



## Thermal tolerance of *Cyclops kolensis* lilljeborg, 1901 (Copepoda: Cyclopoida) and its relationships with pessimal to optimal performance

Vladimir B. Verbitsky<sup>\*</sup>, Andrey K. Grishanin, Elena N. Medyantseva, Olga A. Malysheva, Valentina I. Lazareva, Svetlana M. Zhdanova, Tamara I. Verbitskaya

*Papanin Institute for Biology of Inland Waters, Russian Academy of Science, 152742, Borok, Nekouz, Yaroslavl, Russia*

### ABSTRACT

*Cyclops kolensis* Lilljeborg, 1901 belongs to the Arctic complex of Palaeoartic species, yet in the past 20 years, its occurrence has extended to the summer months in waterbodies with high water temperatures. This species is considered one of the most active migrants from the northern waterbodies in the Volga reservoir cascade to the Volga delta. Here, we explored the ranges of the preferred and avoidance temperatures of *C. kolensis* from two geographically isolated populations. Thermal tolerance was measured in a thermogradient installation and compared to the temperatures at which members of these populations occurred in their source waterbodies. Temperature preference was determined using the “chronic” method. Individuals of *C. kolensis* possessed a bimodal final temperature preferendum of 2–6 °C and 13–21 °C, which corresponds to the optimal thermal conditions of the species in a pond. These ranges were the same for individuals of both populations irrespective of the geographical location and water temperature of their source waterbodies. The temperature range of normal performance was 2–4 to 21–25 °C, and the pessimal temperature ranges were from 1–2 to 3–4 °C and from 22–25 °C to 26–30 °C. These temperature ranges coincide with field observations over a recent 20-year period of temperature conditions under which the species develops in nature. Our results allow us to characterize *C. kolensis* as an ecologically plastic species, which, despite its strong association with the cold-water *Complex* species, is adapting to a wider temperature range as global warming occurs.

### 1. Introduction

Knowledge of the thermal preferences of aquatic organisms is very important, as temperature is a main factor directly impacting the physiology of ectotherms, which react to thermal changes in the environment, avoiding lethal temperatures and pursuing optimal temperature ranges (Reynolds and Casterlin, 1979). Interest in the thermal adaptations of ectothermic species has expanded as evidence of global climate change accumulates. This is particularly true for species living in the Palaeoartic and Holarctic regions, where the largest temperature fluctuations over historical records have been reported (Jansen and Hesselein, 2004; Geerts et al., 2015).

A primary adaptation of hydrobionts is thermoregulatory behavior, wherein individuals react to temperature according to their thermopreferendum. For an aquatic organism, the final thermal preference (FTP) is innate and specific (Reynolds and Casterlin, 1979; Britz and Hecht, 1987). Preferential temperatures are good indicators of the optimum temperatures for hydrobionts in nature (Jobling, 1981; Britz and Hecht, 1987; Kelsch and Neill, 1990; Golovanov, 1995; Lamkemeyer et al., 2003; Verbitsky et al., 2014). Preferential temperatures coincide with optimal temperatures for physiological processes such as metabolism, reproduction and growth (Buckle et al., 1996; Hernandez et al.,

1995; Díaz et al., 2002). According to Nichelmann (1983), an animal's body is subjected to minimal heat stress within the preferential temperature range. The boundaries of animals' natural ranges are also often determined by temperature, acting as a limiting factor (Hayward et al., 2003; Jansen and Hesselein, 2004).

*Cyclops kolensis* Lill. belongs to an Arctic complex of Palaeoartic species. A number of authors consider it the most common species of cold-loving *Cyclops* (Rylov, 1948; Nikolaev, 1972; Monchenko, 1974; Dziuban and Rivier, 1976; Shurganova, 1984, 1989; Blank et al., 2009). Its distribution encompasses the Palaeoartic and part of the Nearctic. *C. kolensis* predominantly inhabits large and deep waterbodies (Elgmork, 1967; Szlauer, 1963; Sarvala, 1979; Santer, 1991; Santer and Lampert, 1995) but is also found in shallow lakes and ponds during spring (Rylov, 1948; Rivier, 2012). It is a common inhabitant of lakes in Poland and the Kola Peninsula and in Siberia from the northern Urals to the New Siberian Islands and Kamchatka (Kozminski, 1936; Elgmork, 1959; Monchenko, 1974; Mazepova, 1978). *C. kolensis* was not found south of the taiga zone in the European part of Russia in the 1950s (Rylov, 1948). However, in the past 20 years, its presence in the summer months and at high water temperatures has been reported (Wærvågen and Nilssen, 2010; Yermolaeva, 2013). *C. kolensis* is considered one of the most active migrants from the northern waterbodies southwards to

<sup>\*</sup> Corresponding author.

E-mail addresses: [verb@ibiw.ru](mailto:verb@ibiw.ru), [werb@ibiw.yaroslavl.ru](mailto:werb@ibiw.yaroslavl.ru) (V.B. Verbitsky).

the Volga reservoir cascade, where it is now widely distributed as far as Volga's delta (The River Volga and Its Life, 1979; Popov, 2007).

The species is not very variable morphologically; even the Lake Baikal forms do not differ significantly from the typical form inhabiting the southern lakes of Sweden (Kozhov, 1963; Lindberg, 1955). This apparent morphological similarity is complemented by constancy at the cytogenetic and molecular genetic levels (Grishanin et al., 2006).

To date there are no data about the preferred and avoided temperatures of *Cyclops kolensis* from different populations.

The aim of the work was to determine the ranges of the preferred and avoided temperatures of two populations of *C. kolensis* separated by 300 km by employing a thermogradient installation and compare the values with field observations of temperature conditions in which these populations develop in nature.

## 2. Materials and methods

### 2.1. Reservoirs in which field distributions were analyzed

The developmental phenology of *C. kolensis* Lilljeborg, 1901 was observed in waterbodies in the Central Federal District of Russia: the Rybinsk reservoir located on the Upper Volga (from 58°24'32" to 57°09'53" N) and Lake Nero, in the Middle Volga basin (from 38°27'30" to 39°26'20" E) (Table 1) (The River Volga and Its Life, 1979). The studied reservoirs differ in area (58 vs. 4550 km<sup>2</sup>), water exchange rate (1.9. vs. 2.2 years<sup>-1</sup>), average depth (1.6 vs. 5.6 m) and location in the Volga system (Litvinov et al., 2009; Poddubny and Litvinov, 2008). The Rybinsk reservoir is weakly eutrophic; Lake Nero is hypertrophic.

### 2.2. Sampling periodicity

In the Rybinsk reservoir, regular annual monitoring was conducted from 6 to 20 sampling stations from May to October in 2008–2014 and from December to March in 2009–2017. The Lake Nero studies were carried out in May to September 2003–2004; winter observations from the 1980s were compiled from Rivier and Stolbunova (1991).

### 2.3. Collection of zooplankton in the field

Copepods were collected using a small Juday net with a diameter of 12 cm and a mesh size of 74 μm. Samples were fixed with 4% formaldehyde. Species determination and linear measurements of animals were performed in the laboratory using StereoDiscovery V12 Carl Zeiss (Germany) and MS-2 LOMO microscopes (Russia). Identification was performed in accordance with Monchenko (1974), Einsle (1993, 1996), and Ueda and Reid (2003).

### 2.4. Zooplankton collection for testing

*Cyclops* individuals were collected using a 74 μm mesh plankton net on March 31, 2014, in the Maryinsky pond of the Vorobyovy Gory preserve, Moscow, Russia (55°42'36" N; 37°32'42" E) at a water temperature of 2.5 °C and in the Barsky pond of Borok settlement, Yaroslavl Region, Russia (58°03'42" N; 38°14'46" E), on April 27, 2014, at a water temperature of 8 °C; on May 5, 2014, at a water temperature of 10 °C

and on April 23, 2018, at a water temperature 1.0–1.5 °C. The latitudinal distance between waterbodies was 300 km. On these dates and in these ponds, *C. kolensis* was the only dominant, large-bodied species of *Cyclops* and was represented by females with eggs. Zooplankton collected in the Barsky pond were placed in a Bogorov's chamber immediately after collection. Each *Cyclops* individual was collected by a pipette using a dissecting microscope. *Cyclops* individuals collected in the Maryinsky pond were maintained in a refrigerator at the same temperature as the water temperature under which they were collected in nature and fed with the microalgae *Nanochlorops* sp. until April 3, when they were placed in a thermal gradient.

