Is the Endemic Fauna of Lake Baikal Affected by Global Change?

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Abstract

Lake Baikal, the largest freshwater lake in the world and UNESCO world heritage site, is inhabited by an exceptionally species-rich, largely endemic fauna which is distinct from faunas from other freshwaters in the Palearctic. With regard to species-richness, extremely high abundance of individuals and high total biomass amphipods (Amphipoda, Crustacea) constitute a major, ecologically highly relevant animal taxon of Lake Baikal. The "immiscibility barrier" of faunas, i.e., the separation of amphipod faunas from Lake Baikal and other Palearctic waters, is believed to be related with the high degree of adaptation of Lake Baikal species to the specific environmental conditions of their habitats; under these conditions they outcompete potentially invasive non-Baikal species that are unable to establish stable populations in Lake Baikal. It is a question of great interest whether the current global change related, massive alterations of temperature and chemical conditions in Lake Baikal will favor potential invasive species. Our molecular and physiological studies with representative endemic Eulimnogammarus species show that these species are indeed equipped to deal with stress from unfavorable environmental conditions and in comparison to a potentially invasive amphipod may not necessarily be more sensitive. However, considerable differences in stress responses among the different species suggest that species shifts in the Lake Baikal ecosystem may occur when environmental conditions continue to change.

The exceptionally unique ecosystem Lake Baikal

Lake Baikal, located in an intracontinental rift zone in the central region of southern Siberia, is the world's oldest (25–30 million years), by volume largest (23,000 km3) and deepest (1,642 m) lake, containing about 20% of the world's liquid freshwater (equivalent to all North American Great Lakes combined) (Rusinek et al., 2012a). As unique ecosystem with exceptionally high degrees of biodiversity and endemism it was designated as a UNESCO World Heritage Site in 1996 (http://whc.unesco.org/en/list/754). So far, 2,595 animal species from Lake Baikal have been identified or described, of which 80% are endemics (Rusinek et al., 2012b; Timoshkin, 2001). This high degree of endemism reflects the long evolutionary history of Lake Baikal in isolation from other freshwater bodies (Timofeyev, 2010).

The fauna of Lake Baikal is represented by two genetically and ecologically different complexes – the Euro-Siberian (Palearctic) fauna inhabiting so called “sors”, which are isolated waters at the shores of Lake Baikal that have connection to the lake, and the “Baikalian” fauna of the open lake (Kozhova and Izmest'eva, 1998). It is indeed a question of great interest why the ”Baikalian” fauna remains majorly distinct from the fauna of sors and adjacent ponds and lakes with species compositions that are commonly found in fresh water systems across northern Eurasia (see Figure 1).

A major factor contributing to the formation of a faunistic “immiscibility barrier” between Lake Baikal and other fresh waters can be seen in the, unique abiotic conditions of Lake Baikal (Mazepova, 1990). The water is classified as ultra-oligotrophic with comparatively very low levels of ions and dissolved organic carbon; oxygen levels are permanently exceptionally high throughout the water column with concentrations close to saturation; and although the water temperature can rise to 20-22°C close to shore in protected shallow bays in summer (Khozov, 1963) it is overall constantly low with 6°C in average (Falkner et al., 1991; Weiss et al., 1991; Yoshioka et al., 2002). The abiotic conditions of Lake Baikal thus show fundamental differences to all other Siberian freshwater systems that are characterized by strong seasonal fluctuations of environmental parameters temperature, oxygen content, osmotic conditions and contents of natural organic compounds. It therefore seems obvious that differences between Lake Baikal and other lakes regarding abiotic conditions may require differences in physiological performance ranges as adaptations of species of the respective faunas to respective conditions. It is assumed that invasions of non-Baikal species into Lake Baikal and formation of stable populations in the lake are precluded by superior performance of the highly adapted species of the endemic fauna of Lake Baikal under these specific conditions which therefore out-compete other, potentially invasive species thus keeping ubiquitous northern Eurasian and Lake Baikal faunas distinct (Timofeyev, 2010).

