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RESEARCH ARTICLE

Daily vertical migrations of aquatic organisms and water transparency as indicators of the potential exposure of freshwater lakes to light pollution

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Abstract

Light pollution, which disrupts the vital functions of organisms, including aquatic organisms, has become widespread in recent years. One of the main biological features of aquatic organisms is the presence of daily vertical migrations (DVM). However, as a result of exposure to artificial lighting, organisms become visible to predators. This leads to disruption of the DVM of aquatic organisms and, accordingly, disruption of the functioning of the reservoir ecosystem. Water transparency plays an important role in predators detecting their prey under light pollution. Based on this, it was hypothesized that the susceptibility of freshwater lakes to light pollution may be indicated by both the presence and intensity of DVM of organisms and water transparency. The study was carried out on lakes Baikal, Hovsgol and Ladoga, which differ in water transparency and the intensity of DVM of amphipods. On the lakes at night, samples were taken using a net to determine the composition of organisms located in the water column, and underwater video observations were carried out at two depths using a video system with a lighting source. As a result, the greatest migratory activity of amphipods was observed in Lake Baikal both at a depth of 0.5-1 m and at 3-6.5 m. In Lake Ladoga, migration activity at both depths was equally weak, and in Hovsgol, little activity was observed at a depth of 3-6.5 m. A comparison of sampling data and video observations showed that the studied lakes contain organisms that can either be attracted to or avoid artificial light from the video system. Since Lake Baikal, of the presented lakes, has the highest water transparency and intensity of DVM of organisms, this lake may be the most vulnerable to increasing light pollution, including those associated with the growth of tourist flows.

Keywords
ALAN, Amphipoda, artificial light at night, Baikal, DVM, Hovsgol, Ladoga

Introduction

Environmental pollution from artificial light has become widespread in recent decades. This type of pollution is called light pollution (LP) or artificial light at night (ALAN) (Rich and Longcore 2006; Hölker et al. 2010a; Bruce-White et al. 2011). Experts estimate that light pollution is increasing at an average rate of 6% per year (Hölker et al. 2010a). In the case of aquatic ecosystems, this is mainly due to increased shoreline lighting, shipping development and fishing. Light pollution is expected to increase sharply by 2060 as the population of coastal areas more than doubles (Neumann et al. 2015). Today, however, up to 76% of the seabed in some gulfs may be affected by artificial lighting (Davies et al. 2020).

In aquatic ecosystems, light pollution has widespread effects on a variety of taxa, including plants, invertebrates and vertebrates (Heise 1992; Nakamura and Yamashita 1997; Camp and Gaffin 1999; Roman et al. 2000; Nowinszky 2004; Ludvigsen et al. 2018; Ayalon et al. 2019; Duarte et al. 2019, Pulgar et al. 2019; Berge et al. 2020; Levy et al. 2020; Meravi and Kumar Prajapati 2020; Vowles and Kemp 2021). It is worth noting that marine ecosystems are now better understood. At the same time, the influence of light pollution on the ecology of crustaceans and fish is most often considered (Navarro-Barranco and Hughes 2015; Luarte et al. 2016; Ludvigsen et al. 2018; Duarte et al. 2019; Garratt et al. 2019; Berge et al. 2020; Davies et al. 2020; Lynn et al. 2021). Among crustaceans, there are a number of groups that are particularly affected by light pollution. For example, both benthic (Nguyen et al. 2020) and planktonic (Davies et al. 2020) members of the Copepoda, which are widely distributed around the world, are photosensitive. For example, observations of *Calanus* spp. Leach, 1816, *Pseudocalanus* spp. Boeck, 1872 and *Oithona similis* Claus, 1866 in Arctic fjords have shown that artificial lighting affects these zooplankton species both at the surface and at depths greater than 80 m (Ludvigsen et al. 2018). Observations of *Tylos spinulosus* Dana, 1853 (Isopoda) along the Pacific coast showed a clear reduction in the abundance of isopods near a light source and a restriction of their intertidal range compared to controls (Duarte et al. 2019). Also on the Pacific coast, locomotor activity and growth rates of the amphipod *Orchestoidea tuberculate* Nicolet, 1849 were studied under the influence of artificial lighting. Significantly higher abundances of *O. tuberculate* were observed at sites with two types of traps with artificial lighting (LED and halogen) compared to control traps without lighting (Luarte et al. 2016). In general, among macroinvertebrates, amphipods can serve as model organisms in studies aimed at investigating the influence of ALAN on hydrobionts (Navarro-Barranco and Hughes 2015; Luarte et al. 2016).

