

Article

Effects of Long-Term Urban Light Pollution and LED Light Color Temperature on the Behavior of a Holarctic Amphipod *Gammarus lacustris* Sars, 1863

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Abstract

Light pollution is becoming more widespread every year, accompanied by the active use of LED lighting. Currently, the ability of organisms to adapt to this pollution and the potential impact of LED lighting of different color temperatures and intensities on organisms remains poorly understood. In this study, we aimed to find out how long-term light pollution affects the behavior of amphipods *Gammarus lacustris*, and to compare their locomotor activity under different lighting conditions, taking into account the factor of shelter from light. The response of individuals was compared in group and individual experiments under daylight, without light, warm and cold LED light up to 30 lx. The individuals were from two populations: the first is not exposed to light pollution (lake No. 14), while the second is affected (the Angara River within the city of Irkutsk). The locomotor activity of amphipods was assessed in daylight, without light, warm and cold light of 2–2.5 lx and 10–11 lx in the presence and absence of shelters from light. As a result of the experiments, adaptive changes in the reaction of *G. lacustris* to warm light were identified in individuals from the Angara River. The importance of LED light color temperature and warm light intensity in determining amphipod response to light was also confirmed. It was found that warm and cold light have different effects on the behavior of *G. lacustris*, and the presence of shelters from light can reduce the negative impact of light pollution in natural conditions.

Keywords: ALAN; light pollution; amphipods; LED; color temperature



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1. Introduction

Natural light is one of the main factors regulating the biorhythms of many organisms, including aquatic organisms [1,2]. Thus, light is the main ecological factor regulating

the daily vertical migrations of phytoplankton [3], zooplankton [4] and zoobenthos, in particular amphipods [5,6]. The main reason for migration is considered to be the protective-food hypothesis. According to it, representatives of zooplankton and zoobenthos float to the upper layers of water to feed at night, thereby avoiding attacks by predators that rely on vision during the daytime. For the same reason, invertebrate drift is observed at night in river ecosystems [7]. Also, natural light sources can be used by many species to orient themselves in space [8–10]. Illumination during the day ranges from about 100,000 lx to about 800 lx at sunset. At night it reaches about 0.3 lx on a full moon and decreases to about 0.001 lx on a moonless clear night and becomes even smaller in cloudy conditions [1,11,12]. At the same time the correlated color temperature of natural daylight can vary from 2,000 K during sunrise to over 10,000 K with a clear, blue sky [13]. Light levels resulting from light pollution very often exceed natural levels at night. As a result, organisms mistake night for “day”. This leads to changes in the biological rhythms of some organisms and in the functioning of entire ecosystems [1,14].

Over the past decade, the annual growth rate of nighttime sky illumination has increased to almost 10% per year [1]. This trend is likely to continue as LED lighting becomes more widespread due to its greater energy efficiency and affordability [1]. Considering that people tend to settle near water bodies and watercourses, since water is of great importance in human life, aquatic ecosystems are subject to strong anthropogenic pressure, including light pollution [15]. There are two types of light pollution: direct and indirect. Direct pollution occurs when artificial light directly hits the water surface and can reach 1000 times brighter than the full moon [11]. For example, illuminance measurements obtained at the ground level from a typical street light vary from 2 to 30 lx within 20 m of the light source, while illuminance from car headlights can exceed 1,000 lx [16]. Indirect pollution is expressed in the form of sky glow, which occurs due to the propagation of artificial light in the atmosphere. It can reach brightness hundreds of times greater than that of the unpolluted sky [17]. In addition, skyglow is enhanced by cloud coverage, so for example, it was enhanced by a factor of 10.1 for one location inside of Berlin and by a factor of 2.8 at 32 km from the city center [18]. Overall, both direct and indirect light pollution have a strong impact on freshwater ecosystems, threatening their biodiversity [1].

Exposure to light pollution can disrupt important behavioral and physiological traits in species that are primarily active at night due to diurnal predators [19]. Even low light levels have been shown to limit vertical migrations of organisms [4,20], and the lights from the ships caused not only vertical but also horizontal movement of arctic zooplankton from artificial light [21]. A variety of experiments show that the effects of different artificial light sources are species-specific, and changes in the behavior of organisms can negatively affect their survival, growth and reproduction [22]. In addition, artificial light, depending on its spectral composition, can have different effects on the behavior [23] and physiology of organisms [24]. In turn, changes in the behavior and physiology of organisms, in the structure and composition of communities [25] due to artificial light sources can lead to disruption of the processing of organic material and the transfer of matter and energy within aquatic ecosystems. However, it is known that ecosystems interact with each other, and thus changes in one ecosystem due to light pollution will likely also affect nearby ecosystems [26]. Although there is sufficient research to demonstrate the negative impact of light pollution on ecosystems, the question of the ability of organisms and ecosystems to adapt to this pollution remains open [27].

To date, there have been relatively few studies that have compared the responses of organisms in aquatic ecosystems that are not exposed to light pollution and those that are exposed to it over a long period of time in natural conditions. However, these few studies have shown a dependence of the structure and composition of organisms on the

level of light pollution [25,28]. A number of examples clearly demonstrate the impact of light pollution on certain species. For example, increasing levels of light pollution reduced the abundance and size of the amphipod *Talitrus saltator* (Montagu, 1808) [29], and also reduced the survival and size of the fish *Amphiprion chrysopterus* Cuvier, 1830 [30]. In turn, in relation to sea urchins *Paracentrotus lividus* (Lamarck, 1816) [31], light pollution increased locomotor activity. In relation to the crab *Neohelice granulata* (Dana, 1851), light pollution decreased the proportion of time spent feeding and sheltering in burrows, but increased the time they spent servicing their burrows [32].

Since there is virtually no data in the literature on the long-term effects of light pollution on aquatic organisms, this study was primarily aimed at (1) studying of the long-term effects of light pollution on amphipods of the species *Gammarus lacustris* Sars, 1863. This species is Holarctic and inhabits a wide range of water bodies, and is also an object of industrial fishing [33]. In addition, different effects of light sources of different spectral composition, but not artificial light intensities, on individuals within the same species have been previously demonstrated for amphipods [6,22,23,34–36]. Also, in connection with the spread of LED lighting in street infrastructure, it makes sense to find out the effect of LED lighting with different color temperatures on organisms, namely warm and cold types of lighting. Warm white light is characterized by a low color temperature (up to 4000 K), while cold white light is characterized by a high color temperature (around 6000 K) [13,37]. We have not found any similar studies for amphipods in the literature, but another study conducted earlier showed that the behavior of Baikal amphipods can be determined by the color temperature of light [38]. Therefore, this work was also aimed at (2) studying the influence of low light levels, color temperature of light and the presence of light shelters on the locomotor activity of *G. lacustris*. Accordingly, the aim of this study was to compare the responses of *G. lacustris* amphipods to different lighting conditions, with and without long-term exposure to light pollution. Additionally, the study aimed to evaluate the locomotor activity of amphipods under different lighting conditions, taking into account the shelter factor, and to compare the effects of warm and cold LED light on the behavior of amphipods.

2. Materials and Methods

2.1. Capture and Acclimation of Amphipods

For the experiments, individuals from two different populations were used, namely, Lake No. 14 and the Angara River (Figure 1). Lake No. 14 is located approximately 1.5 km from the village of Bolshiye Koty, located on the shoreline of Lake Baikal. Lake No. 14 is one of the artificially created reservoirs as a result of gold mining carried out on Lake Baikal in the 19th century. This lake is located in a forest where there is no direct or indirect light pollution. Individuals from the Angara River were collected in the area of the Upper Embankment and the Academic Bridge in the city of Irkutsk. The Angara River within the city of Irkutsk has been exposed to both direct (light sources on the bridge and along the embankment) and indirect (sky glow in the city) light pollution for a long period of time. Comparison of the values of intensity of stable nighttime light radiation in Bolshiye Koty Bay (mean = 45.3 W/cm²/sr, median = 49.1 W/cm²/sr) and along the Upper Angara Embankment (mean = 1.4 W/cm²/sr, median = 1.5 W/cm²/sr) using Earth remote sensing data showed differences in average intensity of more than 30 times [39]. Direct measurements of the illumination level and color temperature of street lamps located near the amphipod collection site were also carried out on the Upper Angara Embankment.