Figure 1. Photograph of a site close to the village Onguryony in the north-west of Lake Baikal. The picture illustrates the "immiscibility barrier" of Lake Baikal and Palearctic freshwater faunas. A typical Lake Baikal shore habitat is in close vicinity and only separated by a narrow stretch of land from a freshwater habitat with a completely different character inhabited by a fauna common in the Palearctic.

Amphipods – dominant benthic organisms in Lake Baikal

Amphipods (Amphipoda, Crustacea) are highly abundant macro-invertebrates that substantially contribute to the overall biomass in Lake Baikal and constitute key components of the benthos from the littoral to abyssal zones. The number of amphipod species in Lake Baikal is exceptionally high and the lake is worldwide one of the hotspots of amphipod species diversity. From animal taxa inhabiting Lake Baikal the Amphipoda taxon has the highest documented diversity and endemicity. All of the so far classified 354 amphipod species and subspecies are endemic to Lake Baikal (Bedulina et al., 2014) and the species number amounts to approximately 20 % of the number of so far described amphipod species from fresh or inland waters worldwide (Väinölä et al., 2008).

The complex taxonomy of amphipods from Lake Baikal is still a matter of debate. Few species, mainly introduced by human activity, such as Gmelinoides fasciatus, Eulimnogammarus cyaneus, E. viridis, and Micruropus wohlii, were found to spread to waters outside of Lake Baikal (Berezina, 2007; Gladyshev and Moskvicheva, 2002; Takhteev, 2000). However, overall, the endemic amphipod fauna is confined to the

Figure 2. Photographs of recently discovered amphipod species endemic to Lake Baikal and of the shore lines where they were found.
Above: *Eulimnogammarus messerschmidtii* Bedulina et Tachteew, sp. n. (blue and red morphs – A, B) and the shore of northern Lake Baikal close to the city of Severobaikalsk.
Below: A yet undescribed species (*Eulimnogammarus* sp. n.) which was found close to the Shaman rock on Olkhon island.

waters of Lake Baikal and ponds and lakes in its vicinity are inhabited by a clearly distinct fauna with Gammarus lacustris as typically predominant amphipod species (Kozhova and Izmest'eva, 1998). Although amphipods from Lake Baikal have intensively been studied over decades there is still a large number of species to discover. Thus, it is assumed that only half of the species making up the endemic fauna of Lake Baikal has been described (Timoshkin, 1999). It is not just deep-water amphipod species that await discovery, but also new littoral species can be found at shores that are relatively well accessible and frequented by humans. Just recently, we published the description of a littoral amphipod species, Eulimnogammarus messerschmidtii that we found on a field trip to northern Lake Baikal close to the city of Severobaikalsk (Bedulina et al., 2014). Another undescribed littoral amphipod species that we found on the Olkhon island at a beach close to the Shaman rock, landmark of Lake Baikal and tourist attraction, still needs to be named (Figure 2). So far, the main focus of studies of amphipods from Lake Baikal has been on taxonomy and ecology and not so much on physiological adaptations to environmental conditions and their molecular basis.

We recently studied two major components of cellular stress response mechanisms in amphipods, so called chaperones or heat shock proteins (hsp) stabilizing the structure of other proteins and cellular transporter proteins from the ABC (ATP binding cassette) transporter protein superfamily that keep out toxic chemicals from cells (Bedulina et al., 2013; Pavlichenko et al., 2015). An important outcome of these studies is that amphipods endemic to Lake Baikal do possess these cellular stress response mechanisms, i.e., these species are equipped to deal with stress caused by adverse environmental conditions, such as temperature or chemical stress.

