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Effect of water temperature on growth and development of red swamp crayfish *Procambarus clarkii* (Girard, 1852)

Volodymyr Koretskyi
Postgraduate Student
National University of Life and Environmental Sciences of Ukraine
03041, 15 Heroiv Oborony Str., Kyiv, Ukraine
https://orcid.org/0009-0002-4733-1176

Iryna Kononenko*
PhD in Agricultural Sciences, Associate Professor
National University of Life and Environmental Sciences of Ukraine
03041, 15 Heroiv Oborony Str., Kyiv, Ukraine
https://orcid.org/0000-0003-3906-3650

Olesia Okhrimenko
PhD in Agricultural Sciences, Associate Professor
National University of Life and Environmental Sciences of Ukraine
03041, 15 Heroiv Oborony Str., Kyiv, Ukraine
https://orcid.org/0000-0001-9867-0595

Ruslan Kononenko
PhD in Veterinary Sciences, Associate Professor
National University of Life and Environmental Sciences of Ukraine
03041, 15 Heroiv Oborony Str., Kyiv, Ukraine
https://orcid.org/0000-0002-7818-2583

Nataliia Rudyk-Leuska
Doctor of Biological Sciences, Associate Professor
National University of Life and Environmental Sciences of Ukraine
03041, 15 Heroiv Oborony Str., Kyiv, Ukraine
https://orcid.org/0000-0003-4355-7071

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**Corresponding author*

Abstract. One of the most widespread commercial crayfish species in world's aquaculture is the red swamp crayfish *Procambarus clarkii*. The aim of this work was to analyse the effect of temperature on growth parameters of *Procambarus clarkii* grown in the water temperature range from 22.0 to 32.0°C with a temperature step of 2.0°C (6 experimental groups in total). During the experiment, theoretical (analysis, systematisation, comparison), experimental (laboratory) and generally accepted research methods were used. The results clearly demonstrated the inhibitive effect of high water temperatures – 30.0°C (Group 5) and 32.0°C (Group 6) – on the growth and development (length and weight gain, survival rate) of crayfish, while the lowest water temperature in this experiment (Group 1, 22.0°C) contributed to more efficient growth and supported survival of crayfish. For example, the final average weight of crayfish in Group 1 (22.0°C) was 15.20 ± 1.97 g, in Group 2 (24.0°C) the average weight was 13.71 ± 1.35 g, crayfish of Group 3 (26.0°C) reached an average weight of 14.85 ± 1.75 g, Group 4 (28.0°C) – 14.08 ± 2.25 g, and in Group 5 (30.0°C) and Group 6 (32.0°C) the average weight was 9.75 ± 2.33 g and 6.60 ± 0.36 g, respectively, which was 1.5 and 2.3 times less than in Group 1. At the same time, the linear growth was more homogeneous and amounted to 8.00 ± 0.29 cm in Group 1, an average of 7.38 ± 0.29 cm in Group 2, individuals of Group 3 had an average length of 7.66 ± 0.22 cm, in Group 4 – 7.42 ± 0.33 cm, and in high-temperature Groups 5 and 6 the average length was 6.80±0.50 cm and 6.04 ± 0.26 cm, respectively. A tendency to decrease the survival rate of crayfish with increasing water temperature in the groups was established. The survival rate in Group 1 at the end of the study was 58.82%, in Group 2 – 41.18%, Group 3 – 47.06%, Group 4 – 41.18%, Groups 5 and 6 experienced the greatest pressure of the temperature on survival – 35.29% and 29.41%, respectively

Keywords: aquaculture; *Procambarus clarkii*; weight; length; survival; thermoregulation; metabolism

Introduction

Considering the difficult situation in which natural crayfish populations are currently in Ukrainian water bodies, it is becoming increasingly important to breed these species in controlled conditions, thereby reducing pressure on natural populations. However, the biological characteristics (slow growth, demanding water quality, etc.) of native crayfish species limit the possibilities for their effective industrial cultivation. Therefore, in terms of researching new highly productive objects of aquaculture among crustaceans, promising is red swamp crayfish *Procambarus clarkii* (Girard, 1852). The prospects for its cultivation are due to its high adaptability to various environmental conditions (in particular, controlled ones), omnivorousness, rapid growth rate, and flexible life cycle, which allows it to survive in various physical and chemical conditions, etc. In addition, given the trends in the development of aquaculture and its potential in Ukrainian water bodies, this species could ideally fit into the structure of multi-trophic aquaculture, the importance of which is underestimated in Ukraine but deserves attention, given the efficiency of its processes and the high potential for commercial yield per unit area (Honcharova *et al.*, 2024).

The natural distribution range of *Procambarus clarkii* is the south-eastern United States, but due to human economic activity, this species has significantly expanded its natural range. A. Ballinger (2022) draws attention to the wide range of introduction of this species outside its natural range – all continents except Australia and Antarctica, which was facilitated, firstly, by the widespread popularity of *Procambarus clarkii* as a species of ornamental aquaculture during the 20th century (Oficialdegui *et al.*, 2025). Only recently, it was recognised as a potential aquaculture species, being included in the list of the 25 most important aquatic alien species introduced into European freshwater and coastal marine waters (Savini *et al.*, 2010). At the same time, according to A. Nota *et al*. (2024), this invasiveness has its advantages, primarily due to the fact that *P. clarkii*, as a more adaptable species, replaces populations of local crayfish that have been lost for certain reasons, which does not always have a positive effect on local ecosystems. As a farmed species, *P. clarkii* is also extremely popular in global aquaculture. It is successfully used commercially in countries where it has developed a significant population of harvestable crayfish. According to FAO (2021), the vast majority of *P. clarkii* production in aquaculture, which is over 2 million tons per year, is currently in China. The same source indicates that *P. clarkii* is the second most cultivated crustacean species in the world.