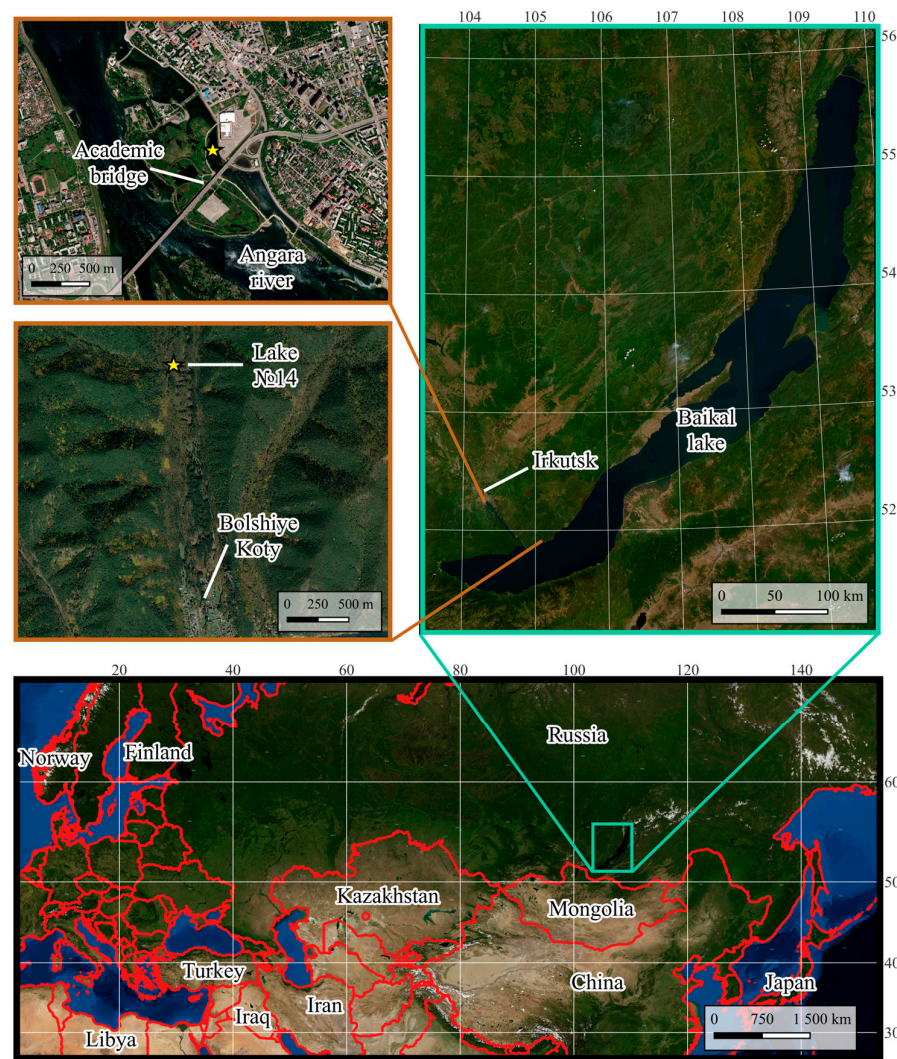


Figure 1. Places of capture (yellow stars) of *G. lacustris* individuals.

For the study, only adult individuals of both sexes were caught using a hydrobiological net in July 2024. Acclimation of individuals was carried out under constant aeration and a water temperature of 16 °C for a week in laboratory conditions. Amphipods were kept in 18 cm × 11.5 cm × 12 cm aquariums (no more than 25 individuals per aquarium). For the maintenance of individuals, tap water was used that had been left to stand for 24 h, and was completely changed in the aquariums every 3 days. The amphipods were fed with dried *Gammarus* sp. after changing the water in the aquariums. These conditions for keeping amphipods are standard at the Institute and are used for conducting experiments, including those lasting at least two weeks [36,38]. In total, at least 250 amphipods were captured from each population for experiments in which the behavior of individuals from different populations under different light conditions was compared. At least 150 individuals were also captured from Lake No. 14 to assess the locomotor activity of amphipods under different lighting conditions with the presence of shelters from light in aquariums. It is worth noting that experiments on the locomotor activity of amphipods without shelters in aquariums were conducted a year earlier (also in July), for which at least 150 individuals were also caught from Lake No. 14, which were then acclimated under the same conditions.

During the acclimation period, the lighting regime for individuals from Lake No. 14 was set at D:N 12:12 h, and for individuals from Angara D:L 12:12 h (D—daylight (from 9:00 to 21:00), N—night without lighting, L—artificial lighting at night). Daylight was provided by overhead lighting in the laboratory and incident light from the window and

was over 70 lx. The color temperature was about 5800 K. To create artificial lighting at night, a video light (YN300 III Pro LED, Shenzhen, China) with a color temperature of 4000 K (150 3200 K LEDs and 1,505,500 K LEDs were lit at the same time) was used, which created an illumination level of about 0.7 lx. This illumination level corresponds to measurements obtained along the coastline on the Upper Embankment during the dark hours of the day (values varied from 0 to 1.6 lx). Light levels were measured using a CEM DT-8809A lux meter (CEM, Macao, China), and color temperature was measured using an OPPL Light-master-II spectrum analyzer (OPPLE, Shanghai, China).

2.2. Comparison of the Behavior of Individuals from Different Populations

To compare the behavior of individuals from different populations under different lighting conditions, group and individual experiments were conducted using a T-shaped aquarium, 10 cm high (Figure 2). At the end of the aquarium, a CN-20FC video light (NanGuang, Shantou, China) was placed with the ability to emit cold (5600 K) or warm (3200 K) light. This resulted in a light gradient from 0.1 lx to 30 lx being created along the long part of the aquarium (100 cm $\times$ 10 cm). In two short branches of the aquarium (15 cm $\times$ 10 cm) the illumination level was 0 lx. Thus, 5 illumination zones were identified in the aquarium: 0 lx, 0.1–1 lx, 1–10 lx, 10–20 lx and 20–30 lx. In group experiments, 20 amphipods from one or another population were simultaneously placed in a 0.1–1 lx zone of the aquarium (a total of 5 replicates for each population). Then the number of amphipods in each illumination zone was noted (distribution of 20 individuals across 5 zones of the aquarium) by manual visual counting in the 1st, 3rd, 5th, 7th and 10th minutes of observation. In individual experiments, instead of 20 individuals, only one was released into the 0.1–1 lx zone (10 replicates for each population), and the choice of the preferred zone by the individual was also noted in the 1st, 3rd, 5th, 7th, and 10th minutes of observation. Experiments were conducted using warm or cold light in a completely darkened laboratory at night (illumination 0 lx). Experiments were also conducted in the dark without the use of lighting and in the daytime with natural lighting (the long part of the aquarium was illuminated by daylight evenly; the short branches of the aquarium were darkened). This experimental design was also previously described by us in a study with another species of amphipod [39].

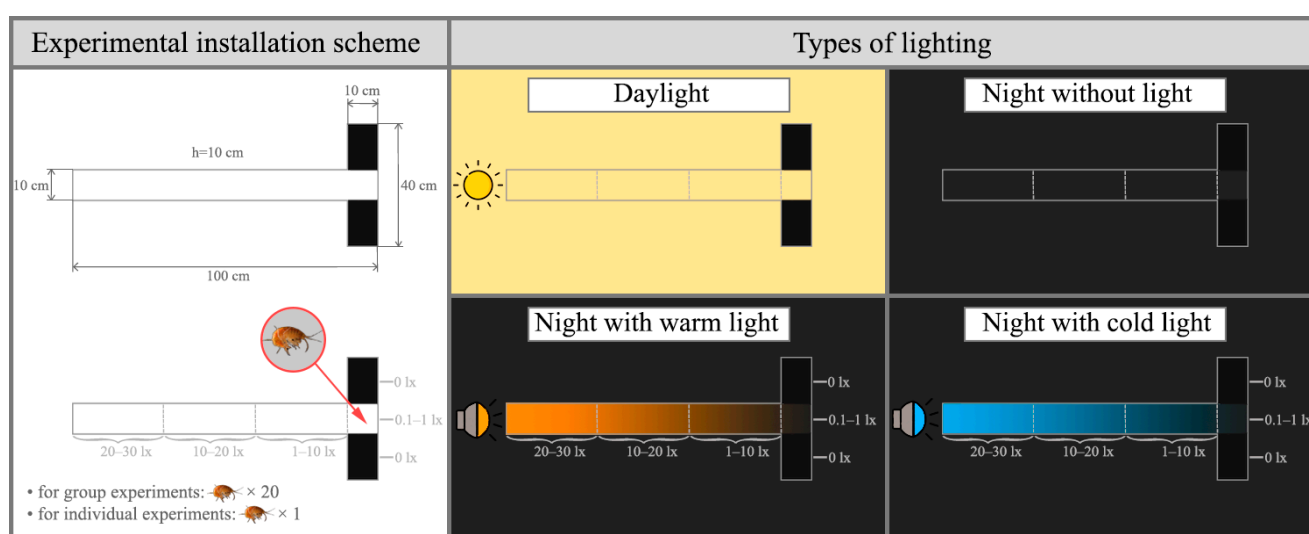


Figure 2. Design of experiments to compare the behavior of individuals from different populations.

2.3. Evaluation of Amphipod Locomotor Activity

For this experiment, only individuals from Lake No. 14 were used. To assess the locomotor activity, 5 individuals were placed in an aquarium measuring 18 cm × 11.5 cm × 12 cm, above which a video camera with the ability to record video at night (due to infrared illumination) and a CN-20FC video light were placed (Figure 3). A total of 6 experiments were conducted with different types of lighting: daylight, night without light (0 lx), warm 2–2.5 lx, warm 10–11 lx, cold 2–2.5 lx, cold 10–11 lx. Artificial light from lamps in the room and natural light coming from windows (≈ 300 lx, ≈ 6000 K) were used as daylight. For each type of lighting, 4 aquariums were taken with 5 amphipods in each. During the experiments, the movements of amphipods were recorded on a video camera for 15 min in each aquarium. The number of individuals per aquarium was primarily determined by the need to facilitate further manual processing of videos of amphipod movements. But at the same time, to ensure the minimum possible sample size (locomotor activity of 20 individuals) for each experiment, including taking into account the time spent on their implementation. All experiments, except for the experiment with daylight, were carried out in the dark with 0 lx illumination in the laboratory. Video recording (as well as lights in four night experiments with artificial lighting) was turned on 30 min after the individuals were placed in the experimental aquariums. All experiments were repeated, but with stones placed in the aquariums as shelters from the light. The size and unevenness of the stones allowed individuals to swim under them and hide in their shadow from the light. A total of 48 video recordings were obtained: 24 video recordings (4 aquariums × 6 lighting conditions = 24 videos) of 15 min each for experiments without shelters in aquariums and 24 video recordings with shelters.

