.1–20.8 °C; *d)* 21.0–22.8 °C; *e)* 22.9–25.2 °C; *f)* 25.3–28.9 °C

Table 1

Parameters of equation (3) of dependence of interlinear interval duration on body weight of marbled crayfish

Temperature range, °C	Average temperature, °C	Weight range of individuals, g	p	q	r*	Average of
15.3 –17.1	16.5	0.148–9.484	45.0	0.2871	0.6382	1.351
17.5–18.9	18.2	0.064–6.950	41.8	0.2185	0.5481	1.295
19.1–20.8	19.7	0.063–6.650	34.0	0.3353	0.7642	1.362
21.0–22.8	22.0	0.200–4.786	24.9	0.5480	0.7100	1.303
22.9–25.2	23.9	0.246–20.52	31.4	0.4275	0.7479	1.333
25.3–28.9	26.2	0.154–4.538	28.3	0.4478	0.7736	1.356

*Correlation coefficient between lgD_m and lgW in the equation (4)

It is important to note that as the body weight of individuals increases, the effect of temperature on the frequency of their molts weakens (Fig. 2).

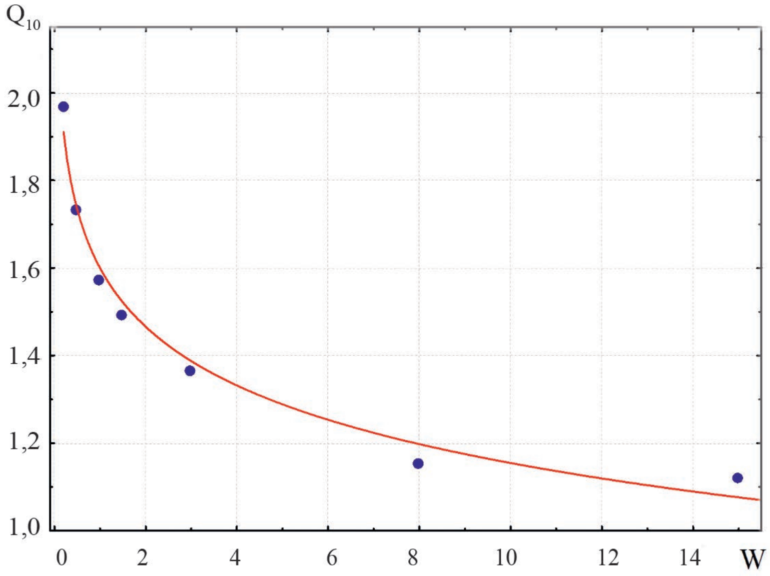

Fig. 2. Dependence between the Q_{10} coefficient for the frequency of molts ($1/D_m$, day^{-1}) and the weight of marbled crayfish individuals (W, g) in the interval 16.5–26.2 °C

The values of $1/D_m$ for the temperatures 16.5 °C and 26.2 °C were calculated using the corresponding equations (3), the parameters of which are given in Table 1.

An increase in the mass of decapod crayfish, which have massive and hard outer integuments, occurs only in the first few days after molting, until the new integuments harden. Therefore, the frequency of molting directly determines the rate of weight growth of crayfish.

The principle of calculating growth curves of individuals is as follows. In the *Excel-2003* editor, a table of 4 columns is built (Table 2). ***The first column*** contains the serial numbers of molts (i). ***The second column*** contains the weights of individuals after the corresponding molt (W_i). The values of the post-molt weight of individuals in any pair of subsequent (W_{i+1}) and previous molts (W_i) can be calculated by the equation:

$$W_{i+1} = \beta W_i, \qquad (5)$$

where β is the ratio of the mass of individuals after the subsequent molt to their weight after the previous molt, expressed in fractions of unity:

$$\beta = \frac{W_{i+1}}{W_i}. \qquad (6)$$

In all temperature intervals, no statistically significant dependence of β values on the weights of individuals was established. Therefore, for further calculations we will use their averaged values for each temperature interval (Table 1).

Table 2

Example calculations of age curves of marbled crayfish per life cycle at temperatures of 25.3–28.9 °C

Number of moult, i_i	W_i, г	D_i days	τ, days	i_i	W_i, г	D_i, days	τ, days
1	**2**	**3**	**4**	**1**	**2**	**3**	**4**
0	**0.007**	3	0	14	0.500	21	138
1	0.010	4	4	15	0.675	24	162
2	0.013	4	8	16	0.915	27	189
3	0.018	5	12	17	1.240	31	220
4	0.024	5	18	18	1.682	35	255
5	0.032	6	24	19	2.281	40	295
6	0.044	7	31	20	3.092	46	341
7	0.059	8	39	21	4.193	53	394
8	0.080	9	48	22	5.686	60	455
9	0.109	10	58	23	7.710	69	524
10	0.147	12	70	24	10.455	79	603
11	0.200	14	84	25	14.177	91	693
12	0.271	16	100	26	19.224	104	797
13	0.368	18	118	27			

Body weight of individuals after each successive molt (W_i) increases exponentially:

$$W_i = W_o \beta^i, \quad (7)$$

where W_o is the average weight of newborn *P. fallax* individuals, which, according to our data, is 0.007 g, i – is the molting serial number.

The third column contains the values of the duration of the subsequent intermolt interval (D_i) for a molted individual with mass W_i, calculated according to (4). ***The fourth column*** records the total values of D with an increasing total, which corresponds to the age of individuals (τ. days) after each successive molt. The age of individuals in our calculations was limited to 780–820 days, which approximately corresponds to the maximum duration of life expectancy of this species in the temperature range of 20–25 °C.

Growth curves for other temperature intervals were calculated in a similar way (Fig. 3).