However, such rapid and intensive development of red swamp crayfish populations in water bodies around the world is still a cause for concern in terms of the impossibility of fully assessing the impact of its populations on local water bodies. Therefore, potential ways to reduce its possible destructive impact or negative pressure on local water bodies are being studied. It is known that *P. clarkii*, as ectotherms, are not capable of independent thermoregulation, and the determining factor for their successful reproduction and development is precisely the water temperature, and its decrease or increase beyond the species optimum causes enormous stress in their organism. It is low water temperatures, especially during wintering, that inhibit the spread of *P. clarkii* in northern latitudes. Furthermore, it has been established that cold stress affects almost all biochemical and physiological processes in crustaceans, including their behaviour, growth and development, reproduction, metabolism, and immunity (and, accordingly, resistance to disease) (Ren *et al.*, 2021).

The only monitoring study conducted so far by L. Peruzza *et al.* (2015) found that populations of *P. clarkii* populations inhabiting the cold-water Brancolo canal (northern Italy) have unique biological characteristics that allow them to complete their life cycle at temperatures that, according to other studies, should inhibit their growth and development and prevent reproduction (Jiang *et al.*, 2024). The results clearly confirm the adaptation of this population to an atypical temperature environment, characterised by an average annual water temperature of 13.32±0.0°C. However, the fertility of females from the cold-water Brancolo canal was 35.0±7.0 eggs compared to 285.0-995.0 eggs in females that reproduce at optimal water temperatures. It is also interesting that in high latitudes, *Procambarus clarkii* reproduces once a year (at the end of summer) and can carry eggs throughout the winter, while in lower latitudes, the species' life cycle includes year-round reproduction with several peaks per year (Chucholl, 2011; Slusar *et al.*, 2023). The results presented indicate that *P. clarkii* is capable of adapting well to new, cold habitats by changing its life cycle.

Regarding the effect of high temperatures on the cultivation of *Procambarus clarkii*, an interesting study by X. Chen *et al*. (2024) found that groups of crayfish kept at a higher water temperature (30.0°C) had correspondingly higher levels of astaxanthin, which developed a rich bright red colouration of the crayfish shell. Thus, the vast majority of studies are aimed at investigating the characteristics of this species' adaptation to water temperature, but they do not answer the question of whether there is an optimal temperature for rapid linear growth and weight gain, sexual maturation, and high survival under controlled industrial farming conditions, or whether it is possible to influence the productivity of *P. clarkii* using this parameter. In addition, the issue of the invasiveness of this species should not be ignored, as against the backdrop of climate change and reduced biotic stability of water bodies, including in Ukraine, it may create conditions that will disrupt the stability of freshwater ecosystems and create conditions for the ideal adaptation of this species. Therefore, it is necessary to understand in more detail the mechanism of adaptation of the red swamp crayfish to the environment and the possible ecological barriers to their successful development in natural ecosystems.

For this reason, the objective of this study was to analyse the impact of different temperature regimes on the growth of *Procambarus clarki* on changes in their growth and survival rates. The study was conducted in accordance with Agreement No. BF/37-2021 (state registration number 0121U113569) within the priority thematic area "Innovative solutions for ensuring the sustainable development of agriculture, forestry, and veterinary medicine in conditions of martial law", applied research "River basin management in the context of climate change".

Materials and Methods

To understand the impact of the aquatic environment on the growth characteristics of the red California crayfish, it was important to study the organism's response not only to temperatures within the species' optimal range, but also to temperatures exceeding its tolerance limit. For this study, young *Procambarus clarkii* aged 20-25 days were used. The study was conducted between June and August 2024 at the Aquaculture Technology Laboratory (V. Kondratyuk Laboratory of Aquatic Bioresources and Aquaculture). The crayfish juveniles for the study was obtained from own broodstock of red swamp crayfish kept in the same laboratory. Six groups were formed for the study in the temperature range from 22.0°C to 32.0°C: Group 1 – grown at a water temperature of 22.0°C, Group 2 – 24.0°C, Group 3 – 26.0°C, Group 4 – 28.0°C, Group 5 – 30.0°C, and Group 6 – 32.0°C. These temperatures were partly within the species optimum range and partly outside the tolerance limits of the organisms, creating extreme conditions (>29.0-30.0°C). A total amount of *Procambarus clarkii* which were used in the experiment, were 102 individuals, 17 in each group. The groups were formed by randomly selecting individuals for each group. The initial weight of the crayfish was 0.2±0.05 g on average, with an average length of 0.2±0.05 g. The crayfish were kept in a freshwater model aquarium system consisting of six 100 L tanks with identical water treatment and cultivation conditions (with an equal number of shelters). Water temperature and dissolved oxygen levels were monitored daily at three measurement points: two stationary points using a JBL Thermometer Premium thermometer and an Aqua-Tech HT-1 electronic thermometer with a remote sensor, and the third using a portable AZ-86021 oximeter.

For feeding at different stages of development, following high-protein compound feeds were used: Alltech Coppens TOP, 0.5-0.8 mm (protein: 60.0%, fat: 16.0%, fibre: 0.3%, ash: 10.7%), Alltech Coppens Vital, 0.5-1.2 mm (protein: 46.%, fat: 10.0%, fibre: 0.09%, ash: 11.9%), Alltech Coppens Advance, 1.5 mm (protein: 54.0%, fat: 15.0%, fibre: 0.3%, ash: 12.0%), Aller Aqua Futura, 0.5-1.0 mm (protein: 64.0%, fat: 9.0%, fibre: 0.5%, ash: 13.0%), Aller Aqua Futura, 0.9-2.0 mm (protein: 64.0%, fat: 9.0%, fibre: 0.5%, ash: 13.0%). At the beginning of the third month of rearing, to increase the content of plant components, the daily diet included Zolotaya Rybka (Gold Fish) Flora feed, 1.7-2.5 mm (protein: 30.0%, fat: 5.5%, fibre: 5.0%, ash: 7.0%) in an amount of 20.0% of the daily feed dose, while Coppens accounted for 50.0% and Aller aqua for 30.0% of the daily feed amount. The daily feed ration was determined based on the total weight of the crayfish and varied from 10.0 to 5.0% depending on age, with the feed fraction increasing according to the size of the individuals. In the daily diet, the weight of Coppens and Aller aqua feed had a 1:1 ratio.