Light pollution has received relatively little attention in freshwater ecosystems. Instances of research include microspectrophotometric studies conducted on Lake Ontario and Lake Cayuga, which revealed substantial impacts of artificial lighting on *Mysis relicta* Lovén, 1862 (Mysida) (Gal et al. 1999). Studies have discovered that light exposure has an adverse impact on the migration of the genus *Daphnia* O.F. Müller, 1785 (Moore et al. 2000). Furthermore, the behaviour and morphology of *D. magna* Straus, 1820 are affected differently by light of different wavelengths and lighting regimes (Li et al. 2022). Exposure to white LED light led to an increase in leaf consumption in freshwater shredders *Gammarus jazdzewskii* Rudolph, Coleman, Mamos & Grabowski, 2018 and *Dikerogammarus villosus* (Sowinsky, 1894) (Amphipoda) (Czarnecka et al. 2021). Additionally, both species exhibited light avoidance when exposed to blue LED light (Czarnecka et al. 2022).

In general, the impact of light pollution on marine and freshwater ecosystems comprises the following negative consequences: alterations in predator-prey relationships, modifications in organism habitats, changes in the feeding behaviour of aquatic organisms and their reproductive success, and disruptions of the spatial orientation and circadian rhythms of organisms (Gal et al. 1999; Moore et al. 2000; Rich and Longcore 2006; Ayalon et al. 2019; Berge et al. 2020; Nguyen et al. 2020; Lynn et al. 2021).

Daily vertical migrations (DVM) are considered one of the important biological features of aquatic organisms in marine and freshwater ecosystems (Greze 1965; Blinn et al. 1988; Nishihama and Hirakawa 1998; Hays et al. 2001; Iguchi et al. 2004; Krapp et al. 2008; Pacheco et al. 2014; Last et al. 2016; Vereshchaka and Anokhina 2017; Dumont 2019). During this phenomenon, at night, either from the bottom or from the water column, aquatic organisms rush to the surface of the reservoir. This phenomenon is primarily characteristic of crustaceans and has been noted in groups such as amphipods (Drolet and Barbeau 2009), isopods (Macquart-Moulin 1992), Antarctic krill (Okkonen et al. 2020), mysids (Vereshchaka and Anokhina 2017), cladocerans (Griffin et al. 2020), ostracods (Pacheco et al. 2014) and copepods (Takahashi et al. 2009). As a rule, DVMs are explained by the fact that at night organisms rise to the surface layer to feed, since predators are inactive during this period of time (Kozhova 1987). However, under conditions of constant artificial lighting, organisms become visible to potential predators and, in turn, more vulnerable, which leads to disruption of migrations. In addition, it must be assumed that the transparency of the reservoir plays an important role in such detection by predators of their victims. The greater the water's transparency, the less scattering and the deeper the light can penetrate into the body of water, consequently impacting a larger quantity of organisms.

DVM of benthic and planktonic communities are also a characteristic phenomenon for Lake Baikal (Karnaukhov et al. 2016, 2019a, 2019b; Takhteev et al. 2019). The main participant in these migrations in Lake Baikal are amphipods (Takhteev et al. 2019). It has been repeatedly noted that amphipods and fish are attracted to artificial lighting (Karnaukhov et al. 2016, 2021). One of the incidental results of these studies was the discovery that the pelagic amphipod *Macrohectopus branickii* (Dybowsky, 1874) exhibits different activity depending on the spectrum of the artificial light source (Karnaukhov et al. 2019b). It is worth considering that amphipods in Lake Baikal are the dominant group of organisms in terms of numbers and include more than 354 species and subspecies (Takhteev et al. 2015). DVM of amphipods were also observed in other large freshwater lakes, such as lakes Hovsgol and Ladoga. However, in these reservoirs the DVM are less pronounced compared to Lake Baikal (Karnaukhov et al. 2019c; Karnaukhov and Kurashov 2020). Moreover, all three reservoirs differ significantly from each other in the level of water transparency.

Given the presence of DVM with varying degrees of intensity in all three reservoirs, we hypothesized that the susceptibility of freshwater lakes to light may be indicated by water transparency and the intensity of DVM of organisms (Karnaukhov et al. 2021). The research aims to examine this hypothesis and assess the potential hazards of light pollution on organisms' migratory behaviour.

Materials and methods

Researched lakes

The studies were carried out on three freshwater bodies of water, namely: in Russia on Lakes Baikal and Ladoga and in Mongolia on Lake Hovsgol. Lakes Baikal and Hovsgol belong to the ancient large lake ecosystems of East Asia. Lake Ladoga, in turn, is the largest freshwater body of water in Europe. Physical-geographical (Table 1) and general characteristics of the assessed lakes are presented below.