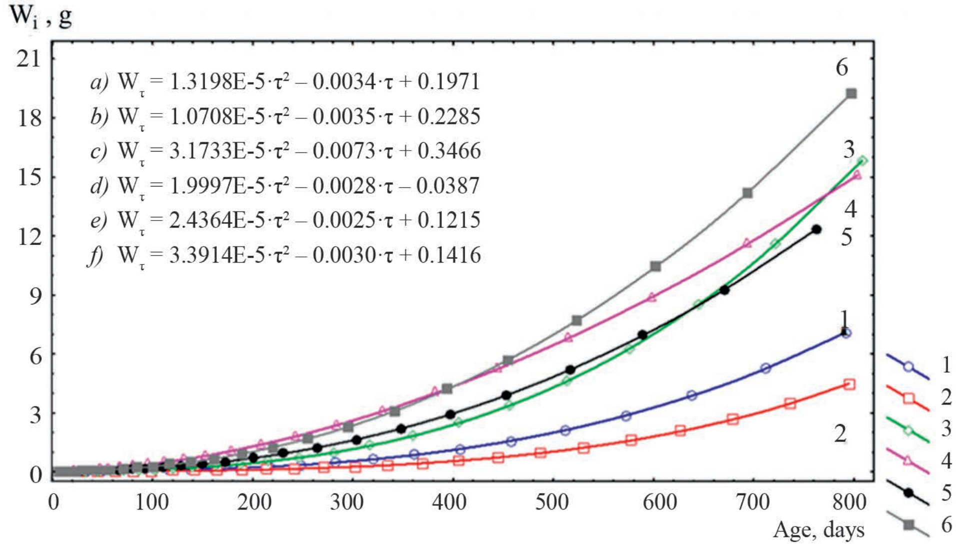

Fig. 3. Parameters of equation (4) and calculated growth curves of *Procambarus virginalis* at different temperature intervals: *a)* 15.3–17.1 °C; *b)* 17.5–18.9 °C; *c)* 19.1–20.8 °C; *d)* 21.0–22.8 °C; *e)* 22.9–25.2 °C; *f)* 25.3–28.9 °C

According to our data [32], individuals began to produce their first clutches already when they reached a body weight of 0.85 to 1.2 g. A definite dependence of this indicator on temperature has not been established. However, in the vast majority of cases, such clutches were unviable and the females quickly discarded them. Viable clutches began to be produced by larger individuals, with a body weight of 1.4 g or more.

The calculated growth curves of *P. virginalis* in all temperature intervals are satisfactorily described by the second-degree polynomial equation:

$$W_\tau = a\tau^2 + b\tau + C, \tag{8}$$

where W_τ is the mass of individuals, g, τ is the age of individuals, days, a, b and C are empirical constants.

The parameters of equations (8) for different temperature intervals are presented in Fig. 3. Based on them, the ages of individuals were calculated when they reached a mass of 1.4 g in these intervals, which corresponds to the duration of the juvenile period (D_j). With an increase in temperature (t, °C), the D_j values of marbled crayfish decrease, and the specific growth rate (r, day^{-1}) during the period of juvenile growth increases (Fig. 2). The relationship between r and t is linear:

$$r = -0.0123 + 0.0019\,t. \tag{9}$$

The value of t at which r = 0 is 6.4 °C. This temperature is the lower temperature limit for the growth of juvenile marbled crayfish (Fig. 4).

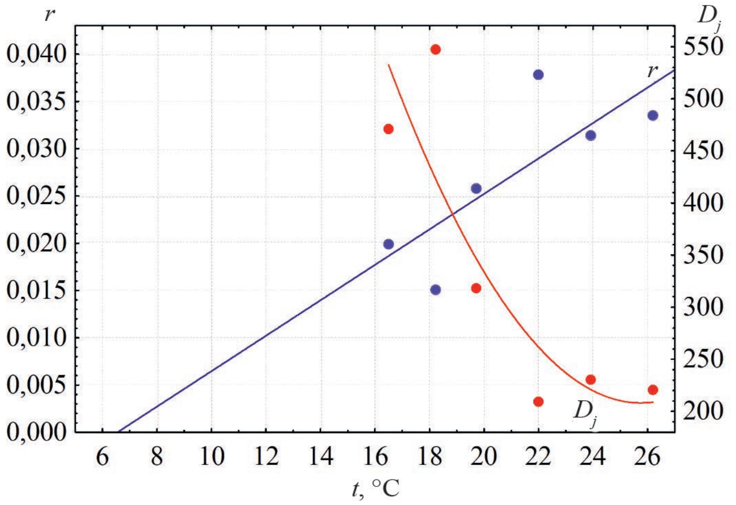

Fig. 4. Temperature dependence of the duration of the juvenile period of marbled crayfish (D_j, day) and the specific growth rate during this period (r, day^{-1})

The t_o value we obtained for the juvenile growth of marbled crayfish is close to the results of R. Seitz, et al. [31]. They experimentally raised newborn individuals of this species constant temperatures of 15 °C, 20 °C, 25 °C and 30 °C until the age of 104–195 days. The value of t_o for the specific growth rate of individuals for the first 100 days of their growth, calculated by us based on the data of these authors, was 7.6 °C.

Consequently, the lower temperature limit for the growth of juvenile marbled crayfish can be taken to be close to 7 °C. From here, the sum of effective temperatures (S_{ef}, degree ·days) for the juvenile period (D_j, day) of this species can be calculated according to:

$$S_{ef} = D_j(t - t_o), \tag{10}$$

where t is the average temperature for the juvenile period.

According to the results of our experiments, the average value of S_{ef} for the juvenile period of marbled crayfish in different temperature intervals is 4316 degree·days. The average weight of newborn marbled crayfish is 7 mg, and the average weight of individuals that have begun to produce viable clutches is 1.4 g. Hence, the increase in the mass of individuals during the juvenile period is 1.39 g. Consequently, the sum of effective temperatures required for an increase in the mass of juveniles by 1 g is equal to 4316 / (1.4 g – 0.007) 3 = 3098 degree·days.