The experimental groups were fed twice a day: the specified feed dose was divided into two parts in a ratio of 30:70 – the first part was administered in the morning, and the second part was administered in the evening. This took into account the natural behaviour of crayfish, which search for food at dusk. The feed was administered at two feeding points located on opposite sides of the aquarium in order to avoid competition or aggressive behaviour by dominant individuals. In general, the same optimal growing conditions (aquarium equipment, feeding, shelter) were created for all six groups, so that only the water temperature differed between the experimental groups.

Intermediate measurements of the length and weight of crayfish were carried out every 10 days. At this time, the number of individuals was also counted to assess their survival rate. Based on the data obtained, the daily feed dose was adjusted. Body weight and length were measured in accordance with general fish biology recommendations using a vernier caliper and measuring tape, as well as TBE-0.21 laboratory scales with a minimum increment of 0.02 g. The conditions for keeping, feeding, and caring for crayfish complied with the requirements of the European Convention for the Protection of Vertebrate Animals used for Experimental and Other Scientific Purposes (1986); Regulation (EU) No. 1143/2014 of the European Parliament and of the Council "On the Prevention and Management of the Introduction and Spread of Invasive Alien Species" (2014), in compliance with the bioethical standards of proper treatment of animals enshrined in the Regulation "On the Protection of Animals Used for Scientific or Educational Purposes at the National University of Life and Environmental Sciences of Ukraine" (2023). The research was carried out with basic funding (contract BF/37-2021 dated 02.08.2021) as part of the applied research project "River Basin Management in the Context of Climate Change".

Results and Discussion

According to the results of daily monitoring of the aquatic environment, the actual water temperature in each experimental group differed from the set experimental temperature, often exceeding the studied level, which was primarily due to weather conditions in the middle and end of the hot summer when the study was conducted. All experimental groups were simultaneously exposed to this influence. The actual temperature regime of all experimental groups is presented in Table 1.

Table 1. *Temperature conditions for the experimental groups of Procambarus clarkii*

Group (experimental, t, °C)	Group 1 (22.0°C)	Group 2 (24.0°C)	Group 3 (26.0°C)	Group 4 (28.0°C)	Group 5 (30.0°C)	Group 6 (32.0°C)
Lowest water temperature	21.3°C	23.8°C	25.8°C	27.1°C	29.7°C	30.9°C
Highest water temperature	24.0°C	26.5°C	28.0°C	30.0°C	32.0°C	34.0°C
Average water temperature during the first month 08.06-30.06	22.2°C	24.5°C	26.5°C	28.9°C	30.8°C	32.4°C
Average water temperature during the second month 01.07-31.07	23.3°C	25.7°C	26.7°C	28.8°C	30.6°C	32.8°C
Average water temperature during the third month 01.08-31.08	23.0°C	25.6°C	26.4°C	29.1°C	30.5°C	32.9°C
Average water temperature during the fourth month 01.09-16.09	22.2°C	24.2°C	26.5°C	28.4°C	30.0°C	31.8°C

Source: authors' development

Based on the data of Table 1, each group experienced slight temperature fluctuations (± 2.0°C) during the study period. For example, the highest daily water temperatures were recorded during the second and third months of cultivation, while the lowest water temperatures were recorded in the last weeks of the study (September). As for other important parameters of the aquatic environment, the content of dissolved oxygen throughout the study period fluctuated within the optimal range for this species: from 5.4 mgO_2/L to 7.7 mgO_2/L; pH – 7.0-8.0. At the beginning of the study, the average weight in all groups was the same and amounted to 0.2 ± 0.05 g, the average body length was 1.5 ± 0.2 cm. The results of the first and all subsequent measurements of the weight of *Procambarus clarkii* carried out every 10 days are presented in Table 2.