### 2.5. Thermogradient apparatus

Temperature preference was determined by the "chronic" method (Reynolds and Casterlin, 1979; Rosetti et al., 1989; Verbitskii and Verbitskaya, 2012; Golovanov, 2013), in which a group of test organisms are placed in a thermogradient apparatus for several days. The FTP measurement device was composed of a Herter tray with a metal floor and walls of transparent acrylic glass with dimensions of 183 cm long × 10 cm wide × 4 cm deep (Fig. 1). In experiment No. 4, two narrow trays were placed in the installation tray; the narrow trays had dimensions of 182 cm long × 4 cm wide × 3.5 cm deep. A horizontal temperature gradient (from 1.6 ± 0.5 °C to 26.7 ± 1.2 °C) along the tray was maintained using a TSS-1 thermostatic device (Russian Federation) with a heating element (0.8 kW) at one end of the tray and a cooling device at the other end. To minimize convection currents and a vertical temperature gradient, the depth of water in the tray was maintained at a depth of 10–12 mm. To monitor and record the water temperature, thermometers were placed every 10 cm along the length of the tray. The number of copepods at a specific location of the tray in the temperature gradient was recorded using a linear scale with 1 mm divisions.

In experiment 1, during the first day of the experiment, the difference in temperature between each 10 cm interval was 1–1.6 °C from thermometers 1 to 5, 0.1–0.4 °C from thermometers 5 to 16, and 1.3–2.9 °C from thermometers 16 to 18. From the 2nd day until the end of experiment 1, the temperature difference between intervals was 0.5–1.5 °C from thermometers 1 to 5, 0–0.3 °C from thermometers 5 to 16 and 0.6–2.5 °C from thermometers 16 to 19. In experiments 2 and 3, throughout the experiments, the interinterval temperature difference was 0.1–2.1–2.3 °C for thermometers 1 through 4, 0.1–0.4 °C for thermometers 4 through 17 and 0.4–0.5 °C to 1.3–1.4 °C for thermometers 17 through 19. Throughout experiment 4, the interinterval temperature difference was 0.1 °C–1.6 °C for thermometers 1 through 5, 0.1 °C–0.8 °C for thermometers 4 through 17 and 0.2 °C–1.4 °C for thermometers 17 through 19.

We recorded the location of individuals simultaneously with temperature. Thus, we avoided time lags between corresponding temperature and location observation of individuals. The design of the device and the detailed methodology is described in Verbitsky et al. (2017).

### 2.6. Experimental procedures

#### 2.6.1. Horizontal thermal gradient method

In experiment 1 (April 3–9, 2014), 55 females with egg sacs from the

**Table 1**  
Description of water bodies, which were observed phenology of *C. kolensis*.

Monogram	Toponym	Latitude (N)	Longitude (IE)	Area, km <sup>2</sup>	Maximum depth (m)	Observation times	Water temperature, °C
RR	Rybinsk Reservoir	58°24'32"	38°27'30"	4550	2100	December–March May–June July–August September–October	0.1–3.4 3–19 17–28 5–17
LN	Lake Nero	57°09'53"	39°26'20"	58	4.7	May–June July–August September	11–21 16–27 7–14

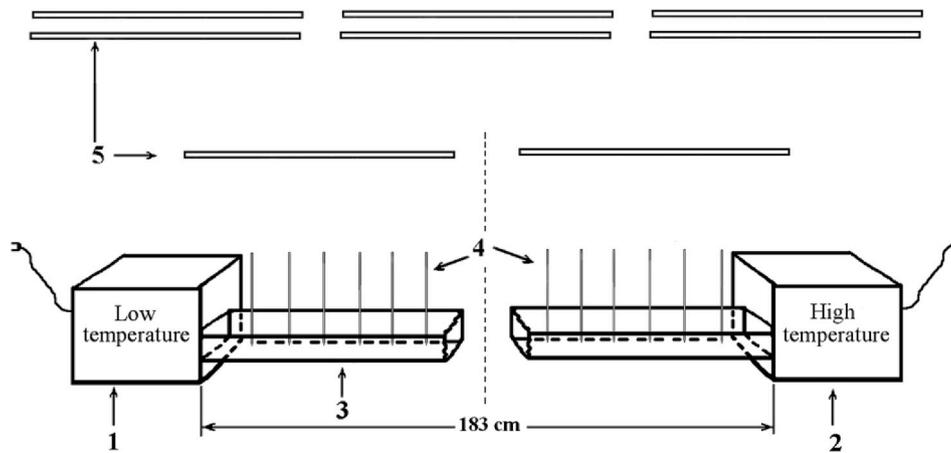


Fig. 1. Schematic diagram of thermogradient apparatus. 1 –refrigerating block, 2 – heat block, 3 – Herter tray, 4 – thermometers, 5 – eight lamps.

Maryinsky pond were placed in a tray into a temperature zone of 2–5 °C. The total number of measurement series was 77, which included a total of 4230 records corresponding to the number of locations of all registered individuals in all series. In experiment 2 (April 27 to May 2, 2014), 42 females from the Barsky pond were placed in a temperature zone of 6–10 °C. The total number of series of measurements was 66, which included 2746 location records. In experiment 3 (May 5–12, 2014), 44 females from the Barsky pond were placed in a temperature zone of 8–12 °C. A total of 103 series of measurements were performed, in which 4537 observations of individual locations were recorded. In experiment 4 (April 23 to May 11, 2018), 70 females from the Barsky pond were placed in tray no. 1 in a temperature range of 1–3 °C. *Cyclops* females were transferred from tray 1 to tray 2 on the 6th day according to the experimental design (Table 2).

In all experiments, a suspension of microalgae *Nanochlorops* sp. was added daily, being evenly dispersed along the entire length of the

chamber at a concentration of  $5.0\text{--}7.5 \times 10^5$  cells/ml. The daily procedures were similar to those of an earlier study (Verbitsky et al., 2017). Before each series of observations, thermometer readings were recorded. Temperature varied within  $\pm 0.3$  °C at each point. The average body size of the adult females, measured as the sum of the lengths of cephalothorax, abdomen and tail furca, was  $1.30 \pm 0.01$  mm.

### 2.7. Determination of preferred and avoided temperatures

To determine preferred and avoidance temperatures, we used the methodology and criteria established by Diaz et al. (1994) and Hernandez et al. (1995). To calculate the average thermal preference for each series of samples, we used the arithmetic average for the modal group of preferred temperatures (Johansen and Cross, 1980). We found the average of the preferred temperature for each day by averaging the data obtained for a series of samples. Then, we summarized the number

Table 2  
Modal ranges and temperatures preferred by *C. kolensis* in experiments in 2018 (April 24, 2018–May 10, 2018).

