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Original Article

Daily vertical migrations of Lake Baikal amphipods: Major players, seasonal dynamics and potential causes

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Abstract: Daily vertical migrations of hydrobionts are widespread in all water bodies, such as small wells and vast oceans. This phenomenon is most common among crustaceans, especially in amphipods. Lake Baikal is one of the most biodiverse freshwater centers containing 354 species and subspecies of amphipods, and almost all of them are endemics. The study's goal was to follow the year-round dynamics of daily vertical migrations of amphipods and pinpoint various environmental factors that affect this process. Observations of amphipod migration were obtained using a remote video system. Based on the results, the vertical migratory activity of amphipods can be tracked during the year. The key factor that reduces migratory activity was found to be the start of the reverse stratification period. It is assumed that Lake Baikal amphipods have no single general reason for vertical migrations, and a few of the driving forces that make different amphipods groups migrate are accumulations of regions positive temperatures that facilitate sex development, food foraging, passive dispersal, search for a partner, and pairing.

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Introduction

Unique characteristics of large water ecosystems include the wide range of hydrobionts and the mutual living patterns of organisms, and interaction with various environmental factors. One such interaction is the daily vertical migration (DVM) of hydrobionts. DVM is the periodical migration of bottom and pelagic organisms toward the upper layers during the night. Observations of DVMs have been conducted for many years, and the content and structure of the migratory community in small water bodies (Blinn et al., 1988; Henri, 2018) to large lake ecosystems, seas, and oceans have been studied (Greze, 1965; Nishihama and Hirakawa, 1998; Hays et al., 2001; Iguchi and Ikeda, 2004; Krapp et al., 2008; Pacheco et al., 2014; Last et al., 2016; Vereshchaka and Anokhina, 2017). The main group that performs DVM is crustaceans, consisting of amphipods (Drolet and Barbeau, 2009), isopods (Macquart-Moulin, 1992), Antarctic krill (Okkonen et al., 2020), mysis (Vereshchaka and Anokhina, 2017), water fleas (Griffin et al., 2020), ostracods (Pacheco et al., 2014) and copepods (Takahashi et al., 2009). The usual reason for such behavior in pelagic organisms is the protection–food factor because it is thought that migration towards upper water layers during the night for forage helps avoid predators that are less active during this time (Kozhova, 1987).

DVMs are widely studied in the Pacific Ocean region, such as the reaction of the pelagic amphipod, *Phronima sedentaria* (Forskal, 1775) to temperature and the possible effect of temperature stress on the vertical migrations process (Elder and Seibel, 2015). Another example is the study of the Pacific Ocean's role in the global carbon cycle, which is based on the carbon transfer by plankton crustaceans, *Metridia pacifica* Brodsky, 1950 and *M. okhotensis* Brodsky,

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Table 1. Video recording sites.

№	Site	Coordinates	Substrate	Depth	Ice coverage
1	Bolshie Koty Bay	51°54'09.9"N 105°04'11.6"E	Small or and medium size pebbles and boulders	3 (3,5) m	January – April
2	Listvenichniy Bay	51°52'05.0"N 104°49'47.0"E	Small or and medium size pebbles and boulders	2 (2,5) m	Not present year-round

1950 via vertical migrations (Takahashi et al., 2009). A study of differences between day- and night-time zooplankton content was done in Chilean Patagonia that showed that plankton biomass and its migration depend on water body stratification (Diaz-Astudillo et al., 2017). Also, hydrobiont-based dependence of DVM on ice coverage, moonlight, wind intensity, and eutrophication levels were studied in various water bodies (Falk-Petersen et al., 2008; Krapp et al., 2008; Pacheco et al., 2014; Last et al., 2016; Okkonen et al., 2020).