Table 2. *Weights of Procambarus clarkii during the study period*

Date	Average M, g (M ± m)					
	Group 1 (22.0°C)	**Group 2 (24.0°C)**	**Group 3 (26.0°C)**	**Group 4 (28.0°C)**	**Group 5 (30.0°C)**	**Group 6 (32.0°C)**
	min/max*	min/max*	min/max*	min/max*	min/max*	min/max*
	μ**	μ**	μ**	μ**	μ**	μ**
18.06	0.25/2.0	0.4/1.9	0.5/1.6	0.3/1.7	0.3/1.5	0.25/0.4
	0.77 ± 0.11	1.02 ± 0.11	1.01 ± 0.09	0.64 ± 0.09	0.58 ± 0.08	0.3 ± 0.01
28.06	0.5/4.6	0.3/3.4	0.6/2.7	0.4/5.1	0.4/2.6	0.3/1
	1.48 ± 0.24	1.61 ± 0.21	1.74 ± 0.16	1.50 ± 0.33	0.89 ± 0.16	0.50 ± 0.07
08.07	1.0/9.8	1.0/5.3	1.5/4.6	1.0/8.1	0.5/4.5	0.3/1.4
	2.68 ± 0.53	2.65 ± 0.33	2.84 ± 0.25	2.15 ± 0.51	1.56 ± 0.31	0.67 ± 0.12
18.07	1.8/14.5	1.0/8.3	1.9/7.5	1.3/13	1.1/7.7	0.5/3.0
	4.07 ± 0.81	3.81 ± 0.55	4.37 ± 0.51	3.37 ± 0.99	2.46 ± 0.71	1.18 ± 0.27
28.07	2.7/15.3	2.2/13.5	2.4/12.5	1.7/14.6	1.4/12.4	1.1/3.2
	5.27 ± 0.88	5.49 ± 0.87	6.08 ± 1.01	4.29 ± 1.19	3.46 ± 1.19	2.07 ± 0.25
07.08	3.4/15.5	2.9/9.6	3.8/18.5	1.9/19.7	1.8/14.4	1.6/4.7
	6.96 ± 1.07	6.53 ± 0.76	8.33 ± 1.6	5.87 ± 1.66	5.78 ± 1.89	3.24 ± 0.38
17.08	4.3/15.9	3.8/14.8	4.3/20.0	2.2/20.5	2.6/20.0	1.6/5.3
	8.45 ± 1.17	8.84 ± 1.48	10.61 ± 1.84	8.01 ± 2.09	6.34 ± 2.33	3.64 ± 0.51
27.08	5.1/19.1	4.2/15.7	5.2/20.8	2.4/20.5	2.6/20	3.0/5.9
	10.55 ± 1.43	9.57 ± 1.25	11.72 ± 1.7	8.25 ± 1.92	7.21 ± 1.95	4.35 ± 0.42
06.09	6.2/19.9	4.9/16.0	6.8/22.0	2.7/20.8	4.1/20.4	3.5/7.1
	12.09 ± 1.5	10.71 ± 1.46	14.06 ± 1.99	9.78 ± 2.64	8.08 ± 2.54	5.61 ± 0.56
16.09	9.3/29.7	6.5/16.6	7.2/21	9.9/22.8	5.7/20.6	5.4/7.4
	15.20 ± 1.97	13.71 ± 1.35	14.85 ± 1.75	14.08 ± 2.25	9.75 ± 2.33	**6.60 ± 0.36**

Note: * – maximum and minimum values; ** – average value; highest and lowest values are highlighted in bold
Source: authors' development

The first measurement of the length and weight of crayfish in the experimental groups 10 days after they were placed in the growing conditions showed a trend of intensive growth in individuals in experimental Groups 1-4 (t range 22.0-28.0°C) (Fig. 1). At the same time, individuals from experimental Group 5 (30.0°C) and especially Group 6 (32.0°C) showed a lag in weight gain. This trend was observed during the first month of cultivation. Thus, at the end of the first month of cultivation, the average recorded weight of individuals in Group 1 (22.0°C) was 4.07 ± 0.81 g, which was 3.86 g more than the initial weight (0.2 ± 0.05 g). The average weight of individuals in experimental Group 2 (24.0°C) increased by 3.61 g relative to the initial weight and was 3.81 ± 0.55 g. The weight of individuals in experimental Group 3 (26.0°C) reached 4.37 ± 0.51 g, which was 4.17 g more than the initial weight and was the largest increase among the experimental groups during the first month of the experiment. In experimental Group 4 (28.0°C), the average weight was 3.37 ± 0.99 g, with an increase of 3.17 g, respectively. Group 5 (30.0°C) reached an average weight of

2.46 ± 0.71 g, and the increase relative to the initial weight was only 2.26 g. Group 6 (32.0°C) was characterised by the lowest average weight among all experimental groups for the first month – 1.18 ± 0.27 g, and accordingly has the smallest increase in average weight relative to the initial weight – only 0.98 g, which was 4.25 times less than the increase in Group 3.

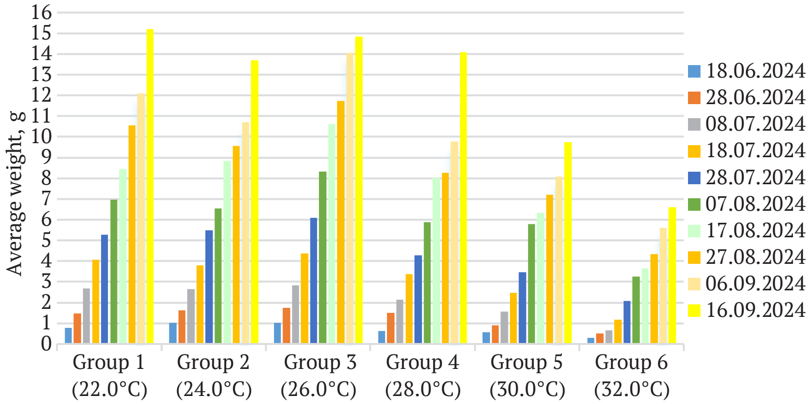

Figure 1. Weight growth of crayfish during the study period
Source: authors' development

The results of the second month of cultivation were also characterised by a rapid increase in body weight in Groups 1-4 (22.0-28.0°C) and moderate growth in Groups 5 (30.0°C) and the smallest in Group 6 (32.0°C). For example, individuals in Group 1 (22.0°C) were characterised by an average increase of 4.39 g during the second month of cultivation. Crayfish in Group 2 (24.0°C) had an average increase of 5.03 g, and Group 3 (26.0°C) again had the largest increase in average weight – 6.24 g. The average weight gain in individuals of Group 4 (28.0°C) during the second month was 4.64 g. Groups 5 (30.0°C) and 6 (32.0°C), which were grown at extremely high temperatures, had an increase of 3.88 g and 2.46 g, respectively, which were the lowest among the experimental groups.