Time, day	Tray	n, ind.	First preferred range			Second preferred range		
			PT <sub>med.</sub> ±S.d., °C*	Modal values, °C	Number of counts (%)	PT <sub>med.</sub> ±S.d., °C	Modal values, °C	Number of counts (%)
1	1	76 ± 3	–	–	–	15.2 ± 0.7	14–16	73.2
2	1	70 ± 6	–	–	–	16.2 ± 1.4	14–19	59.9
3	1	73 ± 5	–	–	–	16.7 ± 1.8	14–20	65.6
4	1	69 ± 4	–	–	–	15.9 ± 1.3	13–20	62.6
5	1	66 ± 5	2.8 ± 0.8	2–4	11.2	14.5 ± 1.2	13–18	48.2
6	1	70 ± 3	2.9 ± 0.9	2–4	12.8	15.7 ± 1.5	13–18	49.9
	2	5	5.1 ± 1.0	1–6	33.3	16.4 ± 1.7	14–19	46.7
7	1	62 ± 4	4.6 ± 1.7	2–7	22.0	17.0 ± 1.8	14–20	50.2
	2	5	9.0 ± 1.7	6–11	22.6	16.2 ± 2.2	13–20	64.2
8	1	60 ± 4	2.3 ± 1.0	1–7	27.0	14.7 ± 1.6	12–17	40.3
	2	5	–	–	–	15.0 ± 1.9	12–18	72.7
9	1	58 ± 2	4.4 ± 1.7	2–7	24.8	15.2 ± 1.6	13–18	46.0
	2	10	3.1 ± 1.7	1–5	12	17.4 ± 1.7	15–20	54.2
10	1	34 ± 3	3.9 ± 1.6	2–6	24.6	14.2 ± 1.4	12–16	42.2
	2	30 ± 3	5.5 ± 2.5	2–10	22.6	15.9 ± 1.6	14–18	55.6
11	1	36 ± 3	3.9 ± 1.6	2–6	24.0	14.3 ± 1.4	12–16	41.1
	2	31 ± 3	6.2 ± 2.2	3–9	24.6	16.2 ± 2.3	13–20	57.7
12	1	31 ± 6	5.1 ± 2.5	2–9	46.8	14.3 ± 1.4	12–16	35.2
	2	31 ± 2	4.0 ± 1.4	3–10	25.5	16.9 ± 3.1	12–21	63.4
13	1	35 ± 4	3.8 ± 1.6	2–10	30.9	14.5 ± 1.4	12–16	36.0
	2	33 ± 5	3.8 ± 1.8	2–7	17.6	16.9 ± 2.7	13–21	60.1
14	1	32 ± 1	3.6 ± 1.5	2–6	27.4	16.3 ± 2.1	13–20	49
	2	32 ± 2	3.6 ± 1.5	2–6	22.7	15.9 ± 3.2	13–21	53.6
15	1	31 ± 2	3.6 ± 1.5	2–6	25.8	16.8 ± 2.0	14–20	45.9
	2	30 ± 2	3.8 ± 1.5	2–6	22.4	16.8 ± 1.7	14–19	46.7
16	1	31 ± 3	3.8 ± 1.5	2–6	21.5	17.0 ± 2.4	13–21	54.5
	2	27 ± 6	5.6 ± 2.6	2–9	20.0	16.7 ± 2.1	14–20	53.9

Note: PT<sub>med.</sub>±S.d. – preferred temperatures ± standard deviation.

of counts for all series for each degree and, based on these amounts, we calculated the percentage distribution of copepods on a scale of degrees. These data were used to calculate the ranges of modal values, preferential temperatures, temperatures of normal performance (TNP), and pessimal and avoided temperatures.

For the range of preferred temperatures, the modal ranges were used, defined as the temperature at which >70% of *C. kolensis* individuals were located. For the TNP range, the temperatures at which >90% of the individuals were located were used (Verbitsky et al., 2014). These temperatures correspond to the natural temperature ranges at which individuals of native populations usually live, grow, feed, and multiply (Kelsch, 1996). The temperatures at which <10% of the individuals were recorded determined the values of the pessimal (or stressful) temperatures at which organisms can survive but not prosper in nature.

To obtain the most objective assessment of the similarities or differences in the distribution of *Cyclops* along the thermal gradient during each experiment, the series of individual position counts for each day of observation were compared using mean values (t-test), medians (Wilcoxon (W)-test), deviations (F-test) and distribution functions (Kolmogorov-Smirnov (KS)-test). In experiment 4, the differences between the distributions in trays 1 and 2 were examined using Spearman's rank correlation coefficient analysis. The values are presented as the mean  $\pm$  SD. All calculations were performed using the statistical package R, version 3.2.2 (R Development Core Team, 2015).

### 3. Results

#### 3.1. Environmental data

In the Rybinsk reservoir, *C. kolensis* occurred from December to June; the maximum population density occurred in May. The main peak of reproduction was from the third week of April to the third week of May, at 5–12 °C (Table 3); in the cold years, the species was observed to reproduce up to the midsummer; i.e., mid-June (13–14 °C) (Lazareva, 2010).

In the shallow Lake Nero, which warms up quickly in the spring, *C. kolensis* bred in the second week of May at 11–12 °C (Table 3). It entered diapause in May/June at a water temperature of 15–19 °C. From July to October, the species was absent from the plankton in both waterbodies.

#### 3.2. Experimental data

##### 3.2.1. Experiment 1

*Cyclops* did not exhibit a strong preference within the narrow temperature range at any point throughout the experiment. Consistently, over 90% of the crustaceans were observed in the range of 4–5 to

19–21 °C (Fig. 2). Comparison of the distribution of data series performed after summing the counts for each day using various statistical tests (t-test, F-test, W-test and K-S-test) revealed no significant differences ( $p > 0.05$ ) in counts among intervals or dates. Three preferred ranges were observed. The first was from 3–5 °C to 6–7 °C (9.8–27.0% of samples), the second was from 9–10 °C to 13–14 °C (17.0–34.8% of samples), and the third was from 15–18 °C to 19–21 °C (32.5–41.6% of samples) (Table 4). We did not calculate the values of final thermal preferendum (FTP) in experiments 1 and 2 and limited ourselves to the average values because in previous studies of other species of *Cyclops*, the FTP was found to manifest starting 5–6 days after copepod placement into the thermal gradient. The average preferred temperature in the indicated ranges was  $4.8 \pm 1.4$  °C to  $6.0 \pm 0.8$  °C,  $11.4 \pm 1.7$  °C to  $12.5 \pm 1.0$  °C and  $17.6 \pm 1.0$  °C to  $19.5 \pm 1.0$  °C. The TNP range was 4–21 °C (97.5–98.4% of counts), and the pessimal values were 3–4 °C and 22–26 °C.

##### 3.2.2. Experiment 2

In the second experiment, *Cyclops* demonstrated a distribution similar to that in experiment 1. More than 85% of the crustaceans occurred in the range of 4–5 °C to 21–22 °C (Fig. 3), and three preferred temperature ranges were distinguished. The first was 5 °C to 6–7 °C (11.1–15.5% of samples), the second was 9–10 °C to 13–15 °C (16.1–28.4%), and the third was 17–19 °C to 21–22 °C (27.7–35.9%) (Table 4). The average selected temperature in the three ranges was  $5.5\text{--}5.6 \pm 0.5$  °C,  $10.5 \pm 1.0$  °C to  $13.6 \pm 1.1$  °C and  $18.6 \pm 1.2$  °C to  $19.2 \pm 1.5$  °C. Starting from the second day, two preferred ranges became evident, one at low values, and one at high values. The range of TNP was 3–4 °C to 21–22 °C (85.4–96.4%), and the pessimal values were 2–3 °C and 23–30 °C.

Starting from the second day, there were no differences between the data series ( $p > 0.05$ ) according to all four statistical tests (t-, W-, F-, and KS-tests) as determined by the daily comparison of the sum of counts of individuals' locations each day in experiments 1 and 2. As a result, there were no differences in average preferred temperature, TNP range or pessimal temperature between experiments 1 and 2, despite the facts that the distance between waterbodies was 300 km in latitude and that the water temperature differed by 6 °C between sites at the time the *Cyclops* individuals were caught.