Lake Baikal is an ancient freshwater body with a large number of endemic species. One of the most species-rich hydrobionts group is amphipods. 354 species and subspecies of amphipods are found in this lake (Takhteev et al., 2015). Lake Baikal amphipods occupy many ecological niches, including a pelagic zone inhabited by the only described freshwater pelagic amphipod, *Macrohectopus branickii* (Dybowsky, 1874) (Rusinek et al., 2012). Both pelagic and benthic amphipods are active participants in DVMs. Studies of DVMs in Lake Baikal have been conducted for more than 20 years; however, most observations were done once in various parts of the lake. Despite this fact, this study revealed several important ecological aspects of the group, for example, the gathering of semi-pelagic amphipods near underwater slopes during the winter months (Karnaukhov et al., 2016b) and different reactions of the pelagic species to artificial lighting (Karnaukhov et al., 2019). In addition, the absence of amphipods in the littoral zone of the lake in the daytime has been repeatedly confirmed (Karnaukhov et al., 2016a; Takhteev et al., 2019). Considering the importance of *M. branickii* in the pelagic community and the function and role of benthic amphipods in maintaining the equilibrium of the littoral community, it is crucial to conduct more rigorous studies of the DVMs by Lake Baikal amphipods (Karnaukhov et al., 2019). Therefore, the goal of this study was to track the year-round dynamics of DVMs and reveal various environmental factors affecting the migratory activities of amphipods.

Material and Methods

Observation sites: The first video recording site of the Lake Baikal amphipod migratory complex was located in Bolshie Koty Bay (Table 1). The site is the gentle littoral platform in the deep part of the bay. Video recordings were conducted every two hours during one full night in the migratory season. Also, additional video recordings were obtained in different months. The second video recording site was located in Listvenichny Bay near the Angara River's source, which is why the site is not covered by ice during the winter. Therefore, video recordings were done once every month during the year.

Sampling and processing of the material: The video recording system contained a metal frame, a GoPro Hero 4 action camera, and one light source, and a thermo-logger iButton was put on the substrate. The video was then recorded for 15 min. During the video processing, done manually every 5 sec, the video was stopped, and the number of migratory organisms was counted. Thus, the measurement unit was the number of specimens per freeze-frame (Karnaukhov et al., 2016a; Takhteev et al., 2019). Also, catching migratory organisms with a Juday plankton net (0.25 m diameter inlet port) was conducted along with video recordings. Sample processing was done in the laboratory according to standard hydrobiological methods (Salazkin, 1984). Organism counting was done in Bogorov counting tray with a stereomicroscope (МБС-10). For each migratory organism, the results were logged in a

Table 2. Mean number of migratory community specimens, Bolshie Koty Bay (2017-2018).

Date / Time		Amphipoda	Fish	*Macrohectopus branickii*
20-21.11.2017	22:00	11.53±0.505	0.392±0.46	0.05±0.016
	00:00	5.139±0.201	0.060±0.018	0.077±0.02
	02:00	3.381±0.165	0.436±0.048	0.022±0.01
	04:00	4.122±0.174	0.348±0.046	0.039±0.014
	06:00	0.116±0.026	0.403±0.039	0.028±0.012
23-24.02.2018	22:00	1.502±0.14	0	0
	00:00	0.116±0.025	0.696±0.034	0
	02:00	0.547±0.054	0	0.00415±0.00413
	04:00	0.564±0.072	0	0.025±0.01
	06:00	0.122±0.026	0.166±0.009	0
27.05.2018	02:00	0.768±0.062	0.06±0.017	0.033±0.014
	04:00	0.039±0.015	0.193±0.03	0
16-17.08.2018	00:00	21.16±0.657	5.74±0.355	0
	02:00	14.409±0.489	7.475±0.482	0
	04:00	5.182±0.207	15.365±0.953	0.028±0.012
	06:00	-	-	-
24-25.11.2018	22:00	0.287±0.04	0.011±0.008	0
	00:00	0.541±0.056	0	0
	02:00	-	-	-
	04:00	-	-	-
	06:00	-	-	-

separate file. Later, the calculations of hydrobionts per m^2 and m^3 were conducted.

Statistical analyses: Statistical analyses of the video recording results and samples were performed using Past.3x software. The Kruskal-Wallis test and Mann-Whitney tests with Bonferroni correction were used.

Results

Analysis of the video recording results in Bolshie Koty and Listvenichny Bays showed the presence of cottoid fish and amphipods, including pelagic amphipod *M. branickii,* in the migratory community (Tables 2, 3). In most cases, the mean number of migrating benthic amphipods was more dominant than the mean number of fish and pelagic *M. branickii*. The maximum mean number of amphipods detected in video recording of the Bolshie Koty Bay was 21.16±0.657 specimens per freeze-frame (night-time on August 16-17, 2018 at 00:00). However, earlier, we had witnessed 80 and sometimes more during the summer and fall (Karnaukhov et al., 2016b). The maximum mean number of amphipods in Listvenichny Bay during the year was 6.967±0.286 specimens per freeze-frame (December 20, 2017).

The dynamics of amphipod abundance during different seasons in the video recordings of Bolshie Koty Bay are shown in Figure 1. High intensity of migratory activity of amphipods was detected in November 2017 and August 2018 (60 specimens per freeze-frame). At the same time, the main peak time of migratory activity cannot be established and is most likely absent in our case. The maximum numbers were detected during 22:00 and 4:00. Migratory activity may be uniform during the night and fluctuations in abundance are caused by biotic (approaching young fish from Coregoninae and Cottoidae families), abiotic (temperature fluctuations, underwater streams, wave activity), and anthropogenic factors (shipping and, as a consequence, artificial lighting). Based on the additional video recordings, an increase in the intensity of migratory activity of amphipods in Bolshie Koty Bay was detected from June to December 2018 and reached 30-46 specimens per freeze frame (irrespective of the month). Data for Listvenichny Bay were organized similarly to Bolshie Koty, for example, according to the seasons (Fig. 2). Increased migratory activity was also detected during the winter.

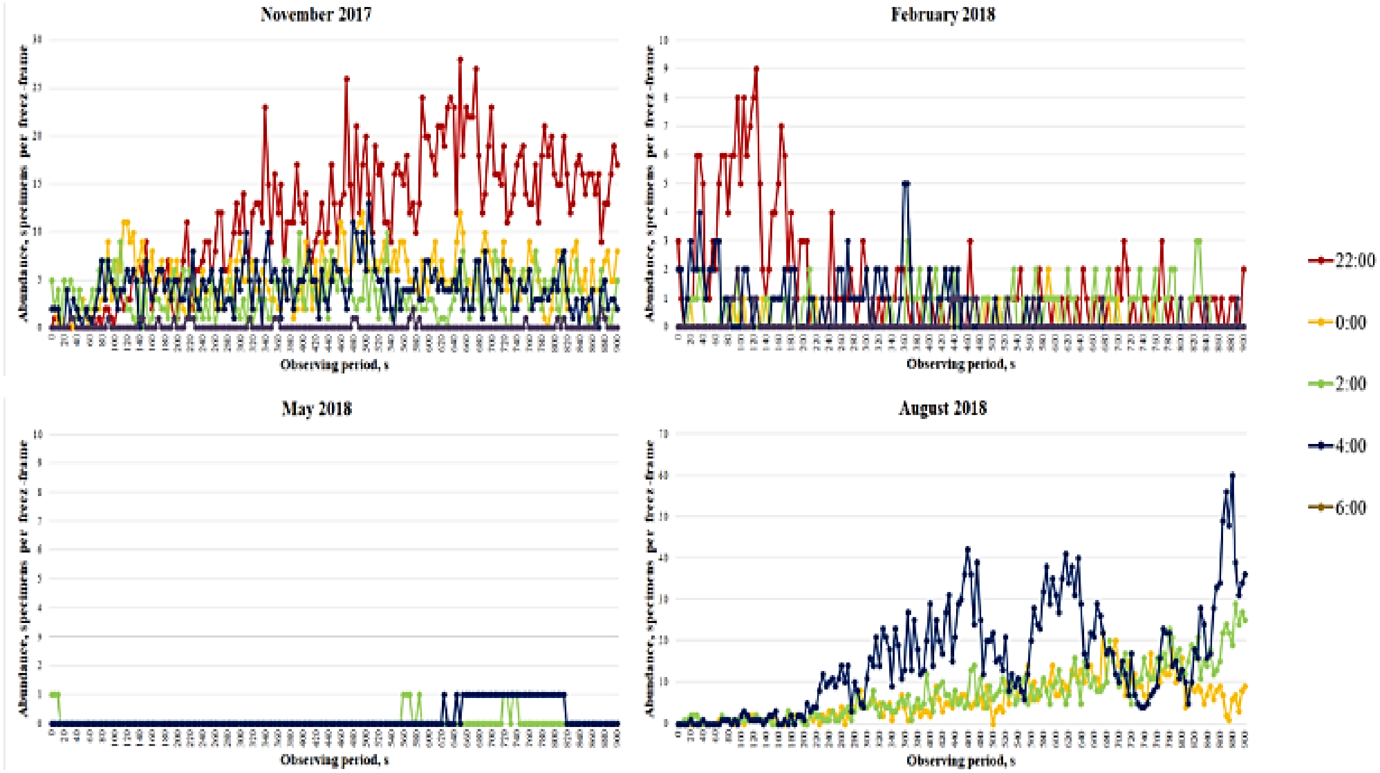

Figure 1. Abundance of amphipods at the observation site in Bolshie Koty Bay during the night across seasons.

Table 3. Mean number of migratory community specimens, Listvenichny Bay (2017–2018).

Date / Time	Amphipoda	Fish	*Macrohectopus branickii*
13.11.17 21:00	2.883±0.127	0.15±0.028	0.906±0.028
20.12.17 21:00	6.967±0.286	0	0
19.01.18 21:00	0.672±0.06	0	0
14.02.18 21:00	-	-	-
18.03.18 21:00	0.033±0.013	0	0
20.04.18 21:00	0	0.044±0.015	0
20.05.18 22:00	0.111±0.027	0.094±0.022	0
19.06.18 23:00	0.917±0.077	0.011±0.008	0
18.07.18 23:00	0.834±0.086	0	0
21.08.18 23:00	1.37±0.086	0.486±0.04	0.011±0.008
20.09.18 23:00	0.105±0.023	0.796±0.03	0.006±0.005
21.10.18 22:00	0.718±0.69	0	0.017±0.009
22.11.18 21:00	0.144±0.026	0.022±0.011	0.094±0.022

The results also showed significant differences between months and seasons, and the Mann-Whitney tests with Bonferroni correction identified strongly expressed differences between months and seasons (Fig. 3). Samples showed the presence of several groups of hydrobionts, including Calanoida, Cyclopoida, Harpacticoida, and Amphipoda (Tables 4, 5). The dominant group of Copepoda collected in Bolshie Koty Bay was Harpacticoida. Its abundance was 2870 specimens per m^2 of the bottom. The subdominant group was Calanoida (251 specimens per m^2 of the bottom). The mean abundance of Cyclopoida was 125 specimens per m^2. The dominant group in Listvenichny Bay was Calanoida, with mean abundance during the whole period of sampling with 1758 specimens per m^2. The subdominant group was Harpacticoida (947 specimens per m^2) and specimens of Cyclopoida had the lowest abundance (71 specimens per m^2).

Among the collected amphipods, several taxa were identified, viz. *Echiuropus levis* Bazikalova, 1945, *E. macronychus sempercarinatus*

Table 4. Abundance of species from migratory communities obtained via the plankton net in Bolshie Koty Bay (per m^2 and m^3).

Date / Time		Amphipoda		Calanoida		Cyclopoida		Harpacticoida	
		$м^2$	$м^3$	$м^2$	$м^3$	$м^2$	$м^3$	$м^2$	$м^3$
23-24.02.2018	22:00	73.3	24.4	0	0	200	66.6	3166.6	1055.5
	00:00	66.6	22.2	373.3	124.4	66.6	22.2	293.3	97.7
	02:00	120	40	0	0	100	33.3	513.3	171.1
	04:00	180	60	0	0	0	0	806.6	268.8
	06:00	40	13.3	6.6	2.2	0	0	133.3	44.4
27.05.2018	02:00	13.3	4.4	360	120	200	66.6	520	173.3
	04:00	0	0	240	80	180	60	160	53.3
16-17.08.2018	00:00	60	20	20	6.6	93.3	21.1	7506.6	2502.2
	02:00	80	26.6	33.3	11.1	80	26.6	10593.3	3531.1
	04:00	86.6	28.8	1720	573.3	286.6	95.5	4520	1506.6
	06:00	26.6	8.8	460	153.3	153.3	51.1	4826.6	1608.8
12.08.2018	00:00	320	106.6	326.6	108.8	506.6	168.8	12406.6	4135.5
24-25.11.2018	22:00	0	0	186.6	62.2	33.3	11.1	126.6	42.2
	00:00	13.3	3.8	166.6	47.62	40	11.43	193.3	55.24
	02:00	0	0	33.3	11.1	13.3	4.4	60	20
	04:00	0	0	93.3	31.1	46.6	15.5	93.3	31.1
	06:00	0	0	0	0	0	0	0	0

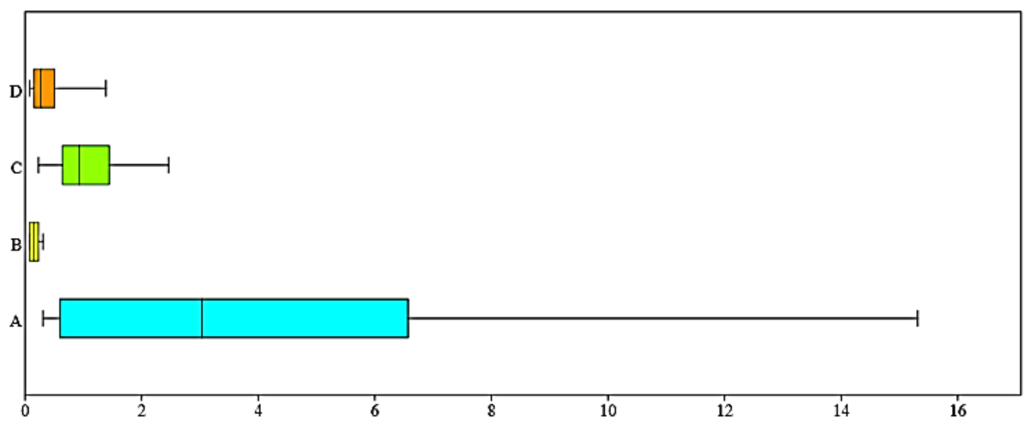

Figure 2. Abundance of amphipods at the observation site in Listvenichny Bay grouped according seasons: A – winter; B – spring; C – summer; D – autumn.

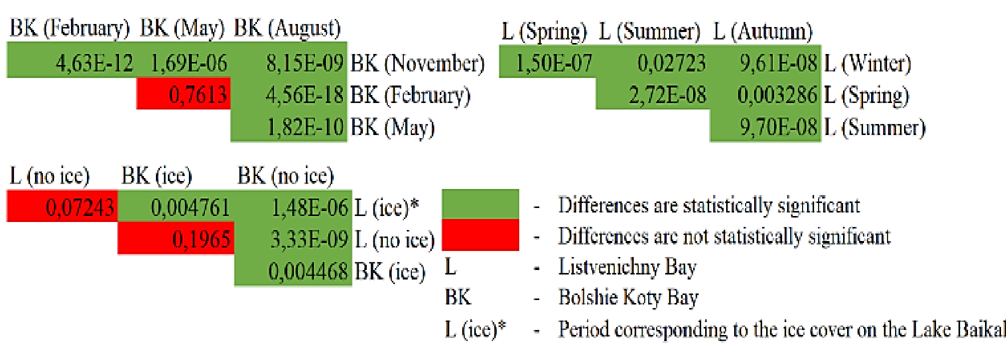

Figure 3. Statistical significance (p) in pair comparisons calculated using Mann–Whitney tests with the Bonferroni correction.

(Bazikalova, 1975), *Gmelinoides fasciatus* (Stebbing, 1899), *Micruropus wohlii wohlii* (Dybowsky, 1874), *Micruopus* sp., *Eulimnogammarus cyaneus* (Dybowsky, 1874), *E.verrucosus* (Gerstfeldt, 1858), *Eulimnogammarus* sp., *Pallasea* sp., and *Brandtia* sp. These species were found in samples at both sites during the entire observation period. However, only *G. fasciatus*,

Table 5. Abundance of species from migratory communities obtained with plankton net in Listvenichny Bay (per m^2 and m^3).

Date / Time		Amphipoda		Calanoida		Cyclopoida		Harpacticoida	
		м^2	м^3	м^2	м^3	м^2	м^3	м^2	м^3
13.11.17	21:00	1100	550	440	220	0	0	4120	2060
20.12.17	21:00	160	80	400	200	0	0	3760	1880
19.01.18	21:00	20	10	560	280	0	0	240	120
14.02.18	21:00	0	0	106.6	53.3	140	70	93.3	46.6
18.03.18	21:00	6.6	3.3	13.3	6.6	6.6	3.3	106.6	53.3
20.04.18	21:00	0	0	0	0	6.6	3.3	353.3	176.6
20.05.18	22:00	6.6	3.3	66.6	33.3	26.6	13.3	26.6	13.3
19.06.18	23:00	40	20	1466.6	733.3	53.3	26.6	46.6	23.3
18.07.18	23:00	20	10	13.3	6.6	0	0	40	20
21.08.18	23:00	240	120	0	0	240	120	720	360
20.09.18	23:00	0	0	12340	4936	0	0	1880	752
21.10.18	22:00	180	72	4400	1760	0	0	500	200
22.11.18	21:00	30	12	3050	1220	450	180	420	168

M. wohlii wohlii, and *Micruropus* sp. were found in Bolshie Koty Bay during the winter (ice-covered period), while during the same time frame, *E. cyaneus* and *Eulimnogammarus* sp. were found at Listvenichny Bay.

Discussion

Daily vertical migrations of Lake Baikal hydrobionts are complex phenomena, and the dominant part consists of amphipods' migrations. The signal factor in starting migration is most likely the level of illumination (Ringelberg, 1995). It is worth noting that the lighting sources used during experiment affect the migratory community in proportion to its increase compared to shooting without lighting. Similar video surveillance without lighting has been carried out repeatedly (Takhteev and Didorenko, 2015). For example, the level of sensitivity to the light for the Lake Baikal amphipods is 0.0001 Lux (Bessolitsyna, 2002; Rudstam et al., 1992; Volkova, 1984). Based on our results, the migration does not stop during the year, but their intensity varies. The observations during the different seasons in Listvenichny Bay vary significantly. However, since there is no ice coverage on this site year-round, it made sense to compare migratory activity during the ice-covered period and period without ice in Bolshie Koty Bay during the same months as in Listvenichny Bay. Such a comparison showed that migratory activity in Listvenichny Bay did not differ during the ice-free and -cover periods in the rest of the lake. Meanwhile, during the ice-free period in Listvenichny Bay, migratory activity did not differ from during the ice-covered period in Bolshie Koty Bay.

At the same time, a comparison of migratory activity during the seasons in Bolshie Koty Bay revealed no significant differences for such activity between February and May (Lake Baikal completely becomes ice-free in May and starts spring mixing the water temperature is relatively low). Our observations showed that migratory activity was low during the February to March period and high during June to December. Based on these facts, we concluded that the main limiting factor for migratory activity is the start of the reverse stratification period. This corresponded to the previous temperature hypothesis of Lake Baikal amphipods DVMs, which states that crustaceans accumulate in the upper water layers in higher temperature regions to speed up their sexual maturation. For example, migrating specimens of the genus *Eulimnogammarus* were only observed in immature individuals. They feed mainly on the food located at the bottom (Morino et al., 2000). However, the DVMs of the Lake Baikal amphipods cannot be explained by only the temperature hypothesis because we can witness migratory activity even during the ice-covered period, even if this event is not intense.

Based on the results, part of the amphipods in the plankton net samples were *G. fasciatus* and specimens of the genus *Micruropus*. Mating in the water column was already mentioned for some non-Lake Baikal amphipods, for example, *Pontoporeia affinis* Lindström, 1855 and *P. rosttrata* (Marzolf, 1965; Yu et al., 1998). Besides, *G. fasciatus* can hunt plankton crustaceans (Bekman, 1962). At both sites, besides amphipods, Calanoida (represented in our study by one species, *E. baikalensis* Sars, 1900), Cyclopoida (*Cyclops kolensis* Lilljeborg, 1901), and Harpacticoida (a number of species) were collected. The dominance of *E. baikalensis* over *C. kolensis* is due to the natural fluctuations of these species in Lake Baikal, while the dominance of Harpacticoida in Bolshie Koty Bay was due to the local distribution. In contrast to the first two taxa, Harpacticoida in Lake Baikal are benthic organisms but actively engaged in daily vertical migrations (Evstigneeva et al., 1991).

The subspecies of *M. wohlii wohlii* and *M. wohlii platycercus* (Dybowsky, 1874) are semi-pelagic amphipods (Takhteev and Didorenko, 2015), often gatherings at night far away from the shore. They were passively transferred by streams (also, the descent to the bottom can be passive without energy costs), including underwater ones and thus can move great distances. Similar migration into pelagic zones can be found among other crustaceans, for example, copepods, ostracods and the amphipod *Hornellia (Metaceradocus) occidentalis* JL Barnard, 1959 (Aldredge and King, 1985). In addition, according to some information, hatching *M. wohlii wohlii* and *M. wohlii platycercus* occur in pelagic zones, which excludes the mass mortality due to predators (Nikolaeva, 1967) and helps juvenile dispersal.

The pelagic amphipod *M. branickii* regularly migrates from a depth of 200-700 m to follow its food source, *E. baikalensis*. However, often individuals of this species can be seen near shore (Karnaukhov et al., 2016a). One reason for this is thought to be upwelling (Didorenko et al., 2020). However, it does not completely explain the migration of *M. branickii* to the shore. *Macrohectopus branickii* migrating to the shore becomes the part of the complex that we can observe in the lake littoral in which both exclusively benthic organisms (benthic amphipods, Harpacticoida, and Cottoidei fish) and exclusively pelagic ones (pelagic amphipod *M. branickii*, *E. baikalensis*, *C. kolensis,* and Coregonidae fish) can be concurrently found. Such conditions facilitate matter and energy exchange between two separate, disconnected lake systems with benthic and pelagic zones.

In addition, one more factor that must be considered affecting the DVM of Lake Baikal amphipods is light pollution. Benthic amphipods are actively attracted to the artificial light sources on the lake shore. These light sources might be visible to potential predators, leading to the depletion of the quality and quantity at some sites (Gliwicz, 1986; Karnaukhov et al., 2021). Besides, artificial light with different wavelengths might also affect pelagic organisms, thus attracting them to the specific Lake Baikal shore locations (Karnaukhov et al., 2019).

Conclusion

Vertical migratory activity of hydrobionts, in particular Lake Baikal amphipods, creates specific conditions for matter and energy exchange between normally disconnected zones of the lake: benthic and pelagic. The exchange did not stop during the year; however, establishing the reverse stratification period caused a significant decrease in the intensity of the vertical migrations. An explanation of migratory activity of all Lake Baikal amphipod diversity with one general cause is not reasonable. Different groups of amphipods have different reasons, such as the search for a mating partner and mating itself, accumulation of positive temperature regions that speed up sexual maturation, search for food, and passive distribution with the help of underwater streams. The general migrants are specimens of the *Echiuropus*, *Gmelinoides* (one species *G. fasciatus*), *Micruropus*, *Eulimnogammarus*, *Pallasea*, and *Brandtia* genera. However, migratory activity is an inherent property of specimens from other Lake Baikal amphipod genera. It should be noted that migration to the surface water during the night in the vicinity of the illuminated parts of the Lake Baikal shore allows amphipods to become exposed to light pollution, making them visible to potential predators. Thus, the DVM phenomenon is a factor that makes migrating species vulnerable to predators during the night in some parts of the coastal littoral.

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