The video recordings obtained during the experiments were processed in 2025 using the ImageJ program (V. 1.53t) and the MTrackJ plugin (V. 1.5.1). The program was used to track the movements of amphipods in aquariums for 15 min. This was performed by constructing movement tracks for each of the five amphipods in one aquarium. After constructing the amphipod movement tracks, tables were obtained containing numerical values of the amphipods' locomotor activity in the form of the distance they traveled in cm.

2.4. Data Analysis

Data visualization and analysis were performed in 2025 using the R programming language (V. 4.4.2). In group experiments, the non-parametric Kruskal–Wallis test was used to determine whether there were statistically significant differences between amphipod distributions across aquarium zones. A nonparametric Dunn's post hoc test with Holm's correction for multiple comparisons was used to compare pairwise amphipod distributions across light levels, observation times, and light types. The Mann–Whitney test was used to determine statistically significant differences between amphipod populations under different lighting conditions. In individual experiments, Fisher's generalized exact test with FDR correction for multiple comparisons was used to detect statistically significant differences in the frequencies of aquarium zone selection by individuals between lighting conditions or populations.

In experiments on the locomotor activity of amphipods, the nonparametric Kruskal–Wallis test was used to establish the presence of statistically significant differences. For pairwise comparison of distances traveled depending on illumination, a nonparametric Dunn's post hoc test with Holm's correction for multiple comparisons was used. To establish statistically significant differences between two samples, differing in the presence or absence of shelters in aquariums, the Mann–Whitney criterion was used. Differences between samples were considered statistically significant at $p < 0.05$.

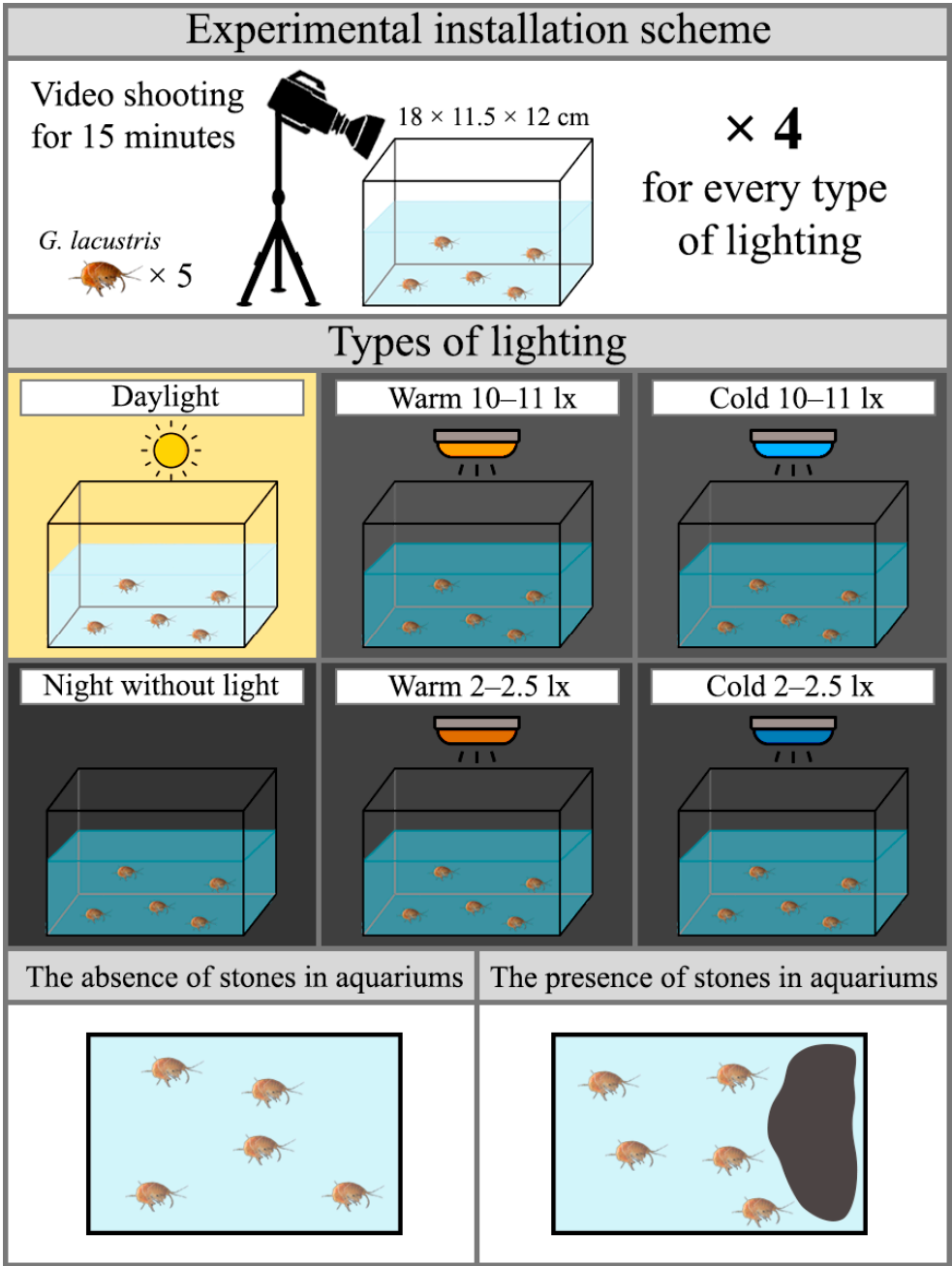


Figure 3. Experimental design for assessing the locomotor activity of amphipods.

3. Results

3.1. Response to Different Lighting Conditions of Individuals from Different Populations in Group Experiments

In experiments with 20 individuals of *G. lacustris* collected from Lake No. 14 (not exposed to light pollution), it was found that lighting conditions influence the distribution of amphipods across the illumination zones in the aquarium (Kruskal–Wallis chi-squared = 10.832, df = 3, *p*-value = 0.01). When comparing samples pairwise, differences were found between daylight and night without light (Figure 4; Table 1).

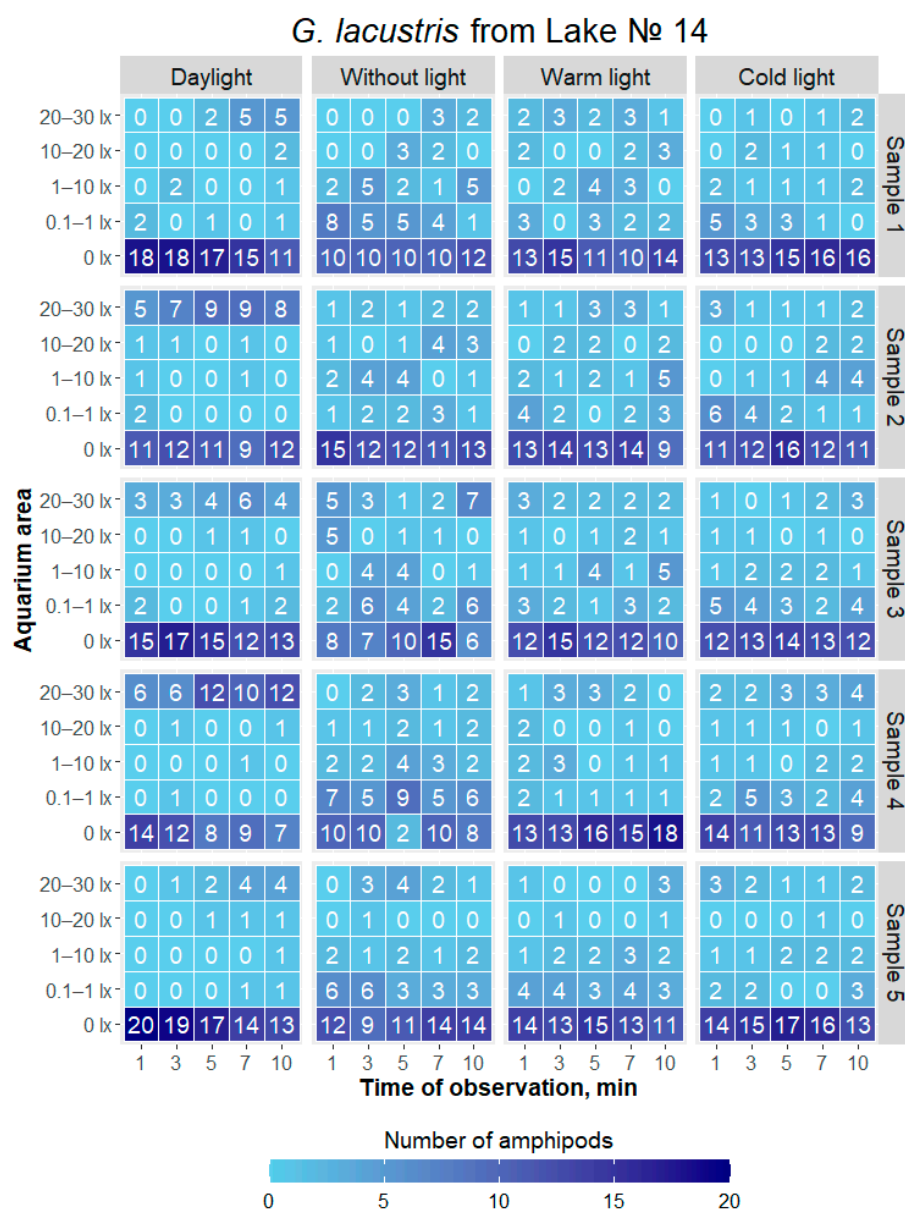


Figure 4. Results of distribution of *G. lacustris* individuals from lake No. 14 across illumination zones in an aquarium depending on observation time, replicates and lighting conditions in group experiments.