The results of the last month of the study showed that the highest average weight was recorded in Group 1 (22.0°C) and amounted to 15.2 ± 1.97 g with an increase in average weight of 15.0 g relative to the initial average weight. Thus, at the end of the study, Group 1 surpassed Group 3 (26.0°C) in terms of average weight, which had the highest average weight during the first and second months of cultivation. Individuals in Group 2 (24.0°C) reached an average weight of 13.71 ± 1.35 g with an increase of 13.51 g. Crayfish in Group 3 (26.0°C) reached an average weight of 14.85 ± 1.75 g at the end of the study, with a weight gain of 14.65 g. In experimental Group 4 (28.0°C), the final average weight was 14.08 ± 2.25 g with a gain relative to the initial weight of 13.88 g. As for Group 5 (30.0°C), the average weight of its individuals was 9.75 ± 2.33 g with an increase of 9.55 g. Crayfish in Group 6, which were grown at the highest experimental temperature of 32.0°C, had an average weight of 6.6 ± 0.36 g at the end of the study, with an increase of 6.2 g, which was the lowest among all studied groups.

In general, during the study period, significant growth asynchrony was observed in all groups, which is typical for crustaceans. In particular, Figure 2 shows individuals from experimental Group 3 (28.0°C) during the intermediate measurement on August 7, which most clearly demonstrated the variability of linear growth and weight gain within the group: the minimum weight was 3.80 g, and the maximum was 18.50 g (Fig. 2). A similar pattern was observed in each group, which is a natural feature of crayfish growth and is not related to study conditions.

Figure 2. Asynchronous growth of individuals in Group 3 (28.0°C) during intermediate measurement

Source: authors' photo

Assessment of the nature of linear growth changes in *Procambarus clarkii* during the study also showed a relationship between water temperature and crayfish body length: in Groups 1-4 (22.0-28.0°C), where cultivation took place within the optimal temperature range, there was intense linear growth, while in Group 5 (30.0°C) and especially in Group 6 (32.0°C), where temperatures were extremely high, moderate linear growth was recorded. The results of linear growth measurements for all six groups during the study period are shown in Table 3.

Table 3. *Linear growth of Procambarus clarkii during the study period*

Date	Average L, cm (M ± m)					
	Group 1 (22.0°C)	**Group 2 (24.0°C)**	**Group 3 (26.0°C)**	**Group 4 (28.0°C)**	**Group 5 (30.0°C)**	**Group 6 (32.0°C)**
	min/max*	min/max*	min/max*	min/max*	min/max*	min/max*
	μ**	μ**	μ**	μ**	μ**	μ**
18.06	2.0/4.0	2.0/3.8	2.3/4.0	2.0/4.0	2.0/4.0	1.8/2.3
	2.94 ± 0.14	3.08 ± 0.15	3.02 ± 0.11	2.67 ± 0.13	2.49 ± 0.15	2.03 ± 0.03
28.06	2.5/5.2	2.2/4.7	2.7/4.5	2.5/5.2	2.5/4.6	2.0/3.1
	3.53 ± 0.17	3.58 ± 0.16	3.82 ± 0.15	3.35 ± 0.20	3.06 ± 0.17	2.78 ± 0.13
08.07	3.0/6.8	3.2/5.5	3.9/5.5	3.0/6.0	2.7/5.0	2.2/3.5
	4.35 ± 0.23	4.26 ± 0.16	4.31 ± 0.12	3.74 ± 0.23	3.57 ± 0.19	2.77 ± 0.14
18.07	4.0/7.6	3.2/6.5	4.2/6.0	3.5/7.5	3.0/6.0	2.5/4.5
	4.85 ± 0.24	4.70 ± 0.26	4.99 ± 0.18	4.52 ± 0.33	4.08 ± 0.31	3.17 ± 0.25
28.07	4.0/8.0	4.0/7.2	4.2/7.2	3.5/7.5	3.5/7.5	3.0/4.8
	5.36 ± 0.28	5.30 ± 0.26	5.57 ± 0.33	4.83 ± 0.35	4.57 ± 0.42	3.97 ± 0.19
07.08	4.8/7.5	4.5/7.0	5.0/8.0	4.0/8.0	4.0/7.8	3.6/5.8
	6.04 ± 0.25	5.94 ± 0.28	6.21 ± 0.38	5.50 ± 0.37	5.11 ± 0.42	4.80 ± 0.27
17.08	5.2/8.0	5.1/8.0	5.5/8.5	4.5/8.3	4.8/8.0	3.6/5.8
	6.50±0.30	6.61±0.40	6.87±0.36	6.16±0.46	5.56±0.46	4.95±0.30

Date	Average L, cm (M ± m)					
	Group 1 (22.0°C)	Group 2 (24.0°C)	Group 3 (26.0°C)	Group 4 (28.0°C)	Group 5 (30.0°C)	Group 6 (32.0°C)
	min/max*	min/max*	min/max*	min/max*	min/max*	min/max*
	μ**	μ**	μ**	μ**	μ**	μ**
27.08	5.8/8.8	5.4/7.7	5.8/8.2	4.5/8.5	4.0/8.0	4.2/5.8
	7.13 ± 0.30	6.80 ± 0.27	7.06 ± 0.27	6.02 ± 0.45	5.56 ± 0.41	4.98 ± 0.23
06.09	6.0/9.0	5.5/8.0	6.2/8.4	4.6/8.5	5.1/8.0	4.9/6.2
	7.41 ± 0.31	6.97 ± 0.32	7.46 ± 0.27	6.37 ± 0.59	5.85 ± 0.45	5.56 ± 0.21
16.09	7.0/10.0	6.2/8.1	6.5/8.3	6.5/8.7	5.8/9.0	5.3/6.7
	8.00 ± 0.29	7.38 ± 0.29	7.66 ± 0.22	7.42 ± 0.33	6.80 ± 0.50	**6.04 ± 0.26**

Note: * – maximum and minimum values of; ** – average value; highest and lowest values are highlighted in bold
Source: authors' development

The fastest linear growth was observed in individuals in experimental Group 1 (22.0°C), which reached 8.00 ± 0.29 cm over three months of the study, increasing their body length by 6.50 cm compared to the initial length (1.5 ± 0.3 cm). The average length of crayfish in Group 2 (24.0°C) increased by 5.88 cm and at the end of the study averaged 7.38± 0.29 cm. At the end of the study, individuals in Group 3 (26.0°C) had an average body length of 7.66 ± 0.22 cm, with an increase of 6.16 cm relative to the initial value. In Group 4 (28.0°C), individuals reached an average length of 7.42 ± 0.33 cm with an increase of 5.92 cm. Crayfish in Group 5 (30.0°C) increased their body length by an average of 5.30 cm and reached an average length of 6.80 ± 0.50 cm. The lowest linear growth results were observed in crayfish from Group 6 (32.0°C): the body length of individuals in this group increased by 4.54 cm, reaching 6.04 ± 0.26 cm at the end of the study period, which was 1.3 times less than in Group 1 (Fig. 3).

