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Is there a Microbial Loop in Lake Baikal?

Manfred Bölter^{a*} and Lyubov R. Izmet's'yeva^b

^a *Institute for Polar Ecology, University Kiel,
1-3 Wischhofstr, Kiel, 24148 Germany*

^b *Scientific Research Institute of Biology
of Irkutsk State University,
PO Box 24, Irkutsk-3, 664003 Russia ¹*

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The occurrence of a microbial loop in the pelagic environment is discussed with regard to hydrological and meteorological effects as well as to the planktological states during the seasons in lake Baikal. Strong local conditions due the melting ice and the sequence of the spring bloom indicate close local interactions between phytoplankton and bacteria. However, missing reports on micro-zooplankton and continuous reports of the roles of the individual organism groups involved in the microbial loop make is difficult to establish the way of matter flow in the lake as a general path. Further, sinking rates of diatoms do not allow a remineralisation of plankton-C and -N in the deep water in its upper photic levels. Thus, microbial mineralized nutrients will stay for long time in the abyssal area of the lake, which can be regarded responsible for its oligotrophic nature in the upper layers.

Keywords: Lake Baikal, limnology, microbial loop.

Introduction

The pelagic system of Lake Baikal is governed by a strong seasonality, great depth and an enormous water body and counts as the largest limnological environment on the Earth. The lake stretches more than 600 km from north to south and thus covers different climatic zones, strongly expressed by the shift in the timing of ice melting in spring / early summer. Another special character is the isolated locality with only small exchange to other water bodies, thus, many

endemic species at all trophic levels evolved. This has formed not only special organisms but also raises the question whether this system has also peculiarities in its ecology and trophic interactions.

A special topic arises about the functioning of the lower organism's food web and its role in production and mineralization. Two scenarios about the pelagic biological processes can be discussed, on the one hand, the traditional sequential food web inclusive its detritus food

* Corresponding author E-mail address: mboelter@ipoe.uni-kiel.de

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web (Wetzel, 2001), on the other hand, the more complex web with various interactive links inclusive the microbial loop (Azam et al., 1983).

The pelagic conditons

The discussion about the pelagic food web in Lake Baikal has been regarded for long time in way of the first scenario, i.e., a step wise trophic food chain, starting with primary producers, mainly diatoms, continuing with herbivorous and carnivorous zooplankton, and ending up with fish, the Baikal seal as a top predator and men. This traditional view has also been accepted for marine systems, e.g., Steel (1974). However, Steel concluded from his fish production studies at marine shelves where he thought about is a missing link in the food web, which later has been recognized as the microbial loop.

In the marine system, two further insights were gained some time ago, which fit later well into the picture of the microbial loop:

i) the two different kinds of primary production, new and regenerated production (Dugdale, Goering, 1967), and

ii) the influence of mechanical energy transfers (Margalef, 1979).

Further, the microbial loop can only work properly with an active community of protozooplankton and, certainly, with a significant contribution of dissolved organic matter which is available to heterotrophic bacteria, generally known as exudates. The question now is: are these items necessary for scenario i or ii present in all its facets in Lake Baikal by which the ecosystem can be describe properly by the one or other picture.

Consequently, the following issues have to be tackled when describing the pelagic processes and following the introduction question about the Lake's way of working:

- physical features of the euphotic zone;
- interactions between water and sediments, i.e., benthic nutrient recycling and benthic pelagic coupling;
- sources (nutrients) for the spring bloom and its dominant phytoplankton;
- features and roles of bacteria during this step in pelagic production;
- role of dissolved organic matter, its source (exudates) and availability;
- seasonal successions of dominant phytoplankton species and communities;
- succession of zooplankton communities;
- fate of particulate organic material, sedimentation and regeneration process;
- which peculiarities are known for Lake Baikal that might make it as a special ecological system?

The structure of the euphotic zone and nutrient regeneration is regulated by physical processes, i.e., stratification, turbulence, upwelling etc. Operationally, Lake Baikal can be divided into three zones, the north, the central and the south basin, just from its bathymetry (Kozhov, 1962; Semovski, 2000). Each of them show individual thaw behaviour in spring and thus different temporal structures in water masses (Killworth et al., 1996; Hohmann et al., 1997) and subsequent shifts in biological processes (Heim et al., 2005), which has been documented by differences in organic material from sedimentation traps by its distinct lipid compositions (Russell, Russell-Mele, 2005) and lead to the question of differences in autochthonous productivity. The pelagic stratification is then reflected by increases in cell numbers of phytoplankton (Jewson et al., 2008). Temperature has been proposed as a driving factor for phytoplankton succession (Richardson et al., 2000), but it seems more likely, as temperature is triggered by radiation and this, in turn, stimulates primary production.

Biological effects

The maintenance of diatoms in the photic zone, which is important for their primary production, can be increased by turbulence from wind and subsequent mixing during spring. The necessity of such turbulence for maintaining diatom production has been described by Margalef (1979). A simulation of disturbance of Lake Baikal actually influenced positively phytoplankton biomass and zooplankton fluctuations (Silow et al., 2001). Turbulent patches are variable in size and time. Wüest and Lorke (2010) found those on scales of 100 m in Lake Baikal.

Some special and local features like thermal bars are able to transport water masses and nutrients to deeper layers (Shimaraev et al., 1993), and locally they can be of great importance for the water mass (and nutrient) budget (Melnik et al., 2006). Such water of elevated salinity is also responsible for bottom water formation (Kipfer et al., 1996), and stimulates bottom currents and lateral transport of dissolved and particulate matter.

Further, the influences of river inputs have to be taken into accounts due to their input of energy and inorganic matter as well as allochthonous sources, like particulate and dissolved organic carbon, bacteria and microbiological processes (Yoshioka et al., 2002; Maksimenko et al., 2008). The input of allochthonous organic C is considered to be nearly 300 kt C yr⁻¹ (Granina, 1997). This holds also true for the main elements of earth alkali metals (Callender, Granina, 1997), and silicon shows highest accumulation rates in sediments and transport rates from rivers. A study of Hohmann et al. (1997) showed the significant influence of Selenga plume for deep-water renewal.

Seasonal effects

The start of the spring bloom is regulated by the increasing light system, and the ice thaw from

south to north. This bloom starts early in spring with the growth of *Aulacoseira baicalensis* or *A. skvortzowii* under the ice (Mackay et al., 2003). This is well confirmed by other reports, e.g., Fietz et al. (2005a), Shimaraeva et al. (2010) who report that this period is strongly dominated by diatoms, here *Stephanodiscus meyerii* and *A. baicalensis*, and *Chrysophyceae*.

During summer (July to September) blooms of small unicellular cyanobacteria were found, dominated by *Synechococcus* sp. or *Synechocystis* sp. (Belykh, Sorokovikova, 2003; Belykh et al., 2006). The numbers of 10⁶ cells ml⁻¹ are close to numbers of heterotrophic bacteria or even exceeding them (Nagata et al., 1994; Straskrabova et al., 2005; Ahn et al., 2006). Summer blooms were also described by dominance of Chlorophyta (*Koliella* and *Monoraphidium*) as well as flagellates (Fietz et al., 2005; Izvestyeva, Silow, 2010). During this time of strong stratification also *Synechocystis limnetica* was found to dominate the pelagial of the south basin (Mackay et al., 2003), an autumn bloom again can be formed again by *A. baicalensis* or other diatoms (Galazi et al., 1978; Ryves et al., 2003). Further, *Rhodomonas pusilla*, a Cryptophyceae species, and Chrysophyceae have been observed (Fietz et al., 2005a; Izvestyeva, Silow, 2010).

The great variability on diatom communities seems to be special feature of this lake, triggered by various environmental