Table 1. Results (*p*-values) of comparison using Dunn's test of distributions of *G. lacustris* individuals from lake No. 14 by aquarium zones for the entire observation period depending on lighting conditions in group experiments.

Type of Lighting	Cold Light	Daylight	Without Light
Daylight	0.1	-	-
Without light	0.7	0.01 *	-
Warm light	0.9	0.08	0.9

* Statistically significant differences.

In addition, statistically significant differences were found in the distribution of amphipods between different illumination zones in the aquarium (Table 2). However, a comparison of the distribution of amphipods by aquarium zones depending on the observation time did not reveal significant differences. That is, amphipods were distributed equally across the aquarium zones in the 1st, 3rd, 5th, 7th and 10th minutes of observation.

Table 2. Results (*p*-values) of comparison using Dunn's test of distributions of *G. lacustris* individuals from Lake No. 14 across aquarium zones in group experiments.

Daylight (Kruskal–Wallis Chi-Squared = 88.289, df = 4, <i>p</i>-Value < 2.2×10^{-16})				
Aquarium area	0 lx	0.1–1 lx	1–10 lx	10–20 lx
0.1–1 lx	$1.9 \times 10^{-11} *$	-	-	-
1–10 lx	$2.2 \times 10^{-13} *$	1	-	-
10–20 lx	$1.6 \times 10^{-11} *$	1	1	-
20–30 lx	0.01 *	0.0003 *	$2.5 \times 10^{-5} *$	0.0003 *
Without light (Kruskal–Wallis chi-squared = 73.573, df = 4, <i>p</i>-value = 3.992×10^{-15})				
Aquarium area	0 lx	0.1–1 lx	1–10 lx	10–20 lx
0.1–1 lx	0.002 *	-	-	-
1–10 lx	$5.1 \times 10^{-8} *$	0.08	-	-
10–20 lx	$8.2 \times 10^{-14} *$	0.0001 *	0.15	-
20–30 lx	$2.3 \times 10^{-9} *$	0.02 *	0.6	0.3
Warm light (Kruskal–Wallis chi-squared = 70.742, df = 4, <i>p</i>-value = 1.582×10^{-14})				
Aquarium area	0 lx	0.1–1 lx	1–10 lx	10–20 lx
0.1–1 lx	$4.3 \times 10^{-6} *$	-	-	-
1–10 lx	$4.3 \times 10^{-8} *$	0.9	-	-
10–20 lx	$1.7 \times 10^{-14} *$	0.017 *	0.16	-
20–30 lx	$2.3 \times 10^{-8} *$	0.9	0.9	0.17
Cold light (Kruskal–Wallis chi-squared = 78.753, df = 4, <i>p</i>-value = 3.2×10^{-16})				
Aquarium area	0 lx	0.1–1 lx	1–10 lx	10–20 lx
0.1–1 lx	$9.7 \times 10^{-5} *$	-	-	-
1–10 lx	$7.7 \times 10^{-9} *$	0.22	-	-
10–20 lx	$2.9 \times 10^{-16} *$	0.0002 *	0.08	-
20–30 lx	$3.5 \times 10^{-8} *$	0.25	0.7	0.049 *

* Statistically significant differences.

For *G. lacustris* caught in the Angara River backwater (subject to light pollution), it was also found that lighting conditions affect the distribution of amphipods across illumination zones in the aquarium (Kruskal–Wallis chi-squared = 51.46, df = 3, *p*-value = 3.904×10^{-11}). When comparing paired samples, differences were found between the following types of lighting: daylight and without light, daylight and cold, without light and warm, without light and cold (Figure 5; Table 3).

Table 3. Results (*p*-values) of comparison using Dunn's test of distributions of *G. lacustris* individuals from the Angara River by aquarium zones for the entire observation period depending on lighting conditions in group experiments.

Type of Lighting	Cold Light	Daylight	Without Light
Daylight	0.007 *	-	-
Without light	0.0004 *	$2.6 \times 10^{-11} *$	-
Warm light	0.2	0.1	$2 \times 10^{-6} *$

* Statistically significant differences.

For amphipods from Angara, as well as for amphipods from Lake No. 14, statistically significant differences were found between different illumination zones in the aquarium (Table 4). Moreover, no statistically significant differences were found between the minutes of observation.

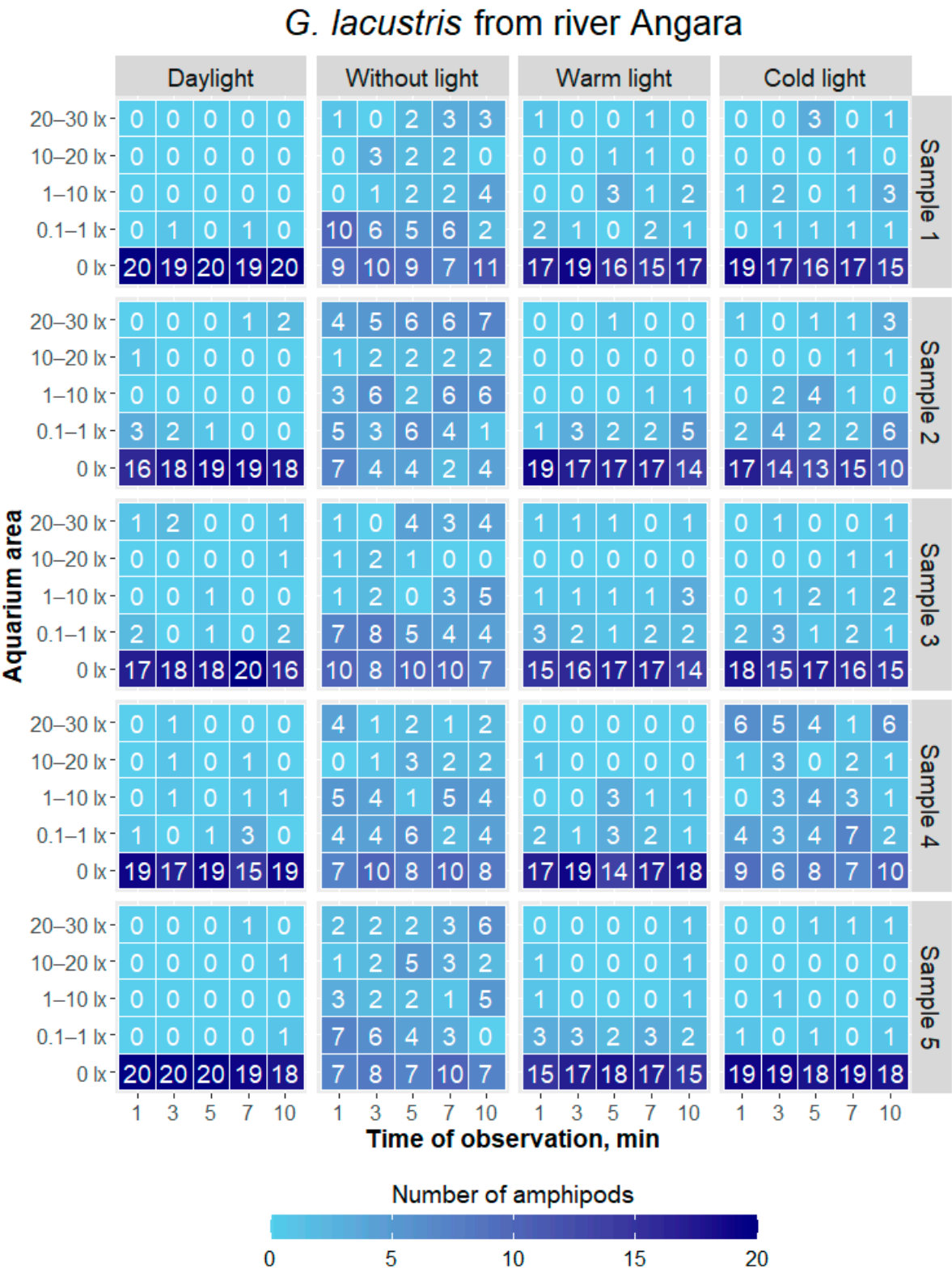


Figure 5. Results of distribution of *G. lacustris* individuals from the Angara River across illumination zones in an aquarium depending on observation time, replicates and lighting conditions in group experiments.