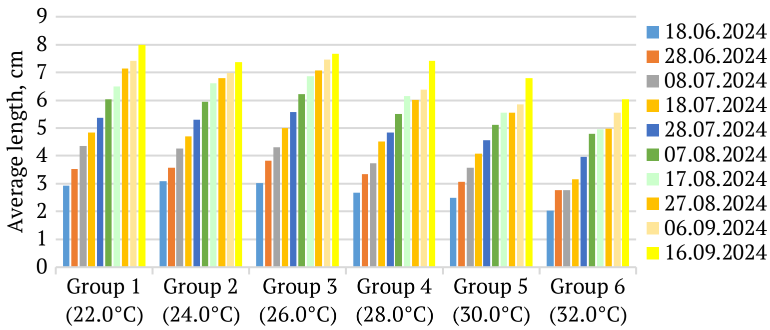

Figure 3. Linear growth of crayfish during the study period
Source: authors' development

Observation of the behavioural reactions of *P. clarkii* during the experimental period showed a typical phenomenon of the cultivation technology of any object in controlled or natural conditions, namely a decrease in the number of individuals, while revealing a direct relationship between water temperature and the number of crayfish in the experimental groups. In this study, the reduction in numbers in some groups was caused by intense cannibalism as a behavioural response to elevated (extremely high) water temperatures (Groups 4-6).

However, it cannot be ruled out that the decline in number could also have been the result of the low vitality of crayfish grown at high temperatures (28.0-30.0°C), since the organism's main resource could have been directed toward thermoregulation, namely cooling the organism, rather than maintaining optimal vital functions. In particular, observations have shown that the highest intensity of mortality and cannibalism was in Groups 5 and 6, which were grown at temperatures beyond the tolerance limits of the organism – 30.0 and 32.0°C, respectively. Table 4 shows general data on changes in the number of *Procambarus clarkii* in six experimental groups throughout the entire study period.

Table 4. *Dynamics of the number of Procambarus clarkii individuals during the study period*

Date	Number of individuals, n*					
	Group 1 (22.0°C)	Group 2 (24.0°C)	Group 3 (26.0°C)	Group 4 (28.0°C)	Group 5 (30.0°C)	Group 6 (32.0°C)
18.06	17.0	17.0	16.0	16.0	16.0	16.0
28.06	17.0	17.0	15.0	14.0	15.0	11.0
08.07	16.0	13.0	13.0	13.0	12.0	10.0
18.07	15.0	13.0	11.0	11.0	9.0	9.0
28.07	14.0	12.0	10.0	10.0	9.0	8.0
07.08	13.0	9.0	9.0	10.0	9.0	7.0
17.08	12.0	7.0	8.0	8.0	7.0	7.0
27.08	11.0	7.0	8.0	7.0	6.0	6.0
06.09	10.0	7.0	8.0	7.0	6.0	6.0
16.09	10.0	7.0	8.0	7.0	6.0	5.0
% survival	58.82	41.18	47.06	41.18	35.29	29.41

Note: * – initial number in all groups – 17
Source: authors' development

It was found that the greatest losses in numbers were observed during the first two months of cultivation, when the juveniles regularly, but asynchronously, moulted (ecdysis), after which, under optimal conditions, the juveniles remained in the metecdysis stage for 1-2 days – a period of formation and strengthening of the new exoskeleton, during which individuals are most vulnerable to cannibalism. However, the experimental groups that were grown at elevated temperatures (Groups 5 and 6) were characterised by a longer period of metecdysis – 2-3 days, remaining vulnerable to environmental factors, primarily cannibalism, for a longer period of time. Thus, survival at the end of the second month of the study underwent significant changes relative to the initial number and amounted to 70.59% in Group 1, 47.06% in Groups 3 and 4, and 41.18% in Groups 2, 5, and 6. The third month of cultivation was characterised by fewer moults (which is a typical feature of crayfish of this age), so survival during the third month remained satisfactory. In particular, in Groups 2, 3, 4, and 5, it was 100% (compared to the second month of cultivation), in Group 1 – 83.3%, and in Group 6 – 71.43%, which indicates a decrease in the intensity of cannibalism due to a decrease in the number of moults in crayfish.

Analysis of the final results of the study showed that the survival rate of crayfish in Group 1 with the lowest cultivation temperature (22.0°C) was 2 times higher than in Group 6 with the highest water temperature (32.0°C) and 1.7 times higher than in Group 5 (30.0°C). At the same time, Groups 2-4 were characterised by approximately the same survival rates of individuals – 41.18-47.06%. This result may indicate an increase in the level of cannibalism and mortality in proportion to the increase in the cultivation temperature. In general, cannibalism, especially during the moulting period of crayfish, is one of the most acute problems in the artificial cultivation of crustaceans (crayfish, shrimp). Special measures, such as placing shelters or coverings, structuring the space, etc., significantly reduce the intensity of its manifestation, but cannot completely eliminate it (Fedorovych *et al.*, 2022a; Ishchuk *et al.*, 2024), so this aspect of crayfish farming technology needs to be studied in more detail.