In all three lakes, one of the main representatives of zoobenthos, both in the number of species (including the number of individuals) and in biomass, are representatives of the order Amphipoda. It is worth noting that the Holarctic species *Gammarus lacustris* Sars, 1863 is common to all three lakes, and the amphipods *Gmelinoides fasciatus* (Stebbing, 1899) and *Micruropus possolskii* Sowinsky, 1915, which are of Baikal origin, are common to lakes Baikal and Ladoga. The last two species are active migrants in Lake Baikal.

Table 1. Physical-geographical characteristics of the studied lakes

Physiographic characteristics	Lake Baikal (Galaziy 1987)	Lake Hovsgol (Bogoyavlenskiy 1989)	Lake Ladoga (Naumenko 2007; Rumyantsev 2015)
Area, km^2	31 500	2 620	17 765
Lake length, km	636	136	219
Maximum width of the lake, km	81	36.5	138
Volume, km^3	23 000	381	848
Average depth, m	730	120	48.3
Number of tributaries of the lake	More than 340	More than 96	About 35
Maximum transparency of the lake, m	40	27	7

Video surveillance and data collection

On each of the three lakes, four points for collecting material were selected for study (Fig. 1), in three of them the depth was in the range of 0.5-1 m, in the fourth – 3-6.5 m, respectively.

On Lake Baikal, the research site was chosen near the village of Bol'shie Koty; on Hovsgol, the study was carried out in the northern part of the lake near the village of Hankh; in Lake Ladoga, observations were carried out near the village named after Morozov and in Svirskaya Bay. Observation in all lakes was carried out in the summer and autumn periods, namely: in September 2018 on Lake Baikal, in June and October 2019 on Hovsgol and from July to August 2019 on Lake Ladoga.

Sampling was conducted during the night at each of the three lakes. The selection of sampling points was based on the depth of 3-6.5 m to establish the migrant organisms' qualitative composition. Samples were collected in triplicate using a Juday plankton net with a 25 cm inlet diameter.

Primary processing of samples collected using a Juday plankton net was performed in a laboratory setting employing standard hydrobiological techniques (Salazkin et al. 1984). Migrant organisms were counted using an MBS-10 stereomicroscope in a Bogorov chamber. Results were documented on a dedicated form for each taxon. The secondary sample processing involved determining the percentage of taxa present.

To investigate the nocturnal migratory community, night-time underwater video observations using a remote system were conducted in addition to sampling. The aforementioned video system has been frequently utilised in Lake Baikal studies (Karnaukhov et al. 2016, 2019b; Takhteev et al. 2019).

The technique for underwater video surveillance is as follows: the video system is lowered to the research point's bottom, where material is recorded for 15 minutes (recording length can vary by up to 5 minutes). The counting of migrating individuals from the video recording is performed manually. While processing the video, the recording is paused every 5 seconds, and the freeze-frame is used to count the total number of all migrant organisms captured in the frame. The result is a unit of measurement such as individuals/freeze-frame (O'Malley et al. 2018; Takhteev et al. 2019). Next, the average number of migrant organisms is calculated for each minute of video surveillance.

The spectral characteristics of the light used in the research were determined using a QE Pro spectrometer (OceanOptics, USA) (Fig. 2). The spectrum of a light source on a video system is characterized by the presence of peaks in the visible range. In this range, both short waves corresponding to blue and long waves corresponding to yellow are observed. The color temperature of the light source, measured using the OPPLE Light Master spectrum analyzer, was 4730 K.