We were unable to find specific data on the growth or lifespan of marbled crayfish in natural reservoirs in the literature. According to our data, its lifespan in the laboratory at an average annual temperature close to 20 °C does not exceed 2–2.5 years, and its maximum weight reaches 15–20 g [32].

According to calculations using equation (8), the age of reaching a body weight of 15 g was reduced by increasing temperature from 1349 to 707 days (Fig. 5). As for the juvenile period, an increase in the specific growth rate in mature females during the growth period from 1.4 to 15 g with increasing temperature, is described by a linear function:

$$r = -0{,}0006 + 0{,}0002t. \tag{11}$$

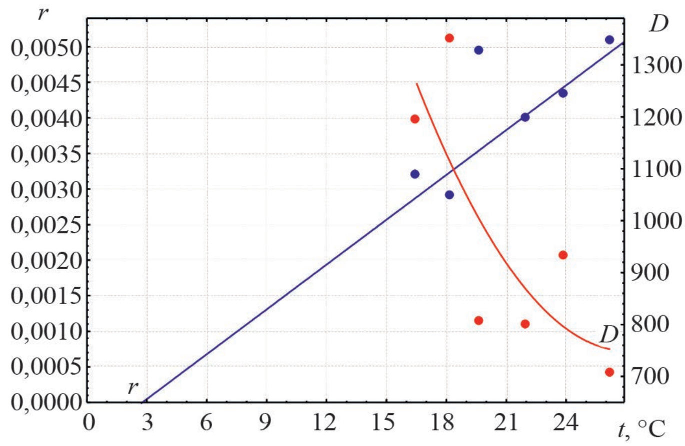

Fig. 5. Temperature dependence of the age at which marbled crayfish individuals reach a body weight of 15.0 g (D, day) and the specific speed of sexually mature individuals (r, day^{-1})

From equation (11) it follows that the lower temperature limit for the growth of sexually mature marbled crayfish is 3 °C, which corresponds quite well to the available literature data. Thus, the survival rate of *P. virginalis* in a natural reservoir in the Czech Republic over a 240-day period, entirely including the winter months, was 25 % [33]. Most of the deaths of individuals occurred precisely during the cold period of the year, when the water temperature dropped to 2–3 °C. At the same time, all surviving individuals did not feed in winter, being motionless and essentially in a state of suspended animation. The exit from it occurred only when the water warmed up in April to 5–7 °C.

In individuals of this species kept from September to April in an outdoor pool, molting was observed even when the water temperature in it dropped to 5.1–9.5 °C [34].

The value of the sum of effective temperatures for the growth period from 1.4 to 15 g in all temperature intervals we studied averages 10 630 degree·days. Therefore, to increase the body weight of sexually mature individuals by 1 g, a sum of effective temperatures equal to 10630: (15.0 – 1.4) ≈ 782 degree·days is required. Since the frequency of molts in sexually mature individuals of marbled crayfish is weakly dependent on temperature, with Q_{10} in the range of 1.15–1.38 (Fig. 2), changes in temperature will have only a small effect on the growth rate of sexually mature individuals.

If the temperature of the water in a reservoir for each day of the year (t_i) is known, the annual sum of temperatures (S_{sum}) of the water in it can be calculated by summing:

$$S_{sum} = \sum_{i=1}^{365} (t_i, °C). \tag{12}$$

However, for the purposes of our research, it is important to know not only the annual sum of temperatures or the average annual temperature, but also the nature of temperature changes throughout the year. However, in most cases, there is no data on daily temperature values in water bodies or in their biotopes where crayfish live. In this case, the annual sum of temperatures can be determined with sufficient accuracy from changes in average monthly temperatures or even from temperatures for individual dates. However, it is desirable that these data cover all seasons of the year or at least the ice-free period.

The curves of annual temperature changes in continental water bodies are not strictly symmetrical for many natural and climatic reasons. The period of the year with maximum temperatures almost always occurs at the end of July – the first half of August. In the reservoirs of the Southern Hemisphere, on the contrary, minimum temperatures are observed during this period of the year. As an example, let's look at the change in average monthly temperatures in the Zaslavskaye reservoir (Table 3).

Annual changes in water temperature in it (t, °C), as in other model reservoirs, are well described by the polynomial equation of a 5th degree:

$$t = a\tau^5 + b\tau^4 + c\tau^3 + d\tau^2 + e\tau + f, \tag{13}$$

where τ is the serial number of the day in the year, counting from January 1st ($\tau = 1$), *a, b, c, d, e* and *f* are empirical constants.

Table 3

Parameters of equation (13) describing annual changes in water temperature (t, °C) in water bodies within the invasion area of *Procambarus virginalis* during the year (τ, ordinal number of days counted from January 1st)

Water body, localisation	Equation
Water body near Jönköping in Southern Sweden	$t = 1{,}4442E^{-10}\tau^5 - 1{,}1117E^{-7}\tau^4 + 2{,}5091E^{-5}\tau^3 - 0{,}0012\tau^2 - 0{,}0513\tau + 4{,}7388$
Zaslavskaye reservoir near Minsk, Belarus	$t = 1{,}3331E^{-10}\tau^5 - 9{,}2227E^{-8}\tau^4 + 1{,}6072E^{-5}\tau^3 + 0{,}0002\tau^2 - 0{,}0837\tau + 4{,}4737$
Water body in Frankfurt am Main, Germany	$t = 1{,}0697E^{-10}\tau^5 - 7{,}5621E^{-8}\tau^4 + 1{,}3638E^{-5}\tau^3 - 0{,}0233\tau^2 - 3{,}0963E^{-5}\tau + 4{,}9113$
Water body in Bratislava, Slovakia	$t = 1{,}2123E^{-10}\tau^5 - 8{,}9101E^{-8}\tau^4 + 1{,}7945E^{-5}\tau^3 - 0{,}0006\tau^2 + 0{,}0097\tau + 3{,}6998$
Plain Dojran Lake, North Macedonia	$t = 9{,}2464E^{-11}\tau^5 - 6{,}578E^{-8}\tau^4 + 1{,}1323E^{-5}\tau^3 + 0{,}0001\tau^2 + 0{,}0061\tau + 5{,}2108$
Monkey Bay of Nyasa Lake, Malawi, East Africa	$t = - 2{,}2873E^{-11}\tau^5 + 1{,}3447E^{-8}\tau^4 - 7{,}9151E^{-7}\tau^3 - 0{,}0005\tau^2 + 0{,}0445\tau + 27{,}6135$