Thus, the studies conducted have examined and established the influence of a wide range of water temperatures on the growth, development, and behavioural responses of the red swamp crayfish under controlled conditions, and it has been established that the optimal temperature range for *P. clarkii* is 22.0 ± 2.0°C. Water temperatures above 28.0°C had a negative inhibitory and, in some cases, lethal effect on crayfish. According to a study by X. Ren *et al.* (2021), as water temperature rises, ectothermic animals need to obtain more energy to maintain an increased metabolism, which leads to a decrease in food consumption rate (in the current experiment, uneaten feed residues were observed precisely in high-temperature groups). However, as the water temperature rises, the rate of catabolism (energy metabolism) in animals exceeds the rate of anabolism (plastic metabolism). This process can be explained in more detail by analysing the work of H. Jiang *et al.* (2024), which studied the effect of different water temperatures (20.0°C – control, 10.0°C and 30.0°C – experimental) on the activity of enzymes (pyruvate kinase (PK), hexokinase (HK) and phosphoenolpyruvate carboxykinase (PEPCK)) in the muscles and hepatopancreas of *P. clarkii*, and changes in the activity of α-amylase (α-AMY) and lipase (LPS) in the intestine and hepatopancreas. Analysing the activity of digestive and metabolic enzymes, H. Jiang *et al.* (2024) found that extremely low (10.0°C) and high (30.0°C) temperatures inhibited their activity levels compared to the control group (20.0°C).

It is obvious that the metabolic and digestive activity of crayfish in the study directly depended on water temperature: extremely high values (above 28.0°C and above, Groups 4, 5, and 6) caused thermal stress, inhibiting the secretion and activity of digestive enzymes and causing metabolic disorders. It is likely that the main expenditure of energy reserves in individuals from high-temperature groups was directed toward thermoregulation, and the activity of digestive enzymes depended on water temperature, affecting the absorption of nutrients from compound feed through various aspects of metabolism, which scaled differently with water temperature.

The optimal water temperature, which was 22.0°C according to the experiment, had a positive effect on the activity of digestive and metabolic enzymes, which manifested itself in the intensive linear-weight growth of individuals, high survival rate, and the appearance of the first females with eggs in this group. At the same time, due to changes in metabolic processes and suppression of digestive enzyme activity, high-temperature Groups 5 (30.0°C) and 6 (32.0°C) were characterised by the lowest linear growth and weight gain and critically low survival rates. The results obtained also coincide with the data of E. Fedorovych *et al.* (2022a), who, having conducted research on the cultivation of various species of crayfish under different temperature and oxygen conditions, found that the best temperature for keeping all the studied species is in the range of 23.0-25.0°C. The negative effect of high temperatures on *P. clarkii* is also described in the work of K. Guo *et al.* (2020), which analysed the intestinal immune response of *P. clarkii* individuals at a temperature of 25.0°C (control) and a stressful temperature of 35.0°C. Based on biochemical analysis of oxidative stress parameters and immune indicators in the intestine, a negative reaction to temperature stress (35.0°C) was established, which manifested itself through increased oxidative stress in the intestine and decreased activity of antioxidant and immune enzymes, which together caused mortality.

An explanation for this result can be found in the work of B. Carreira *et al.* (2017), which studied the feeding of crayfish with different feeds at different temperatures. The results of the studies indicate a decrease in the efficiency of animal feed consumption at higher temperatures, since juveniles fed an animal diet were unable to maintain high growth rates during a prolonged heat wave; and a decrease in the efficiency of plant diets at low temperatures, since juveniles accumulated fewer reserves at lower temperatures when fed a plant-based diet. Similar results regarding an increase in herbivory with increasing water temperature were also investigated by P. Zhang *et al.* (2020), who proved that an increase in temperature increases the herbivory of ectothermic hydrobionts. Along with this, a study of other crustacean species conducted by P. Kovtun & S. Merzlov (2023) demonstrated a significant impact of diet composition, in particular the inclusion of vermiculture biomass, on their productivity.

In the study conducted by the authors of this paper, compound feed with a high protein content (46.0-64.0%) was used to feed crayfish of all groups, including high-temperature ones, and only at the beginning of the third month of cultivation was compound feed with a high fibre content (5.0%) introduced into the crayfish diet in an amount of 20.0% of the daily ration, which was obviously insufficient to maintain normal metabolic processes in individuals from high-temperature Groups (5 and 6). However, this study did not consider the aspect of food selectivity in favour of animal or plant feed for feeding *P. clarkii* at different water temperatures, but the data presented may be useful in future studies for compiling a daily diet for crayfish.

All of the above-mentioned studies lead to one common conclusion: high water temperatures have an undeniable negative impact on crayfish survival, which is also confirmed by this study. It has been found that in juvenile crayfish from high-temperature groups, the metecdysis period (the period after moulting until the formation of a new exoskeleton, which, according to S. Galib *et al.* (2022), is a period of defencelessness for crayfish) lasted 2-3 days, compared to 1-2 days in crayfish at temperatures of 22.0-26.0°C. Thus, individuals from Groups 5 and 6 remained more vulnerable to environmental factors for a longer period of time, primarily to cannibalism, which actively progressed due to the asynchrony of the moulting process itself. The longer period of metecdysis is associated with the functioning of the endocrine system, which regulates the secretion of the substance chitin synthase, which is used to form a new exoskeleton, which was apparently suppressed by high water temperatures. At the same time, the neuroendocrine system of crayfish and related molecules regulate the behaviour of crayfish and physiological processes, including the perception of environmental factors, which could affect the thermotolerance and aggressive behaviour of individuals from high-temperature groups (Ren *et al.*, 2021; Fedorovych *et al.*, 2022b). As crayfish grow, the problem of cannibalism decreases as the frequency of moulting decreases.