Table 4. Results (*p*-values) of comparison using Dunn’s test of distributions of *G. lacustris* individuals from the Angara River by aquarium zones in group experiments.

Daylight (Kruskal–Wallis Chi-Squared = 78.586, df = 4, <i>p</i>-Value = 3.472×10^{-16})				
Aquarium area	0 lx	0.1–1 lx	1–10 lx	10–20 lx
0.1–1 lx	$1.6 \times 10^{-7} *$	-	-	-
1–10 lx	$5.6 \times 10^{-13} *$	0.3	-	-
10–20 lx	$2.3 \times 10^{-12} *$	0.4	1	-
20–30 lx	$8.5 \times 10^{-11} *$	0.9	1	1
Without light (Kruskal–Wallis chi-squared = 61.508, df = 4, <i>p</i>-value = 1.398×10^{-12})				
Aquarium area	0 lx	0.1–1 lx	1–10 lx	10–20 lx
0.1–1 lx	0.017 *	-	-	-
1–10 lx	$1.5 \times 10^{-6} *$	0.1	-	-
10–20 lx	$3.5 \times 10^{-12} *$	0.0001 *	0.11	-
20–30 lx	$1.1 \times 10^{-6} *$	0.1	0.9	0.11
Warm light (Kruskal–Wallis chi-squared = 92.921, df = 4, <i>p</i>-value < 2.2×10^{-16})				
Aquarium area	0 lx	0.1–1 lx	1–10 lx	10–20 lx
0.1–1 lx	0.004 *	-	-	-
1–10 lx	$7.1 \times 10^{-9} *$	0.02 *	-	-
10–20 lx	$2.9 \times 10^{-15} *$	$8.5 \times 10^{-6} *$	0.1	-
20–30 lx	$1.2 \times 10^{-13} *$	$7.1 \times 10^{-5} *$	0.2	0.6
Cold light (Kruskal–Wallis chi-squared = 72.433, df = 4, <i>p</i>-value = 6.952×10^{-15})				
Aquarium area	0 lx	0.1–1 lx	1–10 lx	10–20 lx
0.1–1 lx	$1.9 \times 10^{-5} *$	-	-	-
1–10 lx	$8.3 \times 10^{-9} *$	0.38	-	-
10–20 lx	$2.7 \times 10^{-14} *$	0.007 *	0.35	-
20–30 lx	$4.7 \times 10^{-9} *$	0.38	0.9	0.36

* Statistically significant differences.

Comparison of the distributions of amphipods from Lake No. 14 and the Angara River under different lighting conditions showed statistically significant differences for daylight and warm lighting (Figure 6; Table 5). That is, individuals caught in the Angara backwater (exposed to light pollution) statistically significantly avoided both natural daylight and artificial warm light to a greater extent, compared to individuals from Lake No. 14.

Table 5. Results (*p*-values) of comparison using the Mann–Whitney test of the distribution of *G. lacustris* individuals from Lake No. 14 and the Angara River by aquarium zones depending on lighting conditions in group experiments.

Daylight (W = 6701.5)		Without Light (W = 8563)		Warm Light (W = 6074.5)		Cold Light (W = 6946.5)	
	River Angara		River Angara		River Angara		River Angara
Lake № 14	0.03 *	Lake № 14	0.18	Lake № 14	0.001 *	Lake № 14	0.12

* Statistically significant differences.

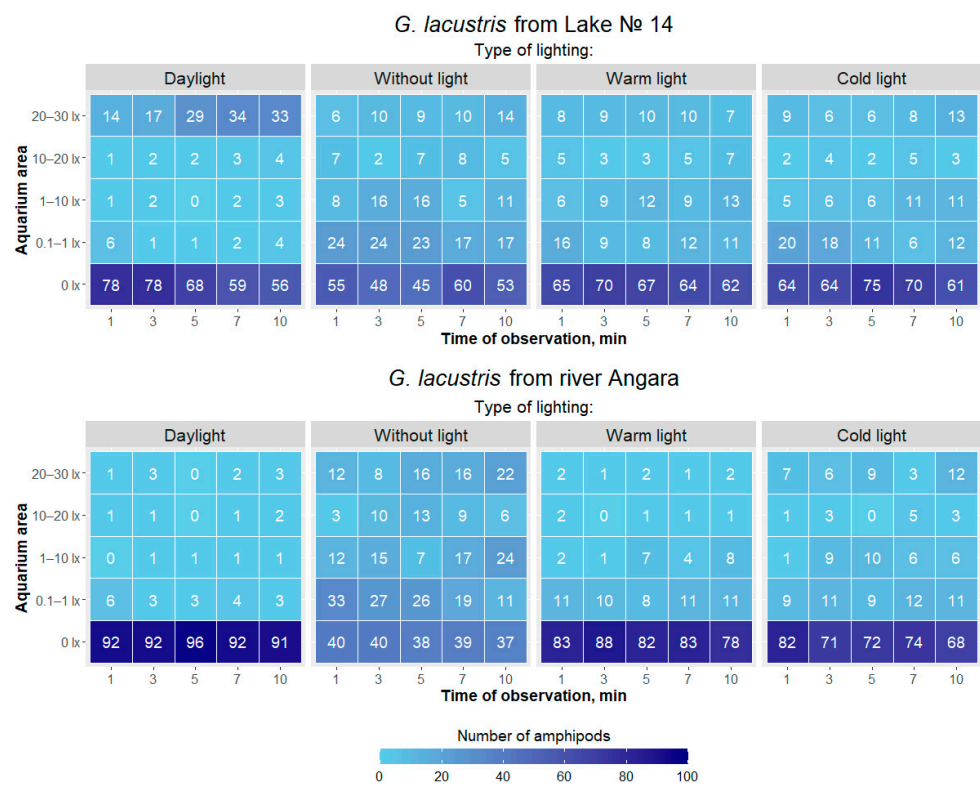


Figure 6. Total distributions of *G. lacustris* individuals from Lake No. 14 and the Angara River by illumination zones in the aquarium depending on the observation time and lighting conditions in group experiments.

3.2. Response to Different Lighting Conditions of Individuals from Different Populations in Individual Experiments

First, about the results of experiments involving *G. lacustris* individuals (individuals were placed in the aquarium individually), caught in Lake No. 14 (not exposed to light pollution). It was found that lighting conditions affect the frequency of individuals choosing lighting zones in the aquarium. In pairwise comparison of samples, differences were found between the following lighting conditions: daylight and cold, daylight and warm, without light and cold, without light and warm (Figure 7; Table 6).

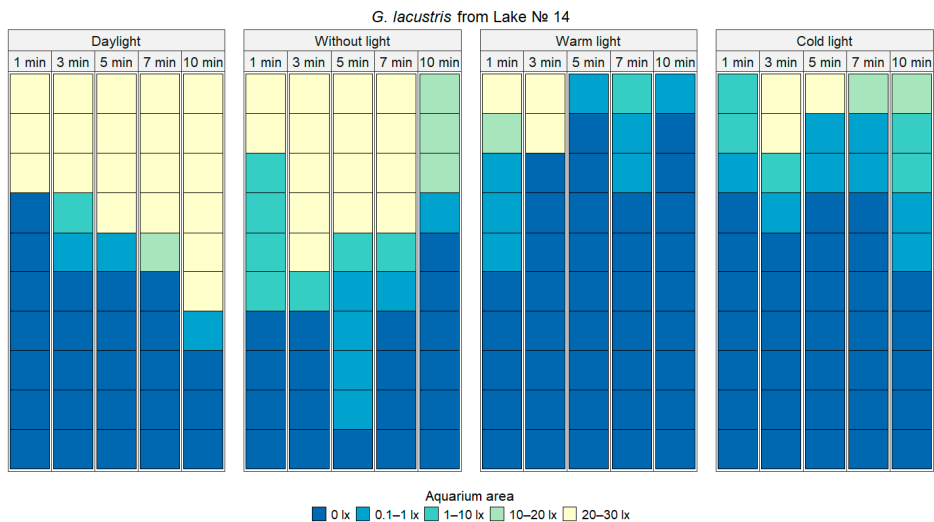


Figure 7. Results of aquarium zone selection by *G. lacustris* individuals from Lake No. 14 depending on observation time, replicates and lighting conditions in individual experiments.

Table 6. Results (*p*-values) of comparison using Fisher's test of the frequencies of aquarium zone selection by *G. lacustris* individuals from Lake No. 14 over the entire observation period depending on lighting conditions in individual experiments.

Type of Lighting	Cold Light	Daylight	Without Light
Daylight	0.0005 *	-	-
Without light	0.01 *	0.1	-
Warm light	0.5	0.0005 *	0.0005 *

* Statistically significant differences.

For *G. lacustris* caught in the Angara backwater (subject to light pollution), it was also found that lighting conditions influence the frequency of individuals' choice of aquarium zones. Differences were found in pairwise comparisons of samples between daylight and without light, without light and cold, without light and warm (Figure 8; Table 7).