The definite integral of function (13) in the range from τ =1st day (January 1) to τ = 365th days (December 31) is the sum of active water temperatures (S_{sum}) in a reservoir for an astronomical year. The values of S_{sum} calculated in this way differ from those determined, according to (12), by no more than 5 % in both directions. This accuracy is quite acceptable for the purposes of this study, given the significant fluctuations in the average annual temperature of water bodies in different years.

The lower temperature limits for the passage of individual stages of ontogenesis in crayfish differ significantly (Fig. 5). The exact lower (τ_{min}, day) and upper (τ_{max}, day) boundaries of these intervals can also be calculated using equation (13), using the t_o values for the corresponding stages of ontogenesis. Integrating equation (12) in the range $\tau_{min} - \tau_{max}$ allows one to determine the sum of temperatures over this range (S_{sum}).

However, for the rates of many biological processes in poikilothermic organisms, the most important factor is not temperature as such, but effective temperature (S_{ef}). It is equal to the difference between the temperature of the environment (t, °C) and the temperature of biological zero, or the lower temperature limit for the occurrence of this process (t_o, °C).

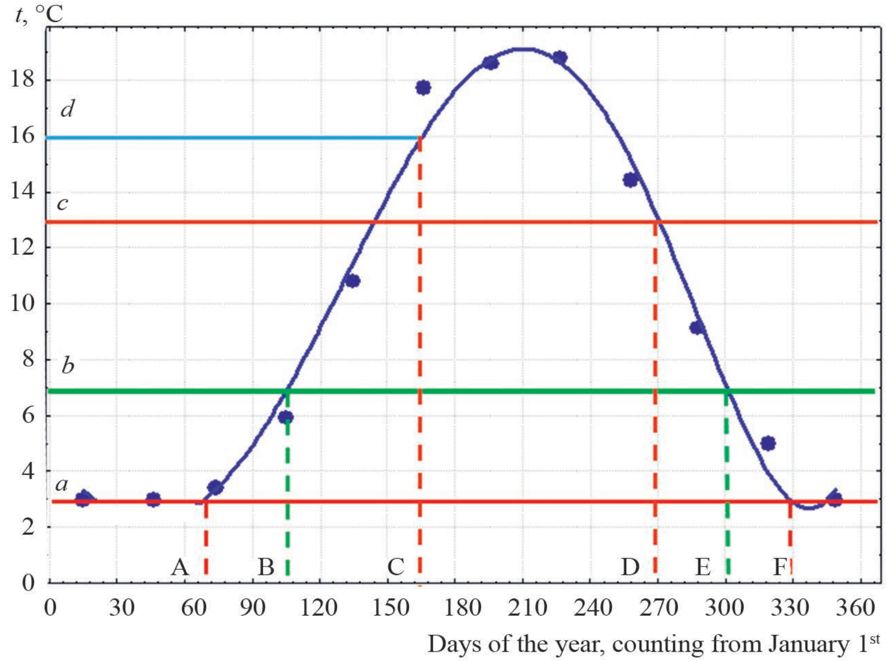

Fig. 6. Changes in monthly temperatures in the Zaslavskaye reservoir in 2023 according to the data of the Internet resource https://seatemperature.info/. The curve is the line of equation (13), the parameters of which are given in Table 3: line *a* – lower temperature limit of growth of sexually mature individuals; line *b* – lower temperature limit of juvenile growth; line *c* – lower temperature limit of embryonic development and growth of newborn individuals; line *d* – temperature of the beginning of clutch emergence by females in natural water bodies of the temperate zone. Range AF – the period of the year when growth of sexually mature individuals occurs. The BE range is the period of the year when juvenile growth occurs. Range CD – the period of the year when embryonic development and growth of newborn individuals occurs

The sum of effective temperatures for the period of the year ($d\tau = \tau_{max} - \tau_{min}$) in which a certain stage of ontogenesis occurs (S_{ef}) can be calculated according to:

$$S_{ef} = \left[\left(\frac{S_{sum}}{d\tau}\right) - t_o\right]\cdot\delta\tau, \tag{14}$$

where S_{sum} is the sum of temperatures for the interval of the year in which a certain stage of ontogenesis occurs, calculated by integrating function (5) in the interval from τ_{min} to τ_{max}, $\delta\tau$ is the duration of this interval (days), t_o is the temperature of biological zero for a given stage of ontogenesis, °C.

However, females of the marbled crayfish in water bodies of the temperate zone begin to lay eggs only after the spring warms up of the water to 16 °C [33], which is significantly higher than the t_o value for the embryonic development of the marbled crayfish, equal to 13.1 °C [34]. This circumstance must be taken into account when calculating S_{ef} according to (14) for time periods in water bodies in which embryonic development of marbled crayfish can actually occur. In this case, this period begins when the water temperature in the reservoir warms up to 16 °C in the spring, and ends when it drops to 13 °C in the fall. In fact, this period of time is the breeding period for marbled crayfish in natural reservoirs.