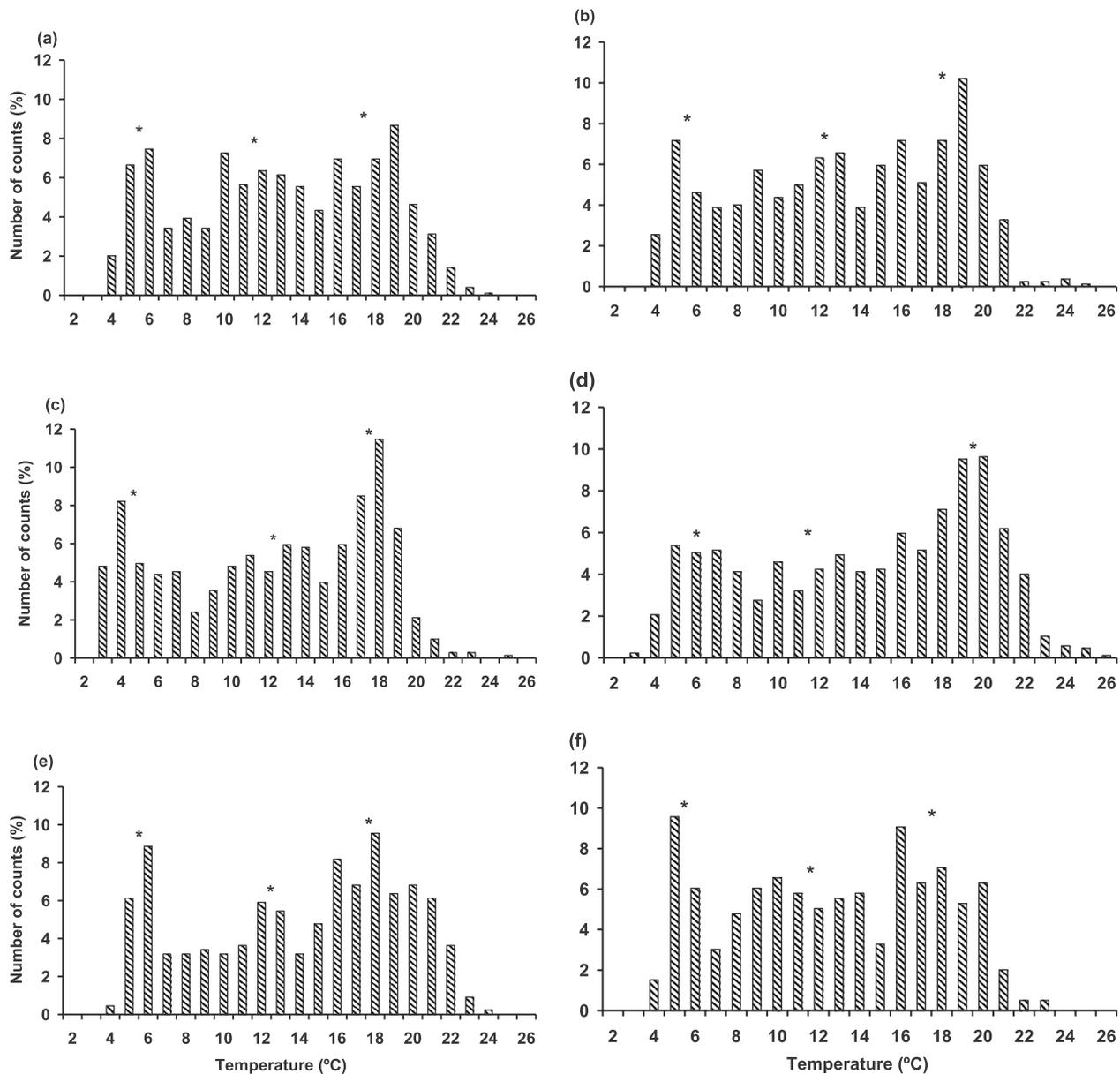
##### 3.2.3. Experiment 3

In the third experiment, the copepods preferred two temperature ranges. The first was 5–7 °C to 9–11 °C (26.5–37.2% of samples), and the second was 14–15 °C to 18–19 °C (30.1–47.5%) (Fig. 4, Table 4). Differences between data series were absent according to all statistical tests ( $P > 0.05$ ). The average preferred temperature ranges were  $7.9 \pm 2.0$  °C to  $8.8 \pm 1.4$  °C and  $16.3 \pm 1.3$  to  $17.0 \pm 1.3$  °C. In this experiment, we

**Table 3**

The months and temperatures at which reproduction and rates of development of *C. kolensis* eggs are maximal in nature.

Basin	Latitude (N)	The period of maximum reproduction	T, °C for eggs development	Authors
Rybinsk reservoir, Russia	58°24'32"N, 38°27'30"E	usually in April–May, rarely in March February–March–April March–April–May March–April – May May	>3.5 (5–12) 0–7 5–9 7–12 3–7	present study Rivier (2010) Lazareva (2010) Rivier (1986), 2012; Lazareva, Sokolova (2017)
Lake Nero, Russia	57°09'53"N 39°26'20"E	April–May	4–11 (12) 4–11	present study Rivier, Stolbunova (1991)
Curonian Lagoon in the Baltic Sea	55°23'20"N 21°06'54"E	November–December–January– February–March	4–7	Frisch (2002)
“_____”	55°23'20"N 21°06'54"E	Early spring	3–11 (6)	Dmitrieva, Semenova (2011)
Lake Heiligensee, Berlin, Germany	52°36' 0"N 13°13' 0"E	in the winter March–April	1–3 5–14	Adrian, Deneke (1996)
Kuibyshev reservoir, Russia	53°26'42"N 49°18'24"E	first half of May	12–13	Timokhina (2000)



**Fig. 2.** The distribution of the counts of individual *Cyclops kolensis* at each location in the temperature gradient in Experiment 1 (4–9 April 2014). a – Day 1, b – Day 2, c – Day 3, d – Day 4, e – Day 5, f – Day 6. \* – Average preferred temperatures.

distinguished the final preferred temperature (FTP) ranges, calculated for 6–8 days as  $8.4^{\circ}\text{C} \pm 1.05$  and  $16.5^{\circ}\text{C} \pm 1.6^{\circ}\text{C}$ . The range of TNP was  $2\text{--}21^{\circ}\text{C}$  (91.2–95.5%), and the pessimal values were  $1^{\circ}\text{C}$  and  $22\text{--}27^{\circ}\text{C}$ .

### 3.2.4. Experiment 4

The fourth experiment was conducted to determine how the two- and three-modal distributions observed in the previous three experiments described above were formed. We placed two parallel inserts, tray no. 1 and tray no. 2, in the installation tray. Seventy females with egg sacs were placed in tray 1. From the first to the fourth day, the *Cyclops* females preferred one temperature range:  $13^{\circ}\text{C}\text{--}20^{\circ}\text{C}$  (62.6–73.2% of records) (Fig. 5a and b, Table 2). Starting on day 5, some *Cyclops* females began to shift to lower temperatures, and two preferred temperature ranges became evident: a more heavily occupied range at  $13\text{--}18^{\circ}\text{C}$  (48.2% of records) and a less occupied range at  $2\text{--}4^{\circ}\text{C}$  (11.2% of records). This trend continued throughout the experiment. At the end of 5 day, we transferred 5 *Cyclops* individuals from the temperature zone of  $24\text{--}27^{\circ}\text{C}$  of tray no. 1 to the same temperature range in tray no. 2. On

days 6 and 7, the females preferred the ranges of  $2\text{--}4^{\circ}\text{C}$  to  $2\text{--}7^{\circ}\text{C}$  and  $13\text{--}18^{\circ}\text{C}$  to  $14\text{--}20^{\circ}\text{C}$  (12.8 and 49% of samples at the lower and higher range, respectively, on day 6, and 22.0 and 50.2% of the samples at the lower and higher range, respectively, on day 7) (Fig. 5c, Table 2). In tray 2, *Cyclops* preferred the ranges  $1\text{--}6^{\circ}\text{C}$  to  $6\text{--}11^{\circ}\text{C}$  and  $14\text{--}19^{\circ}\text{C}$  to  $13\text{--}20^{\circ}\text{C}$  (33.3 and 46.7% of records at the lower and higher range, respectively, on day 6, and 22.6 and 64.2% of records at the lower and higher range, respectively, on day 7).