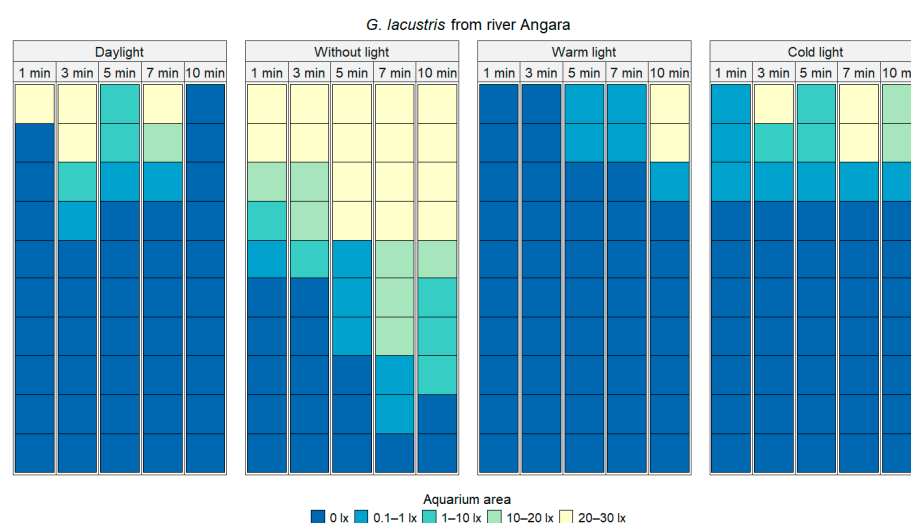


Figure 8. Results of selection of aquarium zones by *G. lacustris* individuals from the Angara backwater depending on the observation time, replicates and lighting conditions in individual experiments.

Table 7. Results (*p*-values) of comparison using Fisher's test of the frequencies of aquarium zone selection by *G. lacustris* individuals from the Angara backwater over the entire observation period depending on lighting conditions in individual experiments.

Type of Lighting	Cold Light	Daylight	Without Light
Daylight	0.6	-	-
Without light	0.0007 *	0.0001 *	-
Warm light	0.2	0.2	10^{-7} *

* Statistically significant differences.

Comparison of the frequencies of choosing aquarium zones by amphipods from Lake No. 14 and the Angara River under different lighting conditions showed statistically significant differences only for daylight (Table 8). That is, individuals caught in the Angara backwater and exposed to light pollution statistically significantly avoided natural daylight to a greater extent, compared to individuals from Lake No. 14.

Table 8. Results (p -values) of comparison using Fisher's test of the frequencies of aquarium zone selection by *G. lacustris* individuals from Lake No. 14 and the Angara River depending on the place where the amphipods were caught and lighting conditions in individual experiments.

Daylight		Without Light		Warm Light		Cold Light	
Lake № 14	River Angara 0.0008 *	Lake № 14	River Angara 0.7	Lake № 14	River Angara 0.6	Lake № 14	River Angara 0.9

* Statistically significant differences.

3.3. Locomotor Activity of Individuals Under Different Lighting Conditions

It was shown that lighting conditions affect the locomotor activity of individuals both in the absence of shelters from light in aquariums (Kruskal–Wallis chi-squared = 69.517, $df = 5$, p -value = 1.292×10^{-13}), and in their presence (Kruskal–Wallis chi-squared = 29.139, $df = 5$, p -value = 2.177×10^{-5}). When comparing the distances traveled by amphipods using the Dunn test, differences were found between different types of lighting. Thus, differences were found between warm and cold types of lighting at both intensities, as well as between the intensities of warm light in experiments without shelters in aquariums (Figure 9; Table 9).

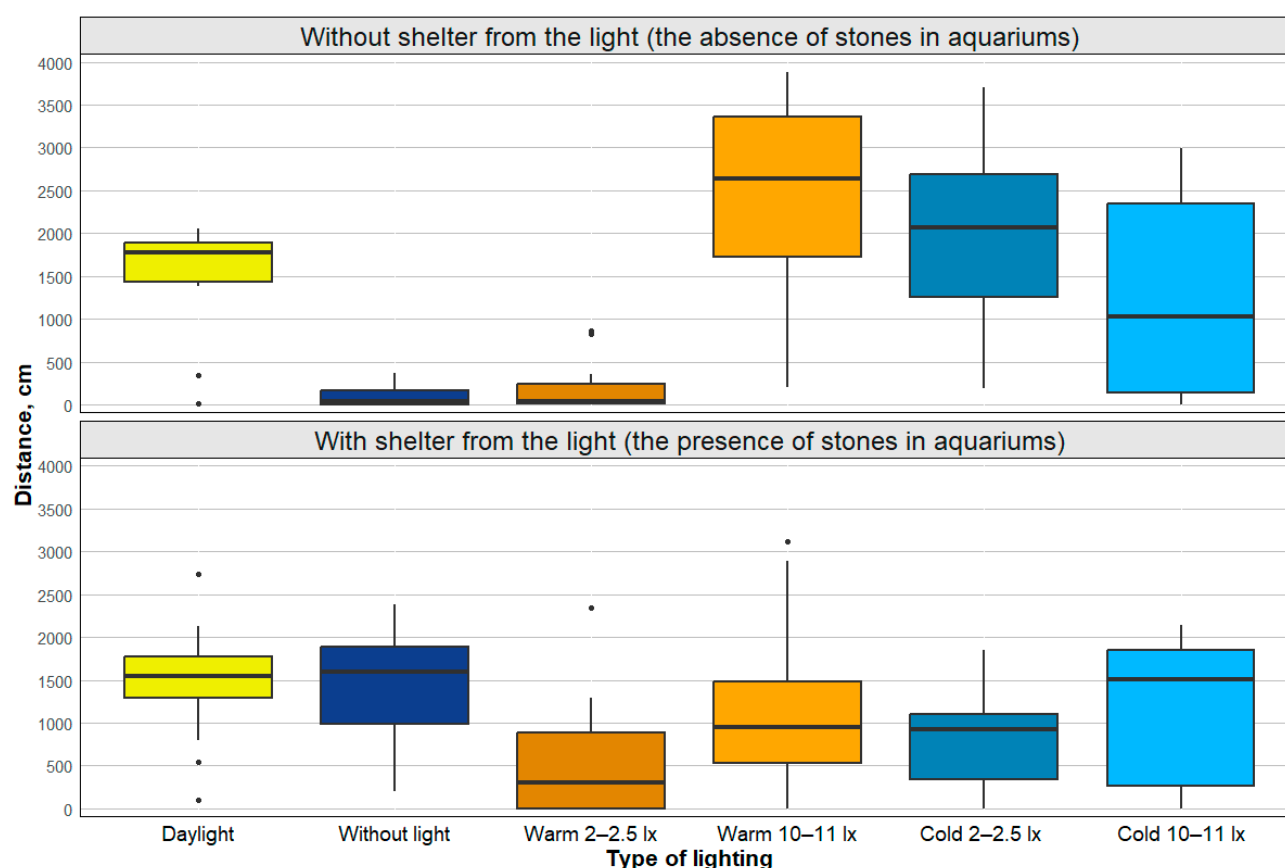


Figure 9. Distance traveled by *G. lacustris* individuals depending on lighting conditions in the absence and presence of shelters in the form of stones in aquariums.

Table 9. Results (*p*-values) of Dunn’s test for pairwise comparison of distances traveled by amphipods of the species *G. lacustris* depending on lighting conditions.

Without Shelter from the Light (the Absence of Stones in Aquariums)					
Type of lighting	Daylight	Cold 10–11 lx	Cold 2–2.5 lx	Without light	Warm 10–11 lx
Cold 10–11 lx	1	-	-	-	-
Cold 2–2.5 lx	1	0.4	-	-	-
Without light	0.0001 *	0.002 *	$1.4 \times 10^{-6} *$	-	-
Warm 10–11 lx	0.2	0.03 *	1	$2.5 \times 10^{-9} *$	-
Warm 2–2.5 lx	0.0004 *	0.006 *	$5.8 \times 10^{-6} *$	1	$1.4 \times 10^{-8} *$
With shelter from the light (the presence of stones in aquariums)					
Type of lighting	Daylight	Cold 10–11 lx	Cold 2–2.5 lx	Without light	Warm 10–11 lx
Cold 10–11 lx	1	-	-	-	-
Cold 2–2.5 lx	0.01 *	0.2	-	-	-
Without light	1	1	0.02 *	-	-
Warm 10–11 lx	0.5	1	1	0.6	-
Warm 2–2.5 lx	0.0003 *	0.01 *	1	0.0005 *	0.1

* Statistically significant differences.

Using the Mann–Whitney test, the values of the distance traveled by amphipods were compared under equal lighting conditions but differing in the presence of shelter in the aquariums. As a result of these comparisons, significant differences were obtained under the conditions of without light, cold 2–2.5 lx lighting and warm 10–11 lx lighting (Table 10).

Table 10. Results of comparison using the Mann–Whitney test of distances traveled by amphipods of the species *G. lacustris* depending on the presence of shelters.