The identification of genetic sequences in amphipods is still challenging as there is a lack of genomic data for this animal taxon which could be used as reference. A recent first genome next generation sequencing (NGS) technology based sequencing campaign of the genome of Eulimnogammarus verrucosus (Rivarola-Duarte et al., 2014), an amphipod endemic to Lake Baikal, can in this respect be seen as pioneering and the obtained data will be of great value for future studies on Lake Baikal amphipods, but may also serve as reference for studies on amphipods in general. The sequenced genome of E. verrucosus appears to be unique in many regards. With a size of about ten Gb (giga bases) it turned out to be surprisingly large, about three times larger than the human genome. The large size cannot be associated with genome duplication as no paralogs of highly conserved genes, so called hox genes, were found, however, the genome appears to contain a high proportion of non-coding DNA, i.e. DNA not coding for any proteins. A comparison of genomes from E. verrucosus and the water flea Daphnia pulex, the closest relative with a well-developed genomic resource, showed only very little sequence similarities indicating that the genomes are quite distinct (Rivarola-Duarte et al., 2014).

Lake Baikal and global change

As a consequence of the drastic alterations of global climate with world-wide increasing mean temperatures and of the global chemosphere resulting from massive releases of man-made chemicals into the environment the abiotic conditions of Lake Baikal have dramatically changed in the last decades and those changes are predicted to continue. Recent models predict a 1.8-5°C increase of the mean global temperature by the year 2100, with increased occurrences of temperature fluctuations and temperature extremes (IPCC, 2007). Simultaneously, the global chemosphere is currently heavily influenced by human activities. The number of chemicals in use by mankind amounts to 100.000, with 10.000 to 30.000 being of environmental concern (Hartung and Rovida, 2009).

Lake Baikal is in one of three areas in the world experiencing the most rapid climate change; the other two regions are the Antarctic Peninsula and northwestern North America (Clarke et al., 2007). All three areas are characterized by long, cold winters. At Lake Baikal, winter air temperatures reach –37°C to –40°C, and the lake freezes for four to five months each year; summer air temperatures soar briefly to 25°C to 30°C in this strongly continental climate (Kozhova and Izmest'eva, 1998).

Despite the enormous temperature buffering capacity of the large water body global warming has caused a 1.21°C increase in the average surface water temperature in the past 50 years (Hampton et al., 2008), a rate twice that of the global average, and the ice-free season has lengthened by 16.1 days between 1868 to 1995 (Magnuson et al., 2000). This is of particular importance for the Lake Baikal ecosystem since ice is arguably the single most important abiotic driver in this lake. The lake’s dominant primary producers and its top predator, the Baikal seal, require ice for population growth. Whereas the spring phytoplankton bloom begins shortly after ice off in temperate-zone lakes the spring bloom occurs under the ice in Lake Baikal and ice is essential for initiating and sustaining this bloom (Moore et al., 2009). Long-term monitoring surveys demonstrated increases of more than 300% in average zooplankton, algae and cyanobacteria abundances since the 1940s as a consequence of increasing temperatures (Hampton et al., 2008). The increase of temperature in the Baikal region will remain substantial in the future. The projected median increase of annual air temperatures will be 4.3°C in 2080-2099 compared to 1980-1999, with 6°C for the median projected temperature increase for the winter months and 3°C for summer (Christensen et al., 2007).

In addition to temperature change industrial pollution and cultural eutrophication are of particular concern for Lake Baikal. The Irkutsk region, containing an industrial corridor with chemical plants and aging industries, lies within the lake’s airshed and industrial chemicals including polychlorinated dibenzo-p-dioxins and dibenzofurans (PCDD/Fs) and polychlorinated biphenyls (PCBs) are carried into the southern basin of the lake by prevailing winds and bioconcentrate in fish, the Baikal seal and in humans (Mamontov et al., 2000). Likewise, perfluorochemicals (PFCs) originating from ongoing contamination from a local source bioconcentrate in Baikal seals (Ishibashi et al., 2008). Other sources of pollutants include the Trans-Siberian railroad, now transporting oil along the southern and eastern shores of the lake, the Baykalsk Pulp and Paper Mill (BPPM), a large deteriorating pulp mill on the southern lake shore, industrial sites in the area of the city Severobaikalsk and agricultural waste water in the Selenga river flowing into Lake Baikal. Eutrophication supposedly from elevated phosphate and nitrate levels in some shallow bays along the Baikal shore was assumed to result from increased tourism and ship traffic with some consequences for the ecosystems in these habitats, such as unusually high abundance of Spirogyra and other algae (Kravtsova et al., 2014; Timoshkin et al., 2014) and in Lisvyanka bay during the summer of 2014 occurrence of frequent deaths of the endemic freshwater sponges that by acting as filter feeders have an important function for water purification. The influx of chemicals and nutrients is anticipated to further increase as a result of thawing permafrost releasing chemicals from soil and increased run-off and erosion into the lake with elevated temperatures.