On day 8, a bimodal distribution ( $1\text{--}7^{\circ}\text{C}$  and  $12\text{--}17^{\circ}\text{C}$ , 27% and 40.3% of records) persisted in tray no. 1, but in tray no. 2, in 72.7% of cases, the *Cyclops* preferred only one range:  $12\text{--}18^{\circ}\text{C}$  (Fig. 5d). At the end of day 8, another five individuals were transferred from the temperature range  $24\text{--}25^{\circ}\text{C}$  of tray no. 1 to tray no. 2. At the end of 9 day, another 20 individuals were transferred from the temperature range of  $22\text{--}27^{\circ}\text{C}$ . From days 9–14, *Cyclops* selected ranges of  $2\text{--}6^{\circ}\text{C}$  to  $2\text{--}10^{\circ}\text{C}$  and  $12\text{--}16^{\circ}\text{C}$  to  $13\text{--}20^{\circ}\text{C}$  (Fig. 5e–g) in tray no. 1 and  $1\text{--}5^{\circ}\text{C}$  to  $3\text{--}10^{\circ}\text{C}$  and  $14\text{--}18^{\circ}\text{C}$  to  $13\text{--}21^{\circ}\text{C}$  in tray no. 2. On days 15–16, the *Cyclops* preferred ranges  $2\text{--}6^{\circ}\text{C}$  and  $13\text{--}21^{\circ}\text{C}$  in tray no. 1 ( $21.5\text{--}25.8^{\circ}\text{C}$  and

**Table 4**  
Modal ranges and temperatures preferred by *C. kolensis* in experiments in 2014.

Time, day	PT <sub>med.</sub> ± S.d., °C	Modal values, °C	Number of counts (%)	PT <sub>med.</sub> ± S.d., °C	Modal values, °C	Number of counts (%)	PT <sub>med.</sub> ± S.d., °C	Modal values, °C	Number of counts (%)
	First preferred range			Second preferred range			Third preferred range		
Experiment 1* (April 4, 2014–April 9, 2014)									
1	5.5 ± 0.5	5–6	9.8	11.9 ± 1.4	10–14	30.9	17.6 ± 1.2	16–19	28.1
2	5.4 ± 0.5	4–7	11.8	12.1 ± 0.8	10–14	17.9	18.0 ± 1.4	15–20	41.6
3	4.8 ± 1.4	3–7	27.0	12.1 ± 1.4	10–14	26.6	17.6 ± 1.0	16–19	32.8
4	6.0 ± 0.8	5–7	15.6	11.6 ± 1.2	10–13	17.0	19.5 ± 1.0	18–21	32.5
5	5.6 ± 0.5	5–6	15.0	12.5 ± 0.5	12–13	17.3	17.9 ± 1.4	16–20	37.7
6	5.4 ± 0.5	5–6	15.6	11.4 ± 1.7	9–14	34.8	17.8 ± 1.5	16–20	34.0
Experiment 2 (April 28, 2014–May 2, 2014)									
1	5.6 ± 0.5	5–6	11.1	12.6 ± 1.8	10–15	28.4	20.0 ± 1.5	18–22	31.0
2	5.5 ± 0.5	5–6	14.6	11.4 ± 1.1	10–13	16.1	20.0 ± 0.7	19–21	27.7
3	5.5 ± 0.5	5–6	12.7	11.0 ± 1.2	10–13	18.1	20.0 ± 1.1	18–21	30.7
4	5.6 ± 0.5	5–7	15.5	11.0 ± 1.4	9–13	19.8	20.0 ± 1.3	18–22	35.9
5	5.6 ± 0.5	5–6	13.2	13.6 ± 1.1	12–15	13.7	19.2 ± 1.5	17–21	35.7
Experiment 3 (May 6, 2014–May 13, 2014)									
	First preferred range			Second preferred range					
1	9.2 ± 1.4	7–11	16.5	18.0 ± 0.8	17–19	29.1			
2	7.9 ± 2.0	5–11	26.5	16.9 ± 1.3	15–19	40.7			
3	8.0 ± 1.9	5–11	37.1	16.8 ± 1.7	15–19	32.5			
4	8.4 ± 1.1	6–10	30.0	17.0 ± 1.3	15–19	47.5			
5	8.5 ± 1.6	6–11	33.8	16.5 ± 1.6	14–19	36.7			
6	8.1 ± 0.8	7–9	28.2	16.6 ± 1.6	14–19	38.3			
7	8.5 ± 1.1	7–10	28.2	16.5 ± 1.6	14–19	37.1			
8	8.8 ± 1.4	7–11	37.2	16.3 ± 1.3	14–18	30.1			

Note: Designations as in Table 2. \* - Cyclops from Maryinsky pond.

45.9–54.5% of the samples) and 2–9 °C and 14–20 °C in tray no. 2 (20.0–22.4 and 46.7–53.9% of samples).

Comparison of the average values of the temperature preferendum from the two trays using Spearman's test showed no differences starting from the 7th day from the beginning of the experiment; i.e., on the second day after the introduction of *Cyclops* from tray 1 to tray 2. There were no differences from day 3 after the start of introduction according to the K–W test or from the 4th day onwards according to the other three tests (Table 5).

Based on the results of the transfer of individuals from tray 1 to tray 2, it can be concluded that under the conditions of the experimental temperature gradient, a *Cyclops* individual can tolerate a wide temperature range but remains in a preferred temperature zone for a long time, resulting in the formation of a two-modal or three-modal distribution along a gradient.

In tray no. 1, the final temperature preferendum (FTP) was 3.7 °C ± 1.5 and 17.0 ± 2.5 °C, and in tray no. 2, it was 3.8 °C ± 1.4 and 16.9 °C ± 2.0 °C. TNP was 2–25 °C in tray no. 1 and 2–24 °C in tray no. 2. The pessimal temperatures in both trays were 1–2 and 25–26 °C (Fig. 5h).