Type of Lighting	<i>p</i> -Value
Daylight	0.2
Cold 10–11 lx	0.7
Cold 2–2.5 lx	0.0002 *
Without light	$2.757 \times 10^{-10} *$
Warm 10–11 lx	0.0008 *
Warm 2–2.5 lx	0.4

* Statistically significant differences.

3.4. Measuring Street Lighting Characteristics

Near the place where the amphipods were caught in the backwater of the Angara River, the illumination level and color temperature of light from street lamps were measured (under the lamps, near the ground). The average color temperature of light was 2254 ± 69 K, and the illumination level was 21.8 ± 2.5 lx. In general, almost the entire Upper Embankment of the Angara River is illuminated at night by lanterns with warm light (Figure 10).

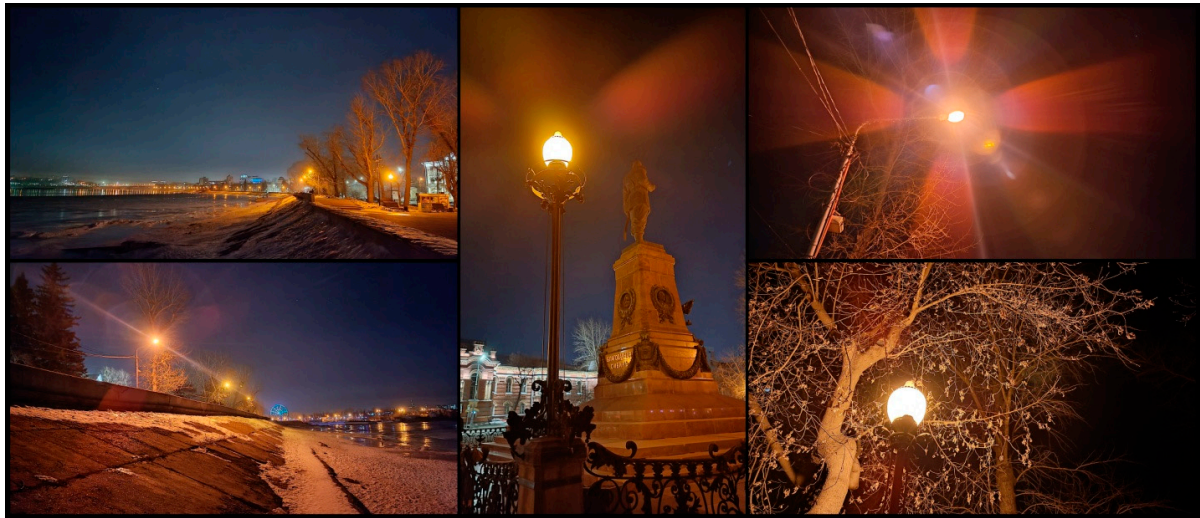


Figure 10. Lighting on the Upper Embankment of the Angara River within the city of Irkutsk, consisting mainly of warm light sources. The photos were taken after full sunset.

4. Discussion

As a result of comparing the behavior of amphipods from different populations under different lighting conditions, it was shown that individuals of *G. lacustris* from a population exposed to urban light pollution in the Angara River statistically significantly avoid natural daylight and artificial warm lighting to a greater extent. It is worth noting that the level of light pollution on the Angara River, where the amphipods were caught, is more than 30 times higher than the values obtained for Bolshiye Koty Bay on Lake Baikal, where there is no indirect impact of light pollution, and the direct impact is practically not expressed [39]. For Lake No. 14, located in the forest 1.5 km from the village of Bolshiye Koty, this difference may be even higher. However, for this study, we did not conduct such measurements using remote sensing data.

Differences in amphipod behavior during the daytime may be associated with the indirect influence of light pollution. For example, when it acts at night, it can inhibit the activity of organisms [23,34,40,41]. As a result, organisms can partially change their daily activity, including during the daytime [7,23]. However, to confirm this hypothesis, it is necessary to conduct a separate study that would include daily observation of the activity of amphipods. At the moment, we associate the change in the behavior of *G. lacustris* during the daytime to a greater extent with increased pressure from predators on the Angara. For individuals from Lake No. 14, the only natural predators are minnows *Phoxinus phoxinus* Linnaeus, 1758. It is worth noting here that they probably pose a danger only to juvenile *G. lacustris*. We assume this because the adult individuals from Lake 14 that we used in this study were active during the daytime in both types of experiments (both in the experiments comparing the behavior of individuals from different populations and in the experiments on locomotor activity with and without shelters). During the day, individuals from the Angara are under pressure from both fish and a large number of birds. The Angara River within the city of Irkutsk is a key wintering ground for ducks, whose numbers can reach several tens of thousands [42]. The dominant duck species during this period, *Bucephala clangula* (L., 1758) and *Anas platyrhynchos* L., 1758, actively feed on invertebrates, including amphipods. Year-round pressure from birds and fish both in winter and summer on the amphipod population in the Angara could have led to more active avoidance of open illuminated areas by individuals during the daytime.

The stronger avoidance of warm lighting by individuals from the Angara may be associated with their adaptation to artificial lighting on the Upper Embankment of the

Angara River. The measured values of the color temperature of the light sources on the Upper Embankment closer to the Academic Bridge were 2254 ± 69 K. This indicates that warm lighting predominates in the place where individuals were captured for the study. It is worth noting that mercury vapor lamps are used to illuminate this embankment. The spectrum of these lamps contains ultraviolet waves, while in LED light sources the presence of ultraviolet is not expressed [43]. It is possible that the avoidance of warm light by individuals is associated with their avoidance of ultraviolet radiation as a protective mechanism [44]. In addition, amphipods may have been under increased pressure from their natural predators during the night, as light makes the individuals visible to them. Most likely, individuals that avoided illuminated areas in the Angara backwater to a lesser extent during the night period were subject to both greater UV exposure and greater pressure from predators. This could have led to survival of individuals with a stronger warm light avoidance response. It is worth noting that we obtained similar results with amphipods of the species *Gmelinoides fasciatus* (Stebbing, 1899) in group experiments (using 20 individuals) [39]. Individuals of *G. fasciatus* captured in the Angara backwater also began to avoid natural daylight and artificial warm light to a greater extent, compared to individuals from a population not exposed to light pollution. The results obtained in this and the present studies show that long-term urban light pollution on the Upper Angara Embankment (several decades) caused adaptive changes in the response of amphipods to warm artificial light. Previously, evolutionary changes as a result of long-term urban pollution have been demonstrated for moths, where urban populations became less attracted to artificial lighting [45]. Morphological changes have also been found in moths over a 137-year period [46].

In general, the behavior of individual *G. lacustris* is consistent with the behavior of a group of individuals from both Lake No. 14 and the Angara backwater. However, the presence of statistically significant differences between populations in the behavior of a group of individuals under warm lighting and their absence in individual experiments may indicate bolder behavior of individuals in a group than individually. More secretive behavior of individuals when exposed to light may be related to defense mechanisms in response to potential predators, since the risk of predation towards individuals decreases with increasing group density [47]. In addition, studies with fish have shown that individuals behave more boldly when they are in a group [48,49]. Some differences in group and individual behavior were also found for *G. fasciatus* [39]. The obtained data, namely the differences in the individual and group response of amphipods to light, should be taken into account when conducting experimental studies using amphipods and artificial light, which is often used in toxicological studies [50–52].

It is also worth noting that when comparing the behavior of *G. lacustris* individuals from different populations, we did not find statistically significant differences between the minutes of observation in all experiments. That is, the amphipods were distributed equally across the aquarium zones both in the first minute after the start of the experiment and every two minutes up until the tenth minute. The results for *G. fasciatus* were similar [39]. Based on the data obtained, we conclude that in short-term tests using light and the participation of amphipods, it is sufficient to record their reaction in the first few minutes of observation. Overall, our finding is consistent with other studies that have shown that 2 min (or less) is sufficient to detect a response to light in motile amphipods [38,50–52]. This time was sufficient to identify differences in the behavior of amphipods from populations not exposed to and exposed to long-term urban light pollution.

Regarding the experiments on the locomotor activity of *G. lacustris*, it can be noted that this species is active during the daytime both with and without shelters in the aquariums. This is confirmed by our results from group and individual experiments with individuals

from Lake No. 14. At the same time, we were somewhat puzzled by the results obtained during the night period without light, namely in experiments with the absence of shelters in aquariums. Considering that in all other experiments of this study, individuals demonstrated activity during the night period without light, including similar activity to daytime activity in individuals from Lake No. 14, we suggest that the low locomotor activity of individuals at night without shelters in aquariums may be associated with the following factors. Firstly, there is the combined effect of the lack of hiding places in the aquariums and the use of infrared light during night (without light) video recording. We were unable to find any data on the effect of infrared light on the behavior of *G. lacustris*, and we can only speculate that direct long-wave light may limit the activity of individuals. Apparently, the presence of rock shelters reduces the impact of infrared light. Previously, various studies have demonstrated the ability of artificial light to suppress the activity of organisms [23,34,40,41,53–55]. And although studies note the fact that crustaceans' eyes are not sensitive to infrared light [56,57], one species of Baikal amphipods, *Macrohectopus branickii* (Dybowsky, 1874), was found to be actively attracted by long-wave (infrared) light [58]. In experiments comparing the behavior of individuals from different populations, there were also no shelters in the form of stones, but at the same time there was no video recording with infrared illumination. Second, the experiments without the use of shelters in aquariums were conducted a year earlier, but in the same month, whereas all other experiments in this study were conducted in the same year and month. And the differences in the nocturnal activity of amphipods could be associated with seasonal or interannual differences in environmental parameters. However, this does not allow us to make any assumptions about the low activity of amphipods during the night period, especially given the approximately equal locomotor activity of amphipods during the daytime in all experiments. Therefore, the questions of the nocturnal activity of amphipods *G. lacustris* and their sensitivity to infrared radiation remain open. And, as we have already noted above, to answer these questions, additional research into the daily activity of amphipods is necessary.