In marbled crayfish, the values of t_o for passing through different stages of life stages in ontogenesis decrease, and the duration and sum of effective temperatures for their passage, on the contrary, increase. Thus, the duration of embryogenesis in him with an increase in temperature from 16–17 ° C to 26–27 °C is reduced from 66–69 days to 21–24 days. The S_{ef} values for the period of embryogenesis average 299 degree·days, and the lower temperature threshold of embryonic development is 13.1°C. In juveniles with a body weight of up to 0.32 g, the lower temperature limit for molting occurs, i. e. body weight growth is the same – 13–14 °C. At the same time, the upper temperature limit for the survival of developing embryos and newborn marbled individuals is a temperature of 27 °C [32].

The lower temperature limit for the growth of juvenile marbled crayfish is 7 °C (Fig. 4), and for mature individuals it decreases to 3 °C (Fig. 5). The age at which the marbled crayfish reaches sexual maturity, even at temperatures ranging from 20 to 26 °C, is at least 200 days, and the average value of the sum of effective temperatures for this period reaches 4316 degree·days.

Therefore, the boundaries and duration of the periods of the year in which these processes can occur in natural reservoirs, as well as the sum of effective temperatures in these periods, will vary significantly (Fig. 6). The parameters of equations (13), which describe the annual variation of temperatures in model reservoirs, are given in Table 3.

The period of the year with temperatures favorable for embryonic development increases as one moves from north to south (Fig. 6). However, temperatures of 27 °C and above are lethal for embryos and newborn juveniles of marbled crayfish [32]. Therefore, in freshwater bodies of the tropical island of Madagascar (an analogue of which is Nyasa Lake), the embryogenesis of marbled crayfish can occur only in the period from April to October, when the temperature in them drops below 27 °C.

On the other hand, the upper temperature limit for the existence of juvenile and mature individuals of this species exceeds 30 °C, so they are able to grow in tropical waters throughout the year.

The boundaries of the passage of individual stages of ontogenesis in *P. virginalis* in model reservoirs and the sum of effective temperatures for these periods are presented in Table 4. The shortest period of the year (only 70 days) with temperatures at which embryogenesis of the marbled crayfish can actually occur occurs in the reservoirs of the South Sweden. However, due to low summer temperatures, the S_{ef} value for this period is only 166 degree·days, or 1.8 times lower than the Sef value required for the embryonic development of marbled crayfish.

Obviously, in such temperature conditions, complete development of clutches in one growing season is impossible. Therefore, the possibility of reproduction of *P. virginalis* populations in the region of Southern Sweden seems very doubtful. However, 13 specimens of marbled crayfish were discovered in the small river Märstaån near Stockholm [26]. However, these authors themselves express reasonable doubts about the ability of this species to create sustainable populations in the waters of Southern Sweden. Most likely, the adult individuals they found in this river were brought there only once.

On the other hand, in the reservoirs of the city of Dnieper (Ukraine), egg-bearing females of *P. virginalis* were found even at the end of October, when the water temperature dropped below 10 °C [35]. Most likely, their clutches were swept out in late summer – early autumn, when the temperature of the reservoir still exceeded 13 °C. In this case, at the end of October, *P. virginalis* eggs could already be in the stage of winter embryonic diapause, typical for crayfish of the temperate zone. At the same time, the ability of eggs and embryos of the marbled crayfish, which is subtropical in its region of origin, to survive a long and cold winter period in water bodies of the temperate zone remains unclear. In any case, we were unable to find information about the presence of egg-bearing females of this species in the waters of Europe during the winter months.

Table 4

Boundaries of individual stages of ontogenesis in *Procambarus virginalis* in natural water bodies and sums of effective temperatures for these periods

Water body, localisation	Sum temperatures in the reservoir for the year, degree·days	Boundaries period of reproduction, embryogenesis and growth of newborns*, days	The sum of effective temperatures for this period, degree·-days	Limits of juvenile growth period*, days	Sum of effective temperatures for this period, degree·days	Limits of growth period of sexually mature individuals*, days	Sum of effective temperatures for this period, degree·days
Water body near Jönköping in Southern Sweden	3158	206 – 275 70	166	133 – 316 184	1083	1 – 20 и 100 – 365 286	2031
Zaslavskaye reservoir near Minsk, Belarus	3442	163 – 275 113	543	105 – 307 203	1567	69 – 330 262	2493
Water body in Frankfurt am Main, Germany	4491	146 – 288 143	850	79 – 321 243	2099	1 – 365 365	3324
Water body in Bratislava, Slovakia	4396	148 – 284 153	837	1 – 365 365	1841	1 – 365 365	3301
Plain Dojran Lake, North Macedonia	5749	122 – 302 201	1550	53 – 329 279	2990	1 – 365 365	4657
Monkey Bay of Nyasa Lake, Malawi, East Africa	9613	110 – 300*** 191	2129	1 – 365 365	7076	1 – 365 365	8518

*In the numerator – ordinal numbers of days of the year, counted from January 1st. The first digit is the day when the water temperature in the reservoir reached 16 °C, the second – when it decreased to 13.1 °C; in the denominator – duration of the period of the year in this temperature range.