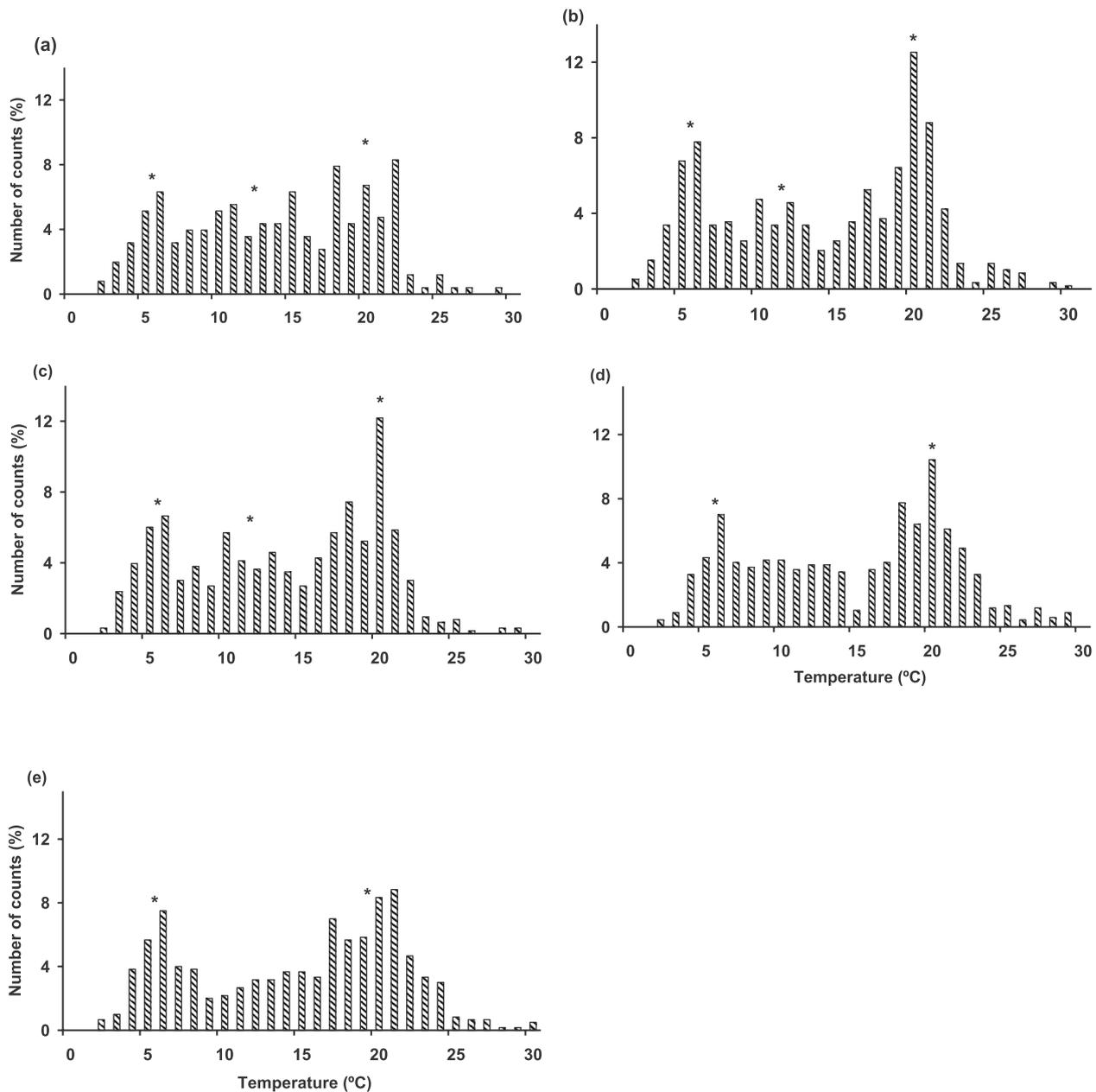
#### 4. Discussion

*Cyclops kolensis* is a common species throughout the entire Volga reservoir cascade (The River Volga and Its Life, 1979). The lack of a pronounced preference of a certain temperature range indicates a considerable thermal plasticity of this species. The observed preference of a wide range of temperatures from 1–5 °C to 18–21 °C contradicts the previously accepted view of this species as a cold-loving stenotherm that typically occurs in this region in winter and early spring (Monchenko, 1974, 1980; Blank et al., 2009; Rivier, 2012; Stolbunova, 2006). According to Monchenko (1974, 1980), individuals of *C. kolensis* appear in plankton at 2 °C, reproduce at 1–8 °C, and proceed to diapause at 12 °C. According to Frisch (2002), they breed from November/December to March at water temperatures of 4–7 °C. The temperature range at which the reproduction and development rate of *C. kolensis* eggs occur in nature are maximal is reported as 3–9 °C (Frisch, 2002; Lazareva, 2010; Lazareva and Sokolova, 2017). According to Rivier (2010, 2012), the

temperature range at which this species exhibits normal vital activity of is 0–3 °C to 12–14 °C, and *Cyclops* enters diapause when the water temperature increases to above 12–14 °C. According to Lazareva (2010), *C. kolensis* individuals reproduce starting from the third week of April to the third week of May at 5–12 °C.

These field observations are in good agreement with the first preferred low temperature range that we observed, but they are not consistent with the second range observed at 13–21 °C. The development of *C. kolensis* populations at higher water temperatures was first reported in the 1990s and subsequently in the 2000–2010s; this development was reported in the autumn-spring period and in the summer months. According to Rivier (2012) and Lazareva and Sokolova (2017), *C. kolensis* breeds at 5–12 °C in the spring until mid-June (at 13–14 °C). Transition to diapause occurs at 12–19 °C. According to long-term observations (Yermolaeva, 2010), *C. kolensis* has two peaks of development in Siberia: the first generation reaches sexual maturity in February–March, the second generation reaches maturity in early June, and adult individuals are found in late July. In the lakes of northern Kazakhstan, *C. kolensis* was caught during the summer at 17.2–19.8 °C (Yermolaeva, 2013). In an oligotrophic Norwegian lake, many reproducing individuals were located in the upper layer from 3 to 10 m at a temperature of 14–20 °C (Wærvågen and Nilssen, 2010). According to Santer and Lampert (1995, p. 609) *C. kolensis* developed well at 20 °C and with high survivorship. According to Melnik (1997) and Arov et al. (2001), *C. kolensis* is the most abundant cyclopoid species in Lake Baikal. It occupies open water year round and is abundant in all lake biotopes when the water temperature exceeds 14–15 °C. The temperature limit for the species in Lake Baikal is approximately 18–20 °C, and the optimum may be approximately 12–14 °C (Kozhov, 1963). These observations are supported by reports by Melnik (1997) and Arov et al. (2001) of the disappearance of *C. kolensis* from Baikal sors (shallow bays typical of Lake Baikal) and in the shallower parts of bays during the periods of maximum water temperatures (>20–22 °C).

Altogether, these data from different studies are in good agreement with the second peak of preference observed at 13–21 °C in experiments 3 and 4. Additionally, our data and literature on the conditions for the development of this species in waterbodies can be explained by the results of previous research (Adrian et al., 1999; Gerten and Adrian, 2002;



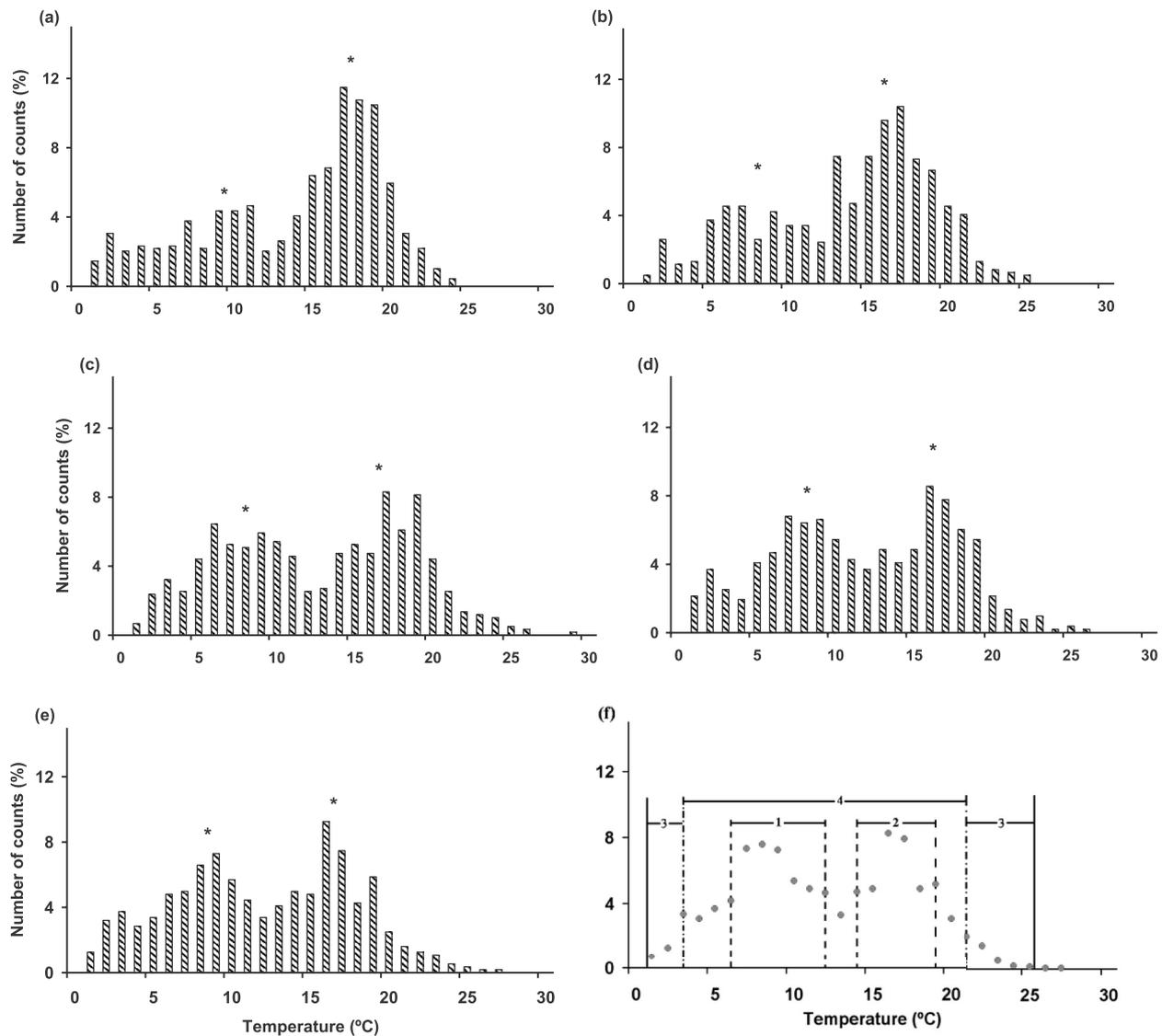
**Fig. 3.** The distribution of the counts of individual *Cyclops kolensis* at each location in the temperature gradient in Experiment 2 (27 April – 2 May 2014). a – Day 1, b – Day 2, c – Day 3, d – Day 4, e – Day 5. \* – Average preferred temperatures.