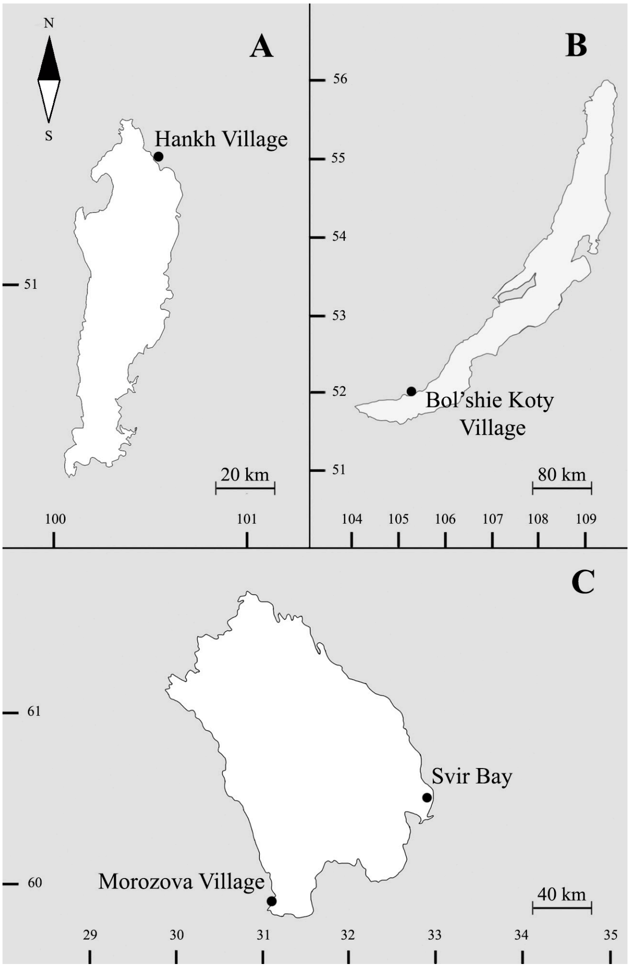

Figure 1. Places of sampling and video observations in the studied lakes: A – Lake Hovsgol; B – Lake Baikal; C – Lake Ladoga.

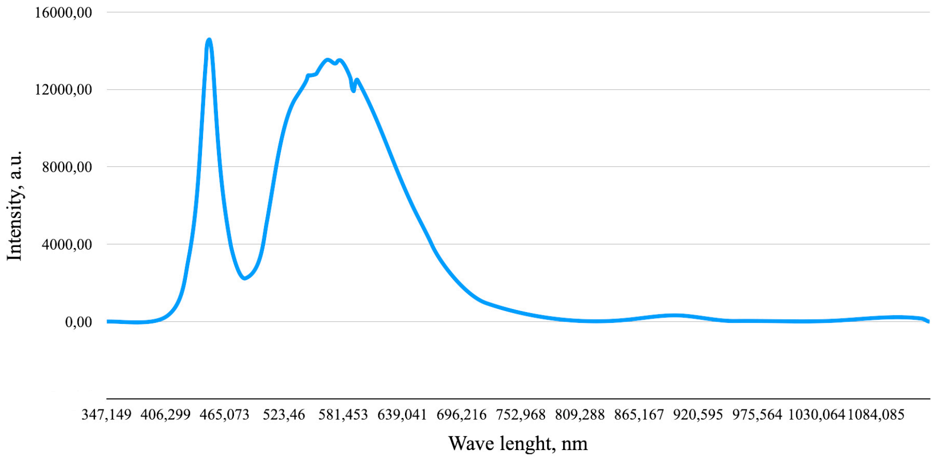

Figure 2. Spectrum of the illumination source on the video system.

To perform statistical analyses on the video surveillance data and generate graphs, we utilized Microsoft Office Excel and Past 3x software packages. Video observation data were entered into a table, where they were subsequently analyzed for normality using the Shapiro-Wilk test (Zacks 1971). Due to the fact that statistical analysis of the abundance of migrating amphipods in the three studied lakes showed an abnormal distribution of samples, we used the Kruskal-Wallis test (Unguryanu and Grjibovski 2014). The test showed that there are statistically significant differences between the medians of these values. Based on this, the Mann-Whitney test with Bonfferoni correction was used (Zacks 1971) and additionally Dunn's post hoc test for pairwise comparison of samples.

Result

The resulting video material helped to establish the number of migrating amphipods at different depths in the three lakes under study, as well as to determine the dynamics of the migratory community.

Statistical processing of data obtained at a depth of 0.5-1 meters at three points and at a depth of 3-6.5 meters showed that among the three lakes, the maximum average number of migrating amphipods is observed in Lake Baikal, namely: 6 ind./freeze-frame for depths of 0.5-1 m and 133 ind./freeze-frame for 3-6.5 m (Fig. 3). In Lake Hovsgol, the maximum average abundance of amphipods was observed at a depth of 3-6.5 m, namely 0.417 ind./freeze-frame, and in Lake Ladoga at both depths it was 0.25 ind./freeze-frame.

Participants in these migrations (except amphipods) in three lakes included fish, as well as representatives of the family Chironomidae in Lake Hovsgol and

Leptodora kindtii (Focke, 1844) in Lake Ladoga (Fig. 4). The greatest population dynamics are observed in fish in Lake Hovsgol – 4 ind./freeze-frame, in amphipods in Lake Baikal – 202 ind./freeze-frame, and in *L. kindtii* in Lake Ladoga – 2 ind./freeze-frame.