Due to the lake's distinct features, such as oligotrophy, cold waters, long residence time, a long pelagic food chain, the high seismicity of the region, and great endemism, its ecosystems may be particularly vulnerable to stress resulting from the current environmental changes (Moore et al., 2009).

Do changes of environmental conditions enable invasive species to enter Lake Baikal?

Freshwater ecosystems are particularly affected by both temperature changes and chemical pollution. Surface runoff and industrial and municipal waste water often end up in streams and lakes and there is a continuous inflow of chemicals into aqueous environments. Increased temperature in concert with chemical stressors result in increased overall stress for organisms (Lannig et al., 2008).

These alterations of environmental conditions are advantageous for species with a superior ability to cope with stress resulting from environmental changes, because they become able to outcompete species that are less stress tolerant. Climate and chemosphere changes favor ubiquitous "generalists" that outcompete indigenous/endemic faunas. Mass occurrences of invasive species, such as for instance shown for certain amphipod species, occur in anthropogenically heavily affected environments (Grabowski et al., 2007; Van den Brink et al., 1991).

It is therefore of great concern that the current environmental changes by global warming and increasing levels of anthropogenic pollutants will lead to a situation where the immiscibility barrier of faunas in Lake Baikal deteriorates. Conditions that have hitherto been the cause of competitive superiority of endogenous Baikal species over ubiquitous Eurasian species may no longer be in place. The circumstance that Baikal species are perfectly adapted to conditions within a narrow range of variation will no longer remain a competitive advantage since environmental conditions may be shifted beyond the limits of optimal performance.

Various cases have shown invasions of non-indigenous species in other ecosystems as a consequence of global climate change and anthropogenic pollution, with success of invasion depending on the degree of stress tolerance (Grigorovich et al., 2008; Stachowicz et al., 2002). Indeed, cases of invasions of species which could be related to environmental conditions, i.e. specifically increased temperature, have also been reported for Lake Baikal; for instance, invading freshwater snails have been found to completely replace the indigenous fauna in certain isolated, shallow bays where comparatively high water temperatures were reached, which was related to a higher degree of thermotolerance of the invasive species (Stift et al., 2004).

On this background, current climate change and pollution can be regarded as substantial threat to the unique ecosystem of Lake Baikal as they may considerably advance replacement of indigenous by invasive species, alterating the Baikal ecosystem. Apart from the tragedy for the world community in case of deterioration of this unique ecosystem, changes of the Lake Baikal ecosystem will also have severe consequences for the local society. For one, local economies dependent on the lake, such as fisheries, may be threatened. Secondly, water supply of local communities may be affected by impaired water quality.

Gammarus lacustris – a potential invasive amphipod species to Lake Baikal?

For addressing the question if changing environmental conditions will enable non-Baikal amphipod species to invade Lake Baikal we chose three species as representative models for experiments. Two of the species, Eulimnogammarus cyaneus and E. verrucosus, are endemic to Lake Baikal and highly abundant littoral species. E. cyaneus inhabits the narrow zone near the water edge and E.verrucosus typically occurs close to shore at water depths from 0 to 6 m. The third species, Gammarus lacustris, can be regarded as potentially invasive species. It is widely distributed in fresh waters of Northern Eurasia, including Siberia (Karaman and Pinkster, 1977). The species occurs in some isolated bays of Lake Baikal, but it is not a typical species of the lake´s fauna (Kozhova and Izmest'eva, 1998; Timoshkin, 2001).