Seebens et al., 2008). In the present study, water temperature, despite being an important factor in the life cycle and phenology of copepods, was weakly correlated with the abundance of *C. kolensis*, and it was impossible to predict *C. kolensis* abundance from water temperature alone.

The existence of more than one FTP zone is not exclusive to *Cyclops kolensis*. For example, the cladoceran *Daphnia magna* was found to prefer two temperature ranges in experiments: 13.3–15.4 °C and 20.2–26.2 °C (Lagerspetz, 2000; Lamkemeyer et al., 2003; Verbitskii and Verbitskaya, 2011, 2012). However, the question of what underlies the above-described behavioral preference of *C. kolensis* remains unanswered. We speculate that there may be two reasons (mechanisms) for this preference. The first involves intraspecific variability, wherein different individuals prefer different temperatures. It is possible that each individual prefers a certain temperature range but that this range differs among individuals. In this case, different temperatures favor

different individuals. This is ecologically adaptive at the population level, because at low temperatures, some individuals will thrive and produce many offspring; others will do so at high temperatures. As a result, the population will be well adapted to seasonal temperature fluctuations. In the context of global climate fluctuations, such a mechanism can help a population persist. The second mechanism is the ability of each individual to move across an entire temperature range while also being able to predominantly occupy the zone (or zones) of most favorable temperatures. To implement such a mechanism, each individual must have high tolerance to temperature variation. At the population level, this mechanism is environmentally beneficial, since it offers a similar advantage as the previously described mechanism: the population has high plasticity with respect to temperature tolerance.

Starting from the second day of the experiment with the two trays, there were no differences between trays 1 and 2, and starting from the third or fourth day, the data series did not significantly differ according



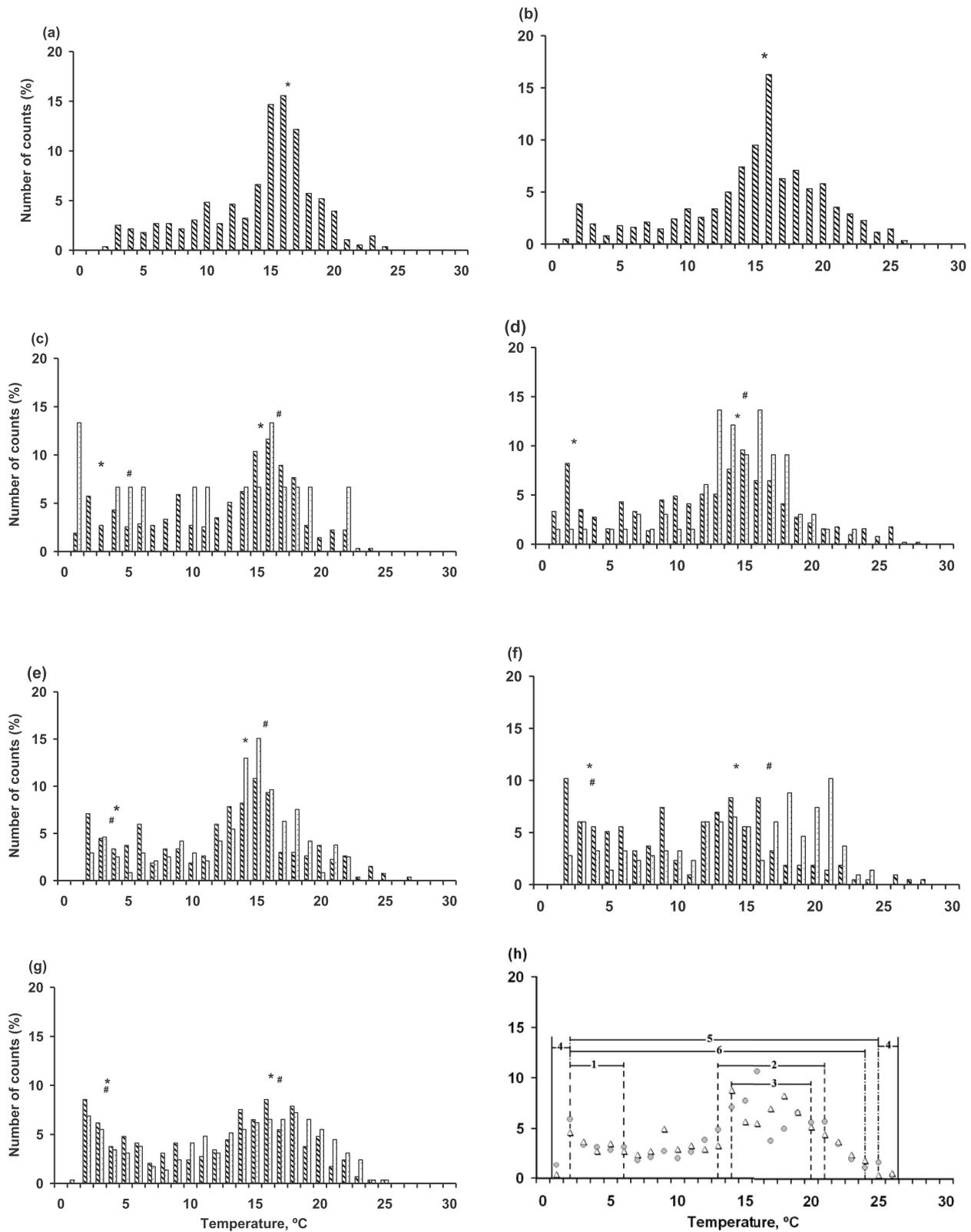
**Fig. 4.** The distribution of the counts of individual *Cyclops kolensis* at each location in the temperature gradient in Experiment 3 (6–13 May 2014). a – Day 1, b – Day 2, c – Day 3, d – Day 4, e – Day 5, f – Day 6–8. \* – Average preferred temperatures. 1,2 – The Final Thermal Preferendum (FTP) equals the Optimum Thermal Conditions (OTC), 3 – Pessimal Temperatures, 4 – Temperature of normal performance (TNP).

to four different statistical tests (Spearman correlation test). Therefore, we can conclude that each individual of *Cyclops kolensis* was able to move throughout the presented temperature range but remained for long periods within two or three specific temperature ranges, which were the same in the different experiments. This pattern was observed regardless of the geographical location and water temperatures of the waterbodies where the *Cyclops* individuals were caught. Thus, *C. kolensis* exhibits the second mechanism of temperature preference. The presence of two ranges of FPT distinguishes *C. kolensis* from other species we have studied that belong to the complex of cold-water species (*C. strenuus* and *C. vicinus*).