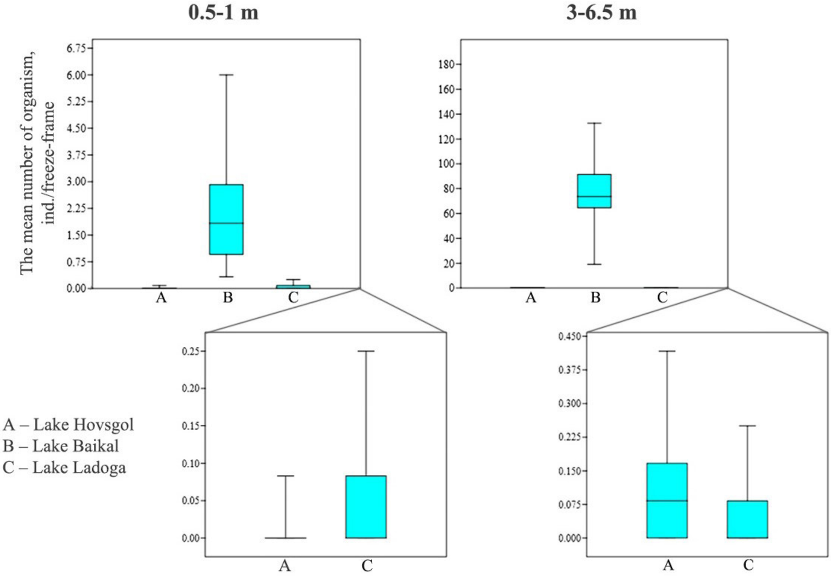

Figure 3. Migration activity of amphipods in the studied lakes at depths of 0.5-1 m and 3-6.5 m.

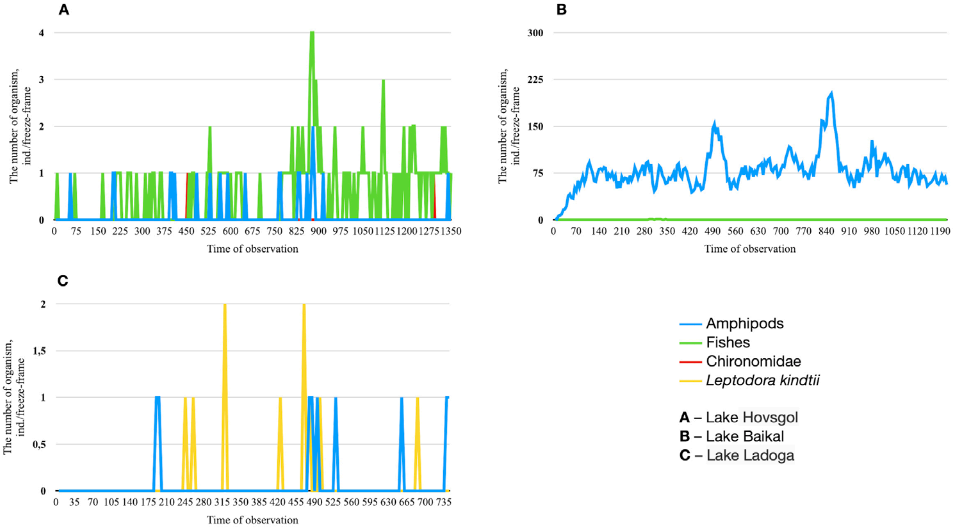

Figure 4. Dynamics of the migratory community in the studied lakes at the time of video observation at a depth of 3-6.5 m.

Statistical analysis of the number of migrating amphipods in the three lakes examined (Table 2) revealed that there is no statistical difference in the level of migratory activity of amphipods between Lakes Hovsgol and Ladoga. However, there are statistically significant differences in the level of migratory activity of amphipods between both aforementioned lakes and Lake Baikal, according to Dunn's post hoc test.

Video observations helped identify some of the migrant organisms attracted to artificial light from the video system and assess their dynamics in all three study lakes. However, this method is suitable for assessing the migratory activity of only part of the taxa from the community of organisms that commit DVM, and does not take into account organisms that avoid light. Therefore, in addition to underwater video observations, we carried out sampling using the Juday plankton net.

As a result of processing samples of the migratory community (and based on literature data), several groups of organisms were noted, which are listed in Table 3. Moreover, among these groups of organisms, the order Mysida is characteristic only of Lake Ladoga. In the samples taken in Lake Hovsgol, organisms such as Harpacticoida and water bugs were not observed, and in Lake Baikal only water bugs were not observed.