As follows, the undoubted advantage of temperature conditions formed in Group 1, which demonstrates the highest percentage of survival and the highest linear growth and weight gain of experimental crayfish, was established. Groups 2-4 are also characterised by satisfactory growth rate, but demonstrate lower survival rates. Also, according to the results of study and analysis of available literature, it was proved inexpedient to grow *P. clarkii* at the temperature conditions formed in Groups 5 and 6, which showed the lowest linear growth and weight gain and the lowest survival rates.

Conclusions

According to the results of the study, the lowest temperatures among the studied ones had a positive effect on the growth and development of *Procambarus clarkii*, while the highest temperature regimes studied, which went beyond the tolerance of the crayfish, showed the lowest efficiency. So, comparing the results obtained, it was found that the highest growth and survival rates were observed in Group 1, which was grown at the lowest temperature among the studied, namely 22.0°C. Groups 2-4 (24.0-28.0°C) showed slightly lower but satisfactory growth and survival rates, but compared to Group 1, these groups were characterised by a lower survival rate. High-temperature Groups 5 (30.0°C) and 6 (32.0°C) were unable to maintain high growth and survival rates.

The influence of high temperatures was also revealed by the results of the assessment of death and cannibalism as a behavioural response of the organism to factors of the external (high temperature) and internal (metabolic processes, activity of the endocrine and neuroendocrine systems) environment. So, the survival rate of individuals in Group 1 (22.0°C) was 2 times higher than in Group 6 (32.0°C). In addition, to the disadvantages of high-temperature cultivation regimes, one can also add naturally higher energy consumption for water heating, which, with large volumes of cultivation, can be high, and most importantly, unnecessary costs. The results obtained have significant potential for the development of an optimised and scientifically sound technology for the cultivation of *Procambarus clarkii*, and can also serve as a basis for further, more in-depth research. In particular, a promising area for further research is to study the effect of the combination of parameters and growing conditions on the physiological parameters and productivity of *Procambarus clarkii* at different stages of ontogenesis.

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Conflict of Interest

None.

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Вплив температури води на ріст та розвиток червоного каліфорнійського рака *Procambarus clarkii* (Girard, 1852)

Володимир Корецький
Аспірант
Національний університет біоресурсів і природокористування України
03041, вул. Героїв Оборони, 15, м. Київ, Україна
https://orcid.org/0009-0002-4733-1176

Ірина Кононенко
Кандидат сільськогосподарських наук, доцент
Національний університет біоресурсів і природокористування України
03041, вул. Героїв Оборони, 15, м. Київ, Україна
https://orcid.org/0000-0003-3906-3650

Олеся Охріменко
Кандидат сільськогосподарських наук
Національний університет біоресурсів і природокористування України
03041, вул. Героїв Оборони, 15, м. Київ, Україна
https://orcid.org/0000-0001-9867-0595

Руслан Кононенко
Кандидат ветеринарних наук, доцент
Національний університет біоресурсів і природокористування України
03041, вул. Героїв Оборони, 15, м. Київ, Україна
https://orcid.org/0000-0002-7818-2583

Наталія Рудик-Леуська
Доктор біологічних наук, доцент
Національний університет біоресурсів і природокористування України
03041, вул. Героїв Оборони, 15, м. Київ, Україна
https://orcid.org/0000-0003-4355-7071

Анотація. В галузі аквакультури одним з найрозповсюдженіших у світі комерційним видом раків є червоний каліфорнійський рак *Procambarus clarkii*. Метою даної роботи був аналіз впливу температурного режиму на параметри росту *Procambarus clarkii* при вирощуванні в діапазоні температур води від 22,0 до 32,0°C з кроком температур 2,0°C (всього 6 дослідних груп). Під час проведення експерименту використано теоретичні (аналіз, систематизація, порівняння), експериментальні (лабораторні) та загальноприйняті у рибництві методи досліджень. Отримані результати чітко продемонстрували пригнічуючий вплив високих температур водного середовища – 30,0°C (Група 5) та 32,0°C (Група 6) – на ріст та розвиток (лінійно-ваговий приріст, виживаність) особин, тоді як найнижча в даному досліді температура води (Група 1, 22,0°C) сприяла більш ефективному росту та підтримувала виживаність раків. Так, кінцева середня маса особин Групи 1 (22,0°C) становила 15,20 ± 1,97 г, у Групі 2 (24,0°C) середня маса складала 13,71 ± 1,35 г, раки Групи 3 (26,0°C) досягли середньої маси в 14,85±1,75 г, Група 4 (28,0°C) – 14,08 ± 2,25 г, а в Групах 5 (30,0°C) і 6 (32,0°C) отримана середня маса складала 9,75 ± 2,33 г і 6,60 ± 0,36 г відповідно, що в 1,5 та 2,3 раза менше порівняно з Групою 1. Водночас показники середнього лінійного приросту мали більш однорідний характер і становили на кінець дослідження у Групі 1 – 8,00 ± 0,29 см, у Групі 2 – в середньому 7,38±0,29 см, особини Групи 3 мали середню довжину 7,66 ± 0,22 см, у Групі 4 – 7,42 ± 0,33 см, а у високотемпературних Групах 5 і 6 середня довжина складала 6,80 ± 0,50 см і 6,04 ± 0,26 см відповідно. Встановлено тенденцію зниження виживаності особин при збільшені температури води у групах. Так, виживаність у Групі 1 на кінець досліджень становила 58,82 %, у Групі 2 – 41,18 %, у Групі 3 – 47,06 %, Групі 4 – 41,18 %, а Групи 5 і 6 зазнали найбільшого тиску температурного показника на виживаність – 35,29 % і 29,41 % відповідно

Ключові слова: аквакультура; *Procambarus clarkii*; маса; довжина; виживаність; терморегуляція; метаболізм