In contrast to species from Lake Baikal G. lacustris may need to tolerate higher fluctuations of environmental conditions, such as temperature changes during the day, as the shallow waters inhabited by the species do not show the buffering capacity of the large water mass of Lake Baikal and due to their limited size do not offer possibilities to escape adverse conditions by migration to other areas. It may therefore be assumed that G. lacustris is better equipped with cellular and physiological adaptations to withstand extreme conditions than the Baikal amphipod species, which in the contrary may have to deal less with fluctuations of environmental parameters in their habitats.

However, our studies show that greater sensitivity to adverse environmental conditions cannot per se be assumed for all Lake Baikal endemics.

Thus, experimental data on temperature sensitivities of the three amphipod species show that indeed a Lake Baikal endemic, E. cyaneus, is least sensitive to temperature stress (Figure 3). At 25°C water temperature, which causes thermal stress in the amphipods, increases in mortalities with time of exposure were found in all three species. However, whereas E. verrucosus was most sensitive with almost 100 % mortality after 24 hrs, mortality was lowest in E. cyaneus and, compared to E. cyaneus, clearly higher in G. lacustris (Figure 3). Based on these findings it appears plausible that E. cyaneus, although endemic to Lake Baikal, nevertheless experiences temperature fluctuations with comparatively large amplitudes or extremes in its habitats. Indeed, temperatures of the shallow waters in the upper littoral, where E. cyaneus is found, can reach maxima above 20°C in the summer (Shimaraev et al., 1994). Further, E. cyaneus can be found in warm waters close to hot springs (own observation). Thus, a high degree of temperature tolerance appears to enable the species to survive in habitats that with regard to environmental conditions are relatively extreme enabling it to escape competition with species that are less temperature tolerant. E. verrucosus, however, as more temperature sensitive littoral species appears to respond to unfavourable temperature conditions by migrating to deeper colder waters as it disappears from the shallow littoral during warm summer periods. It is only found in the shallow littoral when the water is cooler, either due to colder climate or due to upwelling of cold water from the deep (Weinberg and Kamaltynov, 1998).