Table 2. Statistical significance (p) in pairwise comparisons calculated using Dunn's post hoc test

No		**Depth 0.5-1 m**			**Depth 3-6 m**	
		Lake Baikal	**Lake Ladoga**		**Lake Baikal**	**Lake Ladoga**
1	Lake Hovsgol	5.17E-19	0.05845	Lake Hovsgol	1.169E-05	0.299
2	Lake Baikal	–	1.60E-12	Lake Baikal	–	3.552E-07

Table 3. Groups of organisms potentially affected by artificial light in the three study lakes

Taxon	**Lake Hovsgol**	**Lake Baikal (Karnaukhov et al. 2021)**	**Lake Ladoga (Karnaukhov and Kurashov 2020)**
Amphipoda	+	+	+
Pisces	+	+	+
Calanoida	+	+	+
Cyclopoida	+	+	+
Harpacticoida	–	+	+
Cladocera	+	+	+
Mysida	(Absent in the lake)	(Absent in the lake)	+
Belostomatidae	–	–	+
Chironomidae	+	+	+

Figure 5 displays the percentage distribution of organisms detected in night time samples. The charts illustrate that Calanoida and Cyclopoida were the only consistently caught groups across all three lakes, while Calanoida was the dominant group in Hovsgol and Ladoga at 82% and 47%, respectively. In Baikal Amphipoda was the dominant group, accounting for 51%.

During the study, the Secchi disk readings indicated a transparency of 14-20 m in Lake Baikal and 2.5 m in Lake Ladoga. Unfortunately, no water transparency data is available for Lake Hovsgol during the time of observation.

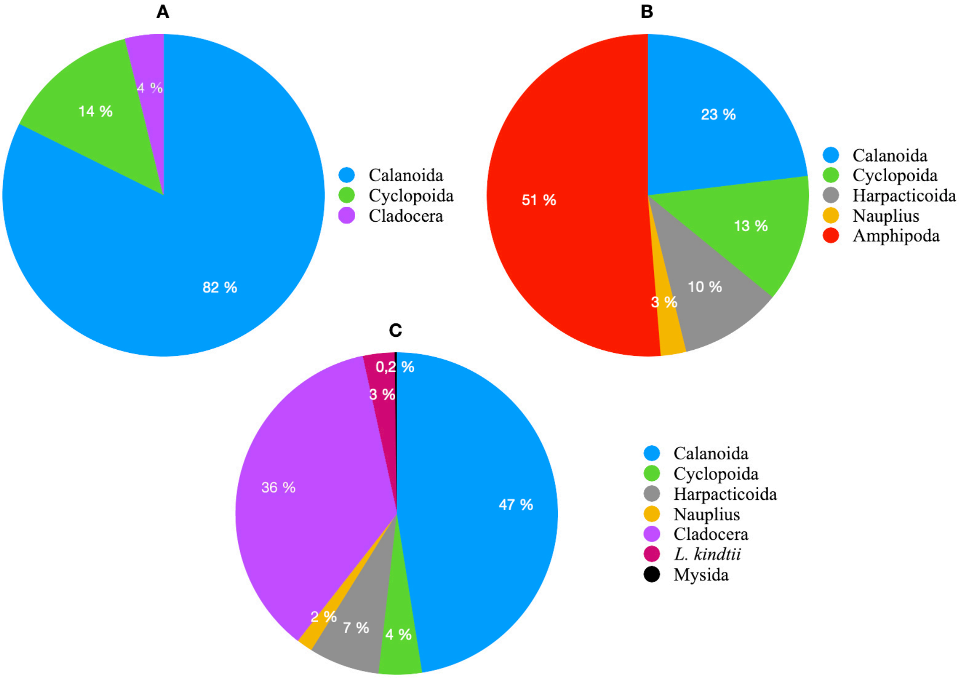

Figure 5. Percentage ratio of groups of organisms found in the water column at night in the studied lakes: A – Lake Hovsgol; B – Lake Baikal; C – Lake Ladoga.

Discussion

Light is a crucial factor in the lives of aquatic organisms, as it serves as an external signal for their biological rhythms. Therefore, it is the primary environmental factor that regulates the daily vertical migrations of zooplankton (Moore et al. 2000) and zoobenthos, in particular amphipods (Navarro-Barranco and Hughes 2015; Karnaukhov et al. 2021). Amphipoda is one of the most abundant groups of macrozoobenthos in the lakes studied, in terms of both quantity and biomass. Meanwhile, the predominant representative of zooplankton in these lakes is the Copepoda subclass, comprising Harpacticoida, Cyclopoida, and Calanoida orders. These organisms from these groups are present in the water column of the lakes investigated at night.