**Until the body weight reached 15 g.

***Period of the year when water temperature did not exceed 27 °C.

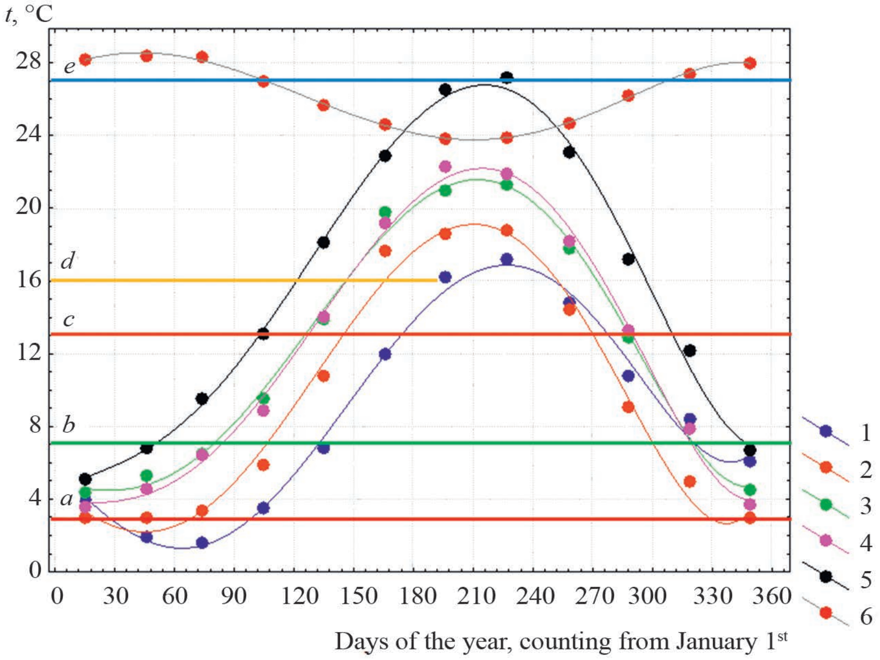

Fig. 7. Annual changes in mean monthly temperature (t, °C) in freshwater bodies in different climate zones in 2023. Based on data from https://seatemperature.info/. 1. Lake in Southern Sweden. 2. Zaslavskaye reservoir (Belarus). 3. A body of water in Frankfurt am Main (Germany). 4. A water body in Bratislava (Slovakia). 5. Doiran Lake (Northern Macedonia). 6. Monkey Bay, Lake Nyasa (Malawi). Line *a* – Lower temperature limit for growth of sexually mature individuals; line *b* – lower temperature limit for growth of juveniles; line *c* – lower temperature limit for embryonic and neonatal growth; line *d* – temperature at which females begin to deploy their clutches in natural waters of the temperate zone; line *e* – upper temperature limit for embryonic and neonatal growth

In more southern reservoirs of Belarus, Germany, Slovakia and North Macedonia, the duration of the reproduction period of the marbled crayfish is significantly longer, and the S_{ef} value in it exceeds the similar value for embryonic development. Consequently, in these reservoirs, females are able to fully tolerate a clutch of eggs, and the juveniles hatched from them can continue to grow for quite a long period of time.

An important limiting factor for natural populations of marbled crayfish is the high mortality of juveniles in winter. Thus, the survival rate of juveniles (average weight 0.9 g) in open concrete tanks in northeastern Estonia from September 2011 to April 2012 was only 8 %. At the same time, the peak of mortality occurred in the coldest months – January and February. In sexually mature individuals (average weight 2.1 g), under the same conditions, survival rate reached 60 % [34].

However, even juveniles that have successfully overwintered in European water bodies are not able to reach sexual maturity during the second growing season in their life cycle. To achieve sexual maturity, juvenile marbled crayfish require a S_{ef} value of over 3000 degree·days. At the same time, the corresponding indicator for the growth period of juveniles in water bodies of Belarus, Germany and Slovakia for the period of the year with temperatures above 7 °C varies within the range of 1567–2099 degree·days (Table 5). The same figure in the warmer Lake Dairen reaches almost 3000 degree·days. However, even if some individuals at the end of this period are able to lay a viable clutch, then in the coming cold period of the year it will most likely die.

Consequently, as a result of the reservoirs of the temperate zone of Europe, newborn individuals of marbled crayfish are able to begin to reproduce only in the third year of life. According to our observations, female marbled crayfish never produced a repeat formula immediately after the juveniles emerged from the previous ones. Always soon after the juveniles hatched from the eggs, the females molted shedding their exoskeleton with the remains of hyaline filaments. They issued repeated egg clutch, and not always, only after another molt. In sexually mature individuals, intermolt intervals, even at temperatures above 20 °C, are quite long – at least 25 days (Fig. 1). Therefore, the second clutch during the growing season in natural reservoirs will develop at rapidly decreasing autumn temperatures, which will negatively affect the survival of embryos.

Therefore, during their third growing season in the reservoirs of Germany and Slovakia, they will be able to produce one clutch, and perhaps two clutches in the warmer reservoirs of the Balkan Peninsula.

In contrast to the reservoirs of Europe, in tropical reservoirs there is no cold period of the year, which limits the growth of not only sexually mature, but also juvenile individuals. Therefore, newborn juveniles are able to reach sexual maturity in them by the age of 200 days and produce up to 3–4 clutches in two seasons of the year with temperatures favorable for embryonic development (below 27 °C).

Reproduction through parthenogenesis significantly increases the invasive potential of the marbled crayfish, since theoretically a new invasive population can be founded by a single mature female that has produced at least one viable clutch during its life cycle. In contrast, the establishment of invasive populations of bisexual crayfish species requires large enough groups of heterosexual individuals to increase the likelihood of their contacts during the breeding season.

However, the reproductive capacity of marbled crayfish is significantly lower than that of bisexual species. In our experiments [32], clutches were produced by no more than 50 % of sexually matured individuals kept in individual vessels. Moreover, up to 80 % of all clutches produced were non-viable. In most cases, breeding females produced one viable clutch during their life cycle, and only in exceptional cases – two such clutches. These results are quite consistent with the available literature data [36]. According to them, among female marbled crayfish kept by US aquarists, 38.5 % did not reproduce, 23.0 % produced only one clutch, and only 38.5 % produced several clutches.

Therefore, low clutch viability and very high mortality of juveniles during the cold season significantly reduce the invasive potential of marbled crayfish. Hence, its spread across Europe is significantly lower than that of other North American invasive species: the signal crayfish *Pasifastacus leniusculus*, the striped crayfish *Faxonius (Orconectes) limosus*, and the red swamp crayfish *Procambarus clarkii*. The first two species originate from the temperate zone of North America and are therefore well adapted to low winter temperatures. In contrast, the red swamp crayfish, like the marbled crayfish, comes from the subtropics of North America.