There are several potential reasons for this behavior. First, it may represent search activity, which has been well studied in fish studies (for example, Nepomnyashchikh and Gremyachikh, 1997; Nepomnyashchikh and Podgornyy, 2003). Second, this behavior may facilitate various life processes (growth, development, nutrition, reproduction) that are optimized at different temperatures. This phenomenon is also well studied in fish (Golovanov, 2013) and may exist in *C. kolensis*, although more research is needed to verify this possibility.

The temperature plasticity of a species is determined by the range of optimal temperatures within which the species is able to perform basic life functions, such as reproduction, growth, development, and feeding. However, the boundaries of optimal temperatures lie within the limits of extreme (limiting) temperatures and within the buffer zones (or stress zones or pessima). Moreover, the values at the upper and lower zones may vary, being physiologically determined. Therefore, with a shift in extreme temperatures for a particular species, the optimum values will shift. According to our data, for *Cyclops kolensis*, extreme temperatures can be considered those below 1 °C and those above 30 °C. These temperatures are avoided by *Cyclops* under experimental temperature-gradient conditions and border the range of tolerance values for the species. The features of the temperature reactions of *C. kolensis* that we discovered, namely, the extended ranges of optimal, tolerant, and critical temperatures, are in good agreement with recent data from the field, which indicate the movement of *C. kolensis* from north to south.

Based on the records in the literature, this movement process began in the second half of the XX century. In the European part of Russia, before the 1950s, *C. kolensis* was not found south of the taiga zone



**Fig. 5.** The distribution of the counts of individual *Cyclops kolensis* at each location in the temperature gradient in 24 April to 9 May 2018. a – Day 2, b – Day 4, c – Day 6, d – Day 8, e – Day 10, f – Day 12, g – Day 14, h – Day 15–18. ▨ – tray 1, □ – tray 2, \* – average elected preferred temperatures in tray 1, # – average preferred temperatures in tray 2. ● – counts from tray 1, Δ – counts from tray 2. 1 and 3 – FTP in tray 2, 4 – Pessimal Temperatures, 5 – Temperature of normal performance (TNP) in tray 1, 6 – TNP in tray 2.

Table 5

Comparison of the distribution of cyclops in two trays of a gradient installation in the experiment 04/24/2018–May 05, 2018 (by average values).

Day	Number of individuals, ind.		Number of counts		r	t	W	K–W test	K–S test
	Tray 1	Tray 2	Tray 1	Tray 2					
6	70 ± 3	5	627	15	0.25 (>0.05)*	6.65 (<0.05) +	2 (<0.05) +	1.6 (>0.05) ++	3.46 (<0.05) +
7	62 ± 4	5	558	53	0.67 (<0.05) **	6.98 (<0.05)	36 (<0.05)	13.1 (<0.05) +	2.91 (<0.05)
8	60 ± 4	5	511	66	0.71 (<0.05)	6.52 (<0.05)	57 (<0.05)	15.7 (<0.05)	2.81 (<0.05)
9	58 ± 2	10	520	83	0.53 (<0.05)	5.79 (<0.05)	106 (<0.05)	11.4 (>0.05)	2.67 (<0.05)
10	34 ± 3	30 ± 3	268	239	0.75 (<0.05)	0.47 (>0.05) ++	291 (>0.05) ++	21.0 (>0.05)	0.97 (>0.05) ++
11	36 ± 3	31 ± 3	321	281	0.71 (<0.05)	0.59 (>0.05)	340 (>0.05)	24.1 (>0.05)	0.82 (>0.05)
12	31 ± 6	31 ± 2	216	216	0.44 (<0.05)	0.0 (>0.05)	401 (>0.05)	18.6 (>0.05)	0.80 (>0.05)
13	35 ± 4	33 ± 5	317	301	0.59 (<0.05)	0.25 (>0.05)	342 (>0.05)	20.0 (>0.05)	0.42 (>0.05)
14	32 ± 1	32 ± 2	292	291	0.82 (<0.05)	0.02 (>0.05)	319 (>0.05)	20.5 (>0.05)	0.57 (>0.05)
15	31 ± 2	30 ± 3	283	272	0.72 (<0.05)	0.22 (>0.05)	353 (>0.05)	18.4 (>0.05)	0.97 (>0.05)
16	31 ± 3	30 ± 3	275	245	0.60 (<0.05)	0.64 (>0.05)	243 (>0.05)	21.7 (>0.05)	1.01 (>0.05)

Notes: r – Spearman Rank Correlation (Tray 1/Tray 2); t – t-test to compare means; W – Mann-Whitney (Wilcoxon) W-test to compare medians; K–W test – Kruskal-Wallis test; K–S test – Kolmogorov-Smirnov test. In brackets – P-values. \*>0.05 – indicate not a statistically significant non-zero correlations; \*\*<0.05 – indicate statistically significant non-zero correlations. +<0.05 – there is a statistically significant difference; ++>0.05 – not a statistically significant difference.

(58°38'N) (Rylov, 1948). However, by the 1960s, after occupying the Volgograd reservoir, it spread into the Lower Volga to the dam of the Volga Hydroelectric Power Plant (48°49'N) (Mordukhai Boltovskoy, Dzyuban, 1976) and was even recorded as far south as the Volga delta (46°20'N) (Kosova, 1970). This species is considered one of the most active migrants from northern waterbodies in the Volga reservoir. In the 1980s, *C. kolensis* was a dominant species in the Rybinsk reservoir from November to May (Rivier, 1986), and in recent years, it was dominant there from November until the end of June (up to a temperature of 18–20 °C) (Lazareva, 2010).

This response of *C. kolensis* to temperature confirms the hypothesis (Cavieres et al., 2016) that individuals of a species occupying different environments under contemporary global warming may show plasticity in their thermal strategies, facilitating survival under a wide range of temperatures.

In ectothermic organisms, metabolism, growth and development rate directly depend on the temperature of the habitat; therefore, the upper boundaries of their temperature optima are close to the upper critical temperatures determined by their physiological and biochemical status. This phenomenon has been reported in a number of publications on fish, lizards, insects and other taxa (Huey and Kingsolver, 1989; Angilletta, 2009; Camacho and Rusch, 2017; Cavieres et al., 2016; Sinclair et al., 2016). *Cyclops kolensis* appears to differ from these other taxa, as evidenced by the high temperature plasticity revealed by the polymodality of the preference distribution. The temperature plasticity of any organism is determined by the specificity of biochemical reactions that ensure the resistance of the organism to extreme low and high temperatures. Therefore, it would be valuable to conduct biochemical studies comparing *C. kolensis* with other species of *Cyclops* of the cold-water complex. Such studies can provide insight into the adaptation mechanisms of species that live in the Palearctic and Nearctic and aid predictions of their responses to heat wave events.

## 5. Conclusion

In chronic experiments using a thermogradient installation, it was revealed that individuals of *C. kolensis* were able to move along the entire temperature gradient. However, they preferred two or three specific temperature ranges, regardless of the waterbody or water temperature from which they were collected. The final thermal preferendum of *C. kolensis* reflects the optimum thermal conditions of  $3.7 \pm 1.5^\circ\text{C}$  to  $8.4 \pm 1.05^\circ\text{C}$  and  $16.3 \pm 1.3^\circ\text{C}$  to  $17.0 \pm 2.5^\circ\text{C}$ , the temperature of normal performance of  $2\text{--}4^\circ\text{C}$  to  $21\text{--}25^\circ\text{C}$ , and the pessimal temperatures of  $1\text{--}3^\circ\text{C}$  and  $22\text{--}27^\circ\text{C}$ . These temperature ranges coincide with numerous field observations of the temperature conditions under which the species develops. Our results and the literature describing natural

populations of this species allow us to characterize *C. kolensis* as an ecologically plastic species. This plasticity has allowed *C. kolensis*, despite its predominant development at low water temperatures, to expand its habitat range southwards and adapt to the higher temperatures observed in recent years.

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