Among aquatic organisms, the most susceptible to light are not only organisms living in the water column, but also organisms that migrate to the upper layers of water. These layers could potentially be penetrated by artificial light from research vessels or illuminated coastal areas. Thus, in the case of navigable lakes, ship lights are a potential source of light pollution for these organisms. For example, a study of the effect of light pollution on Arctic marine ecosystems showed that the working light from a research ship directly affects organisms up to a depth of 200 m in a radius of more than 0.125 km^2 around the ship (Berge et al. 2020). The lakes we studied are also navigable, and therefore artificial light from ships in these lakes can potentially affect both organisms that constantly live in the water column and organisms that find themselves there as a result of DVM. In our study, based on the results of sampling and video observations, the following groups of organisms are potentially exposed to light pollution from ships: fish, Amphipoda, Mysida, Copepoda (Harpacticoida, Cyclopoida, Calanoida), Cladocera and, in particular, *L. kindtii*. We hypothesize that light pollution may affect a variety of organisms through both low-intensity artificial light generated by coastal lighting and high-intensity artificial light generated by waterborne transport. In addition, it is clear that the effects of light pollution are species specific (Navarro-Barranco and Hughes 2015; Bolton et al. 2017; Garratt et al. 2019; Jackson and Moore 2019; Fischer et al. 2020; Czarnecka et al. 2021, 2022; Manríquez et al. 2021). Based on this, assessing this impact on specific organisms from the studied lakes is the task of future detailed studies. At present, it has only been reliably established that light, in the spectrum of which the peak of long-wave radiation predominates over the peak of short-wave radiation, attracts individuals of the Baikal pelagic amphipod *M. branickii*, thereby affecting its migratory activity (Karnaukhov et al. 2019b).

Another important factor influencing the degree of exposure of freshwater lakes to light pollution, in our opinion, is water transparency. As previously stated, artificial light in marine ecosystems can affect organisms down to a depth of at least 200 m. However, if in marine ecosystems the difference in water transparency is sufficiently smoothed out and is characterized by high light transmittance, then water transparency in different lakes varies greatly (Kling 1988; Bigham Stephens et al. 2015). As for the freshwater lakes we studied, the maximum transparency is observed in Lake Baikal and is 40 m during periods of homothermy (Rusinek et al. 2012). It is known that the transparency of the water of Lake Baikal allows one to capture light penetrating through the water column even at a depth of 400 m or more (Hunt et al. 1996). However, the water transparency of Lake Baikal, as in other freshwater lakes, may differ in different areas of the lake and be subject to seasonal fluctuations, decreasing to several meters, for example, during periods of water bloom (Rusinek et al. 2012). Little research has been done on the transparency of water in Lake Hovsgol, but the available data allow us to judge the maximum transparency of 27 m and seasonal variations of ±10 m (Bogoyavlenskiy 1989). As for

Lake Ladoga, for the period of open water the average water transparency is 2.9-3.0 m with a standard deviation of 0.9 m, while the seasonal variation of transparency, as in other lakes, is heterogeneous in different areas of the lake (Naumenko 2007). During our research in Lake Ladoga, which has the least transparency of the three lakes, we already stopped seeing the light from the video system when it descended to a depth of only 6 m, while in lakes Baikal and Hovsgol at this depth the light was clearly visible.

In our study, we selected three lakes with different transparency and tried to assess their susceptibility to light pollution. To do this, through sampling, we determined the composition of the community of organisms at night in water bodies, as well as the reaction of organisms to artificial light using a video system with a light source.

The highest migration activity among the studied lakes is observed in Lake Baikal both at a very shallow depth (0.5-1 m) and at a slightly greater depth – 3-6.5 m. We see that with depth the number of migrants in front of the video system in Baikal increases, as they are attracted from a larger area due to the high transparency of the water in the lake. In a lake with low transparency, in our case it is Lake Ladoga, the migratory activity of amphipods is the same at both depths, since low transparency prevents artificial lighting from attracting organisms from a larger area. In Lake Hovsgol, transparency is also relatively high, as in Lake Baikal, however, we observe the migratory activity of amphipods only at a depth of 3-6.5 m and then hundreds of times less than in Lake Baikal at the same depth.

It is interesting that amphipods and chironomids are absent in the samples taken at Hovsgol, although they are found in video recordings. It can be assumed that amphipods and chironomids living in Lake Hovsgol are not active participants in the DVM, or their population density is so low (Goulden et al. 2006) that it is not possible to record the presence of their migrations during the night. And their presence in video recordings can be explained by the fact that they are attracted by artificial light from the video system, however, in this case, their number (measured in ind./freeze-frame) is not large. However, it is worth noting the fairly large number of fish recorded on video. Based on this, we should not exclude from attention the possibility of fish eating amphipods and chironomids attracted to the light, thereby explaining the small number of victims in the video recording. An increase in predatory activity in fish in the presence of artificial lighting at night was observed both in studies on Lake Baikal (Karnaukhov et al. 2021) and in studies on other water bodies (Bolton et al. 2017). In this study, we did not note a high abundance of fish in video recordings from Lake Baikal, but it was noted in previous studies (Karnaukhov et al. 2016). Therefore, the phenomenon of predators consuming prey in the presence of artificial lighting at night can also be observed on Lake Baikal.