The native area of the signal crayfish in North America covers the extreme south of British Columbia (Canada), the states of Washington, Oregon, Idaho and northern California (USA). It is not highly resistant to elevated temperatures, which limits its ability to move into warmer subtropical regions. The optimal temperature for the development of eggs of this species in artificial conditions is 12–14 °C, at which their survival rate reaches 90–98 %. For individuals under one year of age, an average annual temperature of 18 °C is considered optimal [37]. However, the maximum growth rate of individuals was noted at 23 °C [38].

In 1961, *P. leniusculus* was first introduced to Sweden and then to other European countries as a potential aquaculture object [26], but it quickly began to spread to natural reservoirs. Now in Europe, among the invasive species of crayfish, the signal crayfish has the most extensive range. It extends from Sweden, Finland and Great Britain in the north, to Spain, Croatia and Greece in the south. At the southern border of its European range, the signal crayfish lives in colder mountain reservoirs. The eastern border of its range is Lithuania, Poland, the Kaliningrad region of the Russian Federation and the Daugava River (Western Dvina) in Latvia, up to the city of Daugavpils in close proximity to the border with Belarus. But in Belarus, despite long-term searches, signal crayfish has not been discovered.

On the other hand, low winter temperatures in natural reservoirs (up to 2–3 °C) do not block the growth of not only adult individuals, but also juveniles of *P. leniusculus*. Thus, their newborn individuals raised in the laboratory from July to May on running water coming from nearby Lake Mälaren (Central Sweden) reached an average weight of 300 mg in October, and over 500 mg in May. At the same time, the water temperature from October to May varied within 2–5 °C. The survival rate of juveniles during the entire period of the experiment reached 40 % [39].

In water bodies of Poland, female of signal crayfish reach sexual maturity at the end of the second growing season (body size 8 cm, weight 16 g) and produce the first clutch of eggs, the young of which will hatch at the beginning of the next growing season [40]. The lifespan of this species in natural reservoirs can lasts 10 years or more. Therefore, females can produce as much as 7–8 clutches during their life cycle.

The striped crayfish *F. limosus* is the first alien crayfish species in Europe. Its maternal range includes the northeastern United States and southeastern Canada. It was first introduced in 1890 to the east of the German Empire (now the territory of Poland) with the aim of introducing it into natural reservoirs to compensate for the sharp decline in the population of the native noble crayfish *A. astacus*, which was the most important in Europe commercial species, due to repeated pandemics of crayfish plague [41]. Then striped crayfish was repeatedly introduced into reservoirs in different regions of Germany, Poland and France, and in the interwar years they were even grown in aquaculture. However, due to its small size and robust outer covers, it was not in great demand on the market.

From the areas of initial introduction and aquaculture, striped crayfish quickly spread across numerous water bodies in Europe. It currently ranges from the Atlantic coast of France to the Balkan Peninsula and from Italy to Lithuania and Latvia. In Belarus *F. limosus* was first discovered in 1997 in the Black Gancha River (a tributary of the Neman River) at the junction of the borders with Poland and Lithuania. In the period from 2003 to 2009, it was recorded in several small rivers of the Western Bug basin. By 2016, this species had spread along the Shchara River up to the city of Slonim, and later along the Viliya River (both tributaries of the Neman River) to the dam of the Vileika Reservoir. In 2022, it was discovered in the Slepyanskaya water system of Minsk [42].

Striped crayfish, compared to signal crayfish, have a significantly wider range of temperature tolerance. It tolerates low winter water temperatures well. At the same time, the range of temperatures favorable for its growth and development is quite wide – from 15 to 33 °C. Therefore, it was successfully acclimatized not only in Europe, but also in much warmer Mexico.

In the reservoirs of the Czech Republic, female striped crayfish lay eggs from the second half of April to the first half of May. In a flow-through incubation unit, where the water temperature varied within 7–17 °C, the duration of embryonic development averaged 46 days. Females hatched in the first half of summer reach sexual maturity in the autumn of the same year with a minimum body size of 45 mm and a weight of 2.25 g [43] and will begin to reproduce in the next growing season. Along with rapid growth and sexual maturation, the spinycheek crayfish is characterized by increased resistance to pollution of water bodies and low oxygen content in water.

Like the signal crayfish *P. clarkii*, the striped crayfish produces one clutch per growing season. Since the life span of the latter does not exceed two to three years, it is capable of producing no more than two clutches during its life cycle.

The maternal area of the red swamp crayfish is northern Mexico, southern and southeastern United States. In the USA, its cultivation began in the 19th century. Now this species is widely cultivated in China, Kampuchea, Thailand, Ethiopia, Canada, Australia and New Zealand, and in recent decades – in Europe, primarily in Spain. However, from crayfish farms it penetrates everywhere into natural water bodies, thus becoming an additional risk factor for native crayfish.

The current range of *P. clarkii* in continental Europe extends from the Iberian Peninsula to Italy, Germany, Austria and Poland. It is also found in the south of Great Britain, in Sicily, Sardinia, Corsica and the Balearic Islands [44]. He also entered the river. Nile in Egypt [45], into reservoirs in the west of the Japanese island of Hokkaido [46].

Despite its subtropical origin, the red swamp crayfish is a highly eurythermic species, capable of existing in a very wide range of temperatures. In reservoirs of Germany and Poland it survives at low winter temperatures close to 2–3 °C, and in Egypt (lower reaches of the Nile River) in summer it exists at temperatures up to 26–29 °C. Embryonic development in this species can occur in the range from 7 °C (150 days) to 31 °C (11–14 days) [45; 47].