In experiments without shelters in aquariums, statistically significant differences in locomotor activity were found between warm and cold types of lighting at both 2–2.5 lx and 10–11 lx. Moreover, the greatest locomotor activity at 2–2.5 lx was observed under cold lighting, and at 10–11 lx—under warm lighting. Overall, the results obtained confirm our hypothesis that the behavior of amphipods will be determined by the color temperature of the LED light, which was also demonstrated by us in another study [38]. In addition, in these experiments we were able to confirm the significance of the illumination level for warm light in determining the behavior of amphipods (statistically significant differences were obtained between 2–2.5 lx and 10–11 lx for warm light but were not obtained for cold light). In a previous study we were unable to confirm the significance of white light intensity (4000 K), but we also obtained borderline results for one amphipod species for warm light (3000 K) [38]. The obtained diverse data once again confirm the species-specificity of organisms' reactions to artificial light [6,22,23,34,36,38]. This species-specificity must be taken into account when developing and planning lighting infrastructure near water bodies to the extent possible [1].

The presence of shelters in aquariums reduced the locomotor activity of amphipods under warm 10–11 lx and cold 2–2.5 lx lighting. Increased locomotor activity under these types of lighting without shelters could be associated with stress [22,59] and active search for shelters from light in the aquarium. Overall, this is consistent with the results of experiments comparing the behavior of individuals from different populations, in which amphipods generally tried to avoid warm and cold light. Cold light of 10–11 lx seems to cause less disturbance to amphipods. This may be due to the fact that these lighting

conditions may be perceived by amphipods as daylight in the early hours when the light intensity is still low. It is worth noting that amphipods have extremely low locomotor activity under 2–2.5 lx warm lighting, both with and without shelters in aquariums. Given that at night without light, the amphipods in the experiments demonstrated moderate activity, it is possible that these lighting conditions inhibit the locomotor activity of amphipods. Similar results have been previously shown for the isopod *Tylos spinulosus* Dana, 1853. The locomotor activity of these isopods was impaired as a result of light pollution [54]. Overall, it is important to note that the presence of shelters from light smoothed out the results of amphipod locomotor activity under different lighting conditions. It is likely that in natural conditions in an environment with a sufficient number of secluded places (rocks, vegetation, structures, etc.) the negative impact of light pollution on individual organisms can be reduced.

It is worth noting that statistically significant differences in the behavior of amphipods under warm and cold lighting are absent in experiments comparing the behavior of individuals from different populations. This to some extent contradicts the results obtained in experiments on locomotor activity, where these differences were obtained. In any case, both types of lighting influence the behavior of *G. lacustris*, causing individuals to avoid light or limit their locomotor activity. Changes in the migratory activity of amphipods in natural conditions due to light pollution can disrupt the exchange of matter and energy of entire aquatic ecosystems or their local areas [4,60,61]. In addition, disruption of amphipod locomotor activity and attraction of individual specimens to light may lead to disruption of predator-prey interactions in aquatic ecosystems [32,35,49,62,63]. This is due to the fact that artificial light at night makes amphipods visible to their natural predators. The potential impact of long-term cool spectrum light pollution on organisms is not yet known. However, it can be assumed that individuals will begin to avoid cool light to a greater extent, as was demonstrated for warm light in the present study. Earlier studies of amphipods demonstrated different responses of individuals within the same species to light of different spectral composition. For example, different responses were observed to light from LED lamps and to light from halogen lamps, as well as to light from high-pressure sodium lamps [6,22,34,35]. In addition, researchers noted a more negative impact of LED light on ecosystems. In the present study, by comparing warm and cold LED light, it is not possible to determine which type of lighting will have a greater or lesser negative effect on amphipods during long-term exposure. However, the results we obtained during the comparison of the behavior of amphipods with and without shelters from light allow us to recommend additional structures for placement in coastal water zones, in particular on the Angara. These structures could create shade and prevent excessive detection of amphipods by predators in areas subject to direct light pollution. The development of such structures requires further research, but perforated small boulders or their analogs could serve as examples. But the most effective way to reduce light pollution in water bodies is to adjust coastal lighting, which includes both reducing the light intensity to the level actually needed and setting the direction of the emitted light [1]. As for the Angara River, the lighting on the Upper Embankment is directed towards the water (Figure 10). And moving the light sources, as well as rotating them by 180°, could reduce the impact of light pollution on the Angara.

One of the shortcomings of this study is that the experiments on amphipods' locomotor activity without shelters in aquariums were conducted a year earlier. All the remaining experiments were conducted at the same time. Considering that for the study in both years individuals were selected in July from the same place, which is subject to minimal anthropogenic influence, and only sexually mature individuals of both sexes were used, we believe that the results of the experiments are comparable. We also consider a shortcoming

of this study to be the fact that during the acclimation of amphipods before the experiments in which the behavior of individuals from different populations was compared, we created artificial light pollution for amphipods from the Angara. The use of artificial light at night during acclimation may have affected the results of experiments with individuals from Angara. However, it is worth noting that during acclimation we used white light (4000 K), and in the experiments—warm (3200 K) and cold (5600 K), and statistically significant differences between populations were found only for warm lighting. At the same time, we believe that the use of artificial light during acclimation was necessary to try to maintain conditions close to natural ones in different populations. We knew that light pollution could potentially have a temporary effect, as shown for the amphipod *Americorchestia longicornis* (Say, 1818), which restored its natural activity level within three days after the removal of artificial light at night [55]. Given this, we may have missed the effects of long-term light pollution by setting the same daily lighting regime for individuals from Angara as for individuals from Lake No. 14. Another controversial issue is the use of a lux meter to measure illumination in experiments. Although many authors use a lux meter in their biological and ecological studies due to its simplicity and availability, this device measures the illumination of only visible light adapted to human vision. At the same time, invertebrates, including crustaceans, can be sensitive to various ranges of the spectrum, including ultraviolet [2]. And for a more accurate characterization of the behavior of organisms, it is desirable to adapt the units of measurement of illumination to their visual spectrum, as, for example, was shown for mysids [20]. However, the measurement of illuminance in lux is standard among lighting designers, lighting engineers, and environmental regulators, so this unit of measurement will remain the preferred one in contacts with other disciplines indefinitely [64].

Further research, as we have already indicated above, could be aimed at a detailed study of the daily activity of amphipods and its changes as a result of exposure to long-term light pollution. Particular attention should be paid to the impact of LED light of different color temperatures, since LED lighting is increasingly used in infrastructure every year. We also consider it interesting to evaluate the influence of infrared lighting on the behavior of amphipods, and its ability to distort the results of studies using night surveillance cameras. Overall, based on the analysis of scientific literature, the issue of adaptive changes in organisms as a result of light pollution remains poorly understood. Future research can be conducted to expand the knowledge base on this issue.

5. Conclusions

This study found that long-term urban light pollution, predominantly characterized by warm light at the research site, induced adaptive changes in the response of amphipods *G. lacustris* to warm artificial light. In addition, the hypothesis was confirmed that the response of amphipods to LED light is determined not only by its color temperature, but also by the level of illumination in the case of warm light. We also found some differences between group and individual behavior of amphipods when exposed to artificial light. In future studies, we suggest paying attention to this when conducting experiments with amphipods and using light.

This study also confirmed that in short-term tests using light and amphipods, recording their responses in the first few minutes of observation is sufficient to detect the effects of light on behavior. However, this only concerns the primary response of amphipods to light in rapid tests, and the question remains open about the behavior of amphipods under longer continuous exposure to light. Comparing warm and cold LED light in this study, it was found that both types of light affected the behavior of *G. lacustris*, causing individuals to avoid the light or limit their locomotor activity. In addition, the presence of shelters from

light mitigates the negative impact of light pollution on amphipods. However, in this study, we were unable to identify the color temperature of LED lighting that would have a greater or lesser negative impact on amphipods in natural conditions.

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Institutional Review Board Statement: The experiments were approved by a special commission of the Research Institute of Biology of Irkutsk State University (Protocol no. 11, dated 11 May 2024). The experiments were carried out in accordance with international ethical standards.

Informed Consent Statement: Not applicable.

Data Availability Statement: All the data used are included in the article. In addition, any data used for this study will be provided upon request by the corresponding author.

Conflicts of Interest: The authors declare no conflicts of interest.

Abbreviations

The following abbreviations are used in this manuscript:

LED	Light-emitting diode
ALAN	Artificial Light At Night

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