In samples taken on Lake Ladoga at a depth of 3-6.5 m, there are also no amphipods, however, they were noted during video observation. It is worth noting that in Lake Ladoga a significant number of amphipods introduced from Lake Baikal was observed in the bottom community at depths of 0.5 and 1 m (Karnaukhov and

Kurashov 2020). However, we do not observe their active migrations, as in Lake Baikal, where these species are members of the migratory community (Karnaukhov et al. 2023). We assume that the difference in the migratory activity of amphipods in these lakes arises due to the large difference in their transparency. In Lake Baikal, amphipods migrate for various reasons (Karnaukhov et al. 2023), but in any case, migrations are expressed in the form of floating to the upper layers of water at night, when amphipods are less visible to potential predators. Perhaps in Lake Ladoga amphipods no longer need to migrate, since amphipods are poorly distinguishable by potential predators both during the day and at night. In addition, perhaps, due to low water transparency, organisms lack the level of illumination that would start and stop, in other words, regulate their DVM. Possession of high photosensitivity and an active reaction to light is observed in those organisms that live in reservoirs with high water transparency, since this contributes to their life activity (Tidau et al. 2021; Marangoni et al. 2022). Thus, adult individuals of the ostracod *Vargula annecohenae* Torres & Morin, 2007 exhibit quite high photosensitivity, the greatest activity of which is observed only when the critical "dark threshold" is reached (the "dark threshold" is reached when less than a third of the Moon is visible or at light intensity 2–3 minutes before the onset of nautical twilight, when the Moon is not illuminated) (Gerrish et al. 2009). Arctic zooplankton exhibits even higher photosensitivity, performing daily vertical migrations even in polar night conditions. Thus, it was shown that Arctic zooplankton is closely related to the ambient light regime and performs synchronized slow vertical migrations in the upper 30 m on a moonless polar night. This occurs even though the Sun at this moment is 8° below the horizon, in addition, zooplankton exhibit a strong escape response from artificial light, observed even down to a depth of 100 m (Ludvigsen et al. 2018).

It should be noted that mysids were found in samples taken in Lake Ladoga, although they were absent from the video recordings. However, in another earlier study, mysids were observed during video observations (Karnaukhov and Kurashov 2020). This discrepancy may be due to the fact that, firstly, there may be a low number of mysids at the observation site of this study, and secondly, mysids may avoid artificial lighting from the video system. The reaction of avoidance of artificial light by mysids was also observed in Cayuga Lake in New York (Gal et al. 1999). In addition to mysids, light avoidance has been reported in other higher crustaceans, such as isopods (Duarte et al. 2019), amphipods (Wolsky and Huxley 1932) and crayfish (Abeel et al. 2016; Fischer et al. 2020). As noted earlier, the reactions of organisms to artificial light are species specific. In this regard, more experiments and observations are needed to more accurately assess the exposure to light of both individual organisms and entire ecosystems.

Baikal has greater transparency compared to other lakes. Consequently, at night, artificial light will penetrate to a greater depth compared to Ladoga and cover a larger area and volume of water mass. In addition, in Baikal the DVM of organisms is most pronounced compared to other lakes we studied, which means light penetrating to depth will affect a potentially larger number of migrating organisms compared to Hovsgol (despite the high transparency of the water in it). From all of the above, it follows that Baikal is the most vulnerable to the effects of artificial light, compared to lakes Ladoga and Hovsgol, and with the increase in tourist flow and illumination of the coastlines, it is also the most susceptible to the negative effects of light pollution.

Conclusion

In all the lakes we studied, there are groups of organisms that could potentially be affected by artificial lighting. The degree of negative impact of light pollution will differ between lakes depending on various factors, for example, the transparency of the water in the lake and the presence of daily vertical migrations among zoobenthos and zooplankton representatives (the population density of zoobenthos and zooplankton representatives will also play an important role).

It is obvious that the degree of light pollution will increase in the coming decades, and therefore it becomes necessary to both regulate the regulatory framework for the use of different sources of artificial lighting with different spectral characteristics, and conduct experiments with living organisms. This will help identify light sources and their spectral characteristics that most negatively affect the life of organisms.

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