The sum of effective temperatures (S_{ef}) calculated by us based on the data of these authors for the embryonic development of *P. clarkii*, equal to 270 degree·days, is close to that for the marbled crayfish – 298 degree·days.

However, the lower temperature threshold of embryonic development (to) in *P. clarkii* is significantly lower than in the marbled crayfish – 9.0 and 13.1 °C, respectively.

In *P. clarkii* populations from water bodies of Europe and Japan, egg-bearing females appear in the second half of summer, when water temperatures reach their maximum annual values [44; 46]. At temperatures ranging from 20 to 25 °C, the duration of embryogenesis does not exceed three weeks. However, females continue to carry hatched larvae until their third molt. According to laboratory experiments, the gestation period of larvae at an average temperature close to 24.5 °C takes another 25 days [46]. If we assume that the lower temperature limit for growth of *P. clarkii* larvae for the first three intermolt periods is the same as for embryonic development (i. e. 9 °C), as established for *P. virginalis* [33], then the total sum of effective temperatures for the periods embryogenesis and gestation of young by females is 270 + 388 = 658 degree·days.

Consequently, in water bodies of the temperate zone with a long autumn-winter period, females of *P.clarkii*, taking into account the late timing of the hatching of juveniles, are capable of producing no more than one clutch of eggs during the growing season. However, even juveniles that have switched to an independent lifestyle will find themselves in conditions of constantly decreasing temperatures in the autumn-winter period, which will significantly reduce their growth rate and lengthen the juvenile period. Therefore, in the temperature conditions of water bodies of the temperate zone, juveniles of this species reach the minimum size of sexually mature individuals (body size 60 mm) at the age of at least 5 months, i. e. will begin to reproduce in the next growing season.

The lifespan of *P. clarkii* in nature is usually no more than 3–4 years. Consequently, during its life cycle, its females are capable of producing 2–3 clutches of eggs. In warmer water bodies of the subtropical and tropical zones, there is no long autumn-winter period, and the age of reaching sexual maturity is reduced to three months. In this case, females can produce two clutches during a long growing season.

In contrast to the above species, *P. virginalis*, although it has a fairly wide range in Europe, is found in only a small number of water bodies. In some of them, only single adult individuals were found one time, the further fate of which remained unknown. A number of populations of this species are also known that have existed for quite a long time. They are found mainly in the southern parts of their range with a warmer climate and long growing and breeding seasons. However, even in the warmer Doiran Lake on the Balkan Peninsula, the marbled crayfish reaches sexual maturity only in the third growing season, i.e. one year later than the signal and striped crayfish. Only on the tropical island of Madagascar can the growth of juvenile and mature female marbled crayfish continue year-round. Therefore, in a few years it not only spread throughout this island, but also became a common and even commercial species here [16].

One of the most important indicators of the invasive potential of alien species is the maximum instantaneous rate of population growth (r_{max}). The higher the r_{max}, the faster the population size increases, which deprives the population with a lower growth rate of food and biotopic resources [22]. The value of r_{max} can be approximately calculated according to:

$$r_{\max} \approx \frac{\ln(\alpha_1\alpha_2 F)}{T}, \tag{15}$$

where α_1 is the survival rate of newborn females in the juvenile period, expressed in fractions of unity, α_2 is the proportion of breeding females in the total number of sexually mature individuals, F is the average number of juveniles born by females during the life cycle, T is the generation time in the population.

The crayfish generation time (T) can be approximately taken equal to:

$$T = \frac{T_1 + T_d}{2}, \tag{16}$$

where T_1 and T_d are the average age of females when they lay their first and last clutches in years. T_d usually corresponds to the maximum lifespan of females under natural conditions.

Fecundity (F) of the listed North American invasive crustacean species is quite comparable. In females of the maximum age and maximum size, it reaches 300–500 eggs. The sex ratio in natural crayfish populations is close to 1:1, hence $\alpha_2 \approx 0.5$. The only exception is the parthenogenetic marbled crayfish, all individuals of which are females, i. e. theoretically it has $\alpha_2 = 1.0$. However, since not all sexually mature females in this species produce viable offspring, the real values of α_2 in its natural populations are most likely significantly lower. The survival rate of all types of crayfish in the juvenile period (α_1) in natural reservoirs is very low, usually no more than 0.01–0.05. Logarithm of the values of α_1, α_2 and F in (15) largely eliminates even their significant (up to 3–5 times) differences in different crayfish species.

Conclusion

Based on (15), the generation time (T) has a significantly stronger effect on r_{max} for crayfish populations than other parameters of the life cycle of the individual. The shorter T, the higher the growth rate of their populations. In water bodies of the temperate zone with a long autumn-winter season periods with low winter temperatures, slowing down or even blocking the processes of embryonic development and growth of female crayfish, the latter are capable of producing no more than one clutch of eggs per life cycle.

In such circumstances the signal, striped and red swamp crayfish, which begin to reproduce already in the second growing season, will have an undoubted advantage not only over the native European noble crayfish *A. astacus*, narrow-clawed crayfish *Astacus leptodactylus*, white-clawed crayfish *Austropotamobius pallipes* and stone crayfish *Aus. torrentium*, but also invasive marbled crayfish, which begin to reproduce 2–3 years later.

This conclusion is confirmed by numerous examples. In Belarus, the striped crayfish is gradually replacing the long-clawed crayfish [48]. The signal crayfish in Sweden and Finland displaces the broad-clawed and long-clawed crayfish [49], in the UK – the white-clawed crayfish [50], and in Germany – the stone crayfish [51]. And such examples are far from unique.

In the foreseeable future, invasive crayfish species in Europe will enter into intense competition with each other, the outcome of which is currently difficult to predict. However, it is quite possible to predict it if, using the model we have developed, we determine the temperature limits for embryonic development, growth and reproduction of individuals and the sum of effective temperatures for passing through these stages of ontogenesis.

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