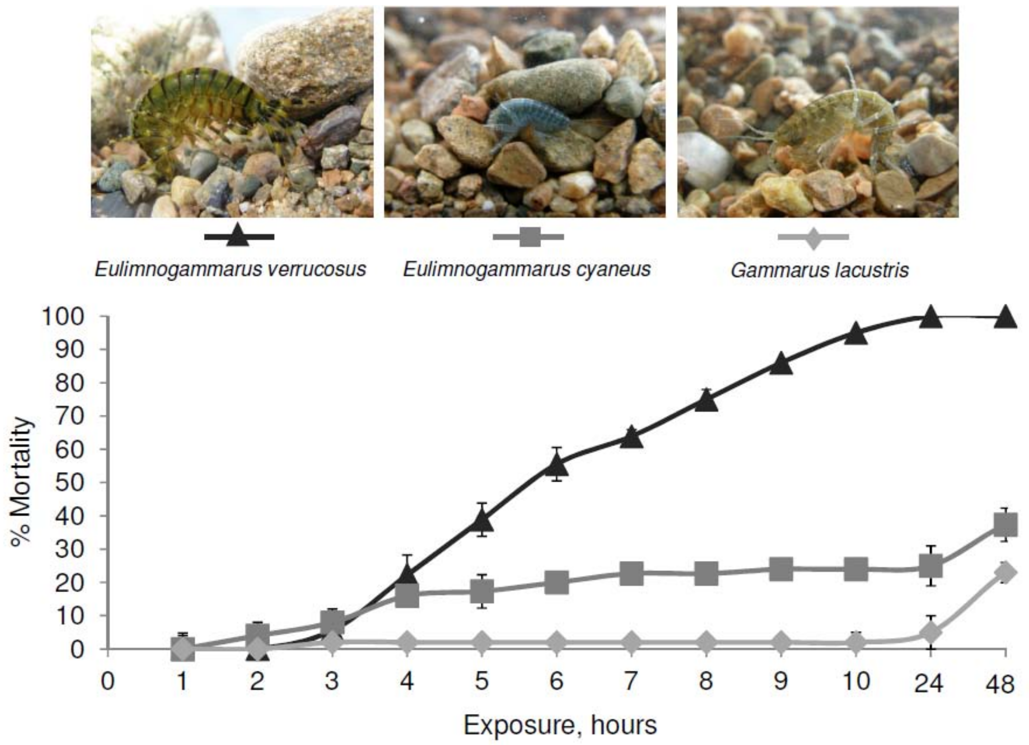

Figure 3. Percent mortalities of different amphipod species, *E. cyaneus*, *E. verrucosus* and *G. lacustris* in dependence of time of exposure to thermal stress (water temperature at 25°C). Upon lab adaptation of wild caught amphipods animals were kept in water tanks in aerated water maintained at 25°C and dead animals were counted and removed from the tank every hour. For details on origin and maintenance of animals and on the experimental set up refer to Bedulina et al. (2013) and Pavlichenko et al. (2014). Data from Bedulina et al. (2013) and Timofeyev (2010). Photographs of amphipods by Vasiliy Pavlichenko.

As outlined above the studied endemic amphipods possess the cellular machinery enabling the organisms to deal with adverse environmental conditions, such as thermal and chemical stress. However, there are species-specific differences in cellular stress response systems that can be seen as reason for differences between species in the degree of tolerance to environmental stress. Thus, the Hsp70 system mitigating destabilizing effects of high temperature on protein structure is more complex and more active in E. cyaneus than in E. verrucosus (Bedulina et al., 2013) and constitutive hsp70 transcript levels are generally higher in G. lacustris and E. cyaneus than in E. verrucosus, with particularly high constitutive HSP70 protein levels in E. cyaneus (Protopopova et al., 2014). These molecular data are thus in line with the different degrees of thermal tolerance indicated by the temperature-related mortalities in those species (Figure 3).

Conclusions

Our data do not indicate that non-Baikal amphipods are generally more stress-tolerant than Baikal endemics. Therefore, continuing environmental changes may not necessarily enable invasive species to occupy new habitats in Lake Baikal since species, such as E. cyaneus, may still be able to deal with changed conditions, especially higher maximum temperatures, and out-compete potential invaders. However, migration of endemic species, such as E. verrucosus, to deeper, cooler waters as a consequence of higher water temperatures may increase the competition pressure in these habitats leading to ecosystem shifts. Changes in the Baikal water chemistry, in particular eutrophication, may lead to dramatic impacts on the Lake Baikal ecosystem, as recently reported, and urgently needs to be addressed by water managers and scientists.

Acknowledgements

We want to thank our colleagues Lena Jakob, Lorena S. Rivarola-Duarte, Anton Gurkov, Denis Axenov-Gribanov, Vasiliy Pavlichenko, Christian Otto, Marina Protopopova, Zhanna Shatilina, Xenia Vereshagina, Hendrik Michael, Inna Sokolova, Irene Fernandez Casas, Wibke Busch, Michael Ginzburg, Hans-Otto Pörtner, Peter Stadler, Rolf Altenburger, Stephan Schreiber, Jörg Hackermüller, Magnus Lucassen, Franz-Josef Sartoris and Michael Evgen'ev, Olga Zatsepina, Vadim V. Takhteev who are or were involved in the activities of our Helmholtz-Russia joint research group LaBeglo ("Lake Baikal and biological effects of global change", HRJRG-221). LaBeglo is funded by the Helmholtz Association and the Russian Foundation for Basic Research (RFBR). Further support was by research scholarships from the DAAD and the Russian Ministry of Science under the joint program "Mikhail Lomonosov," by the Russian Foundation for Basic Research (projects 14-04-00501, 15-04-06685), Russian Science Foundation (project 14-14-00400) and by the foundation of "Goszadanie" from the Ministry of Education and Science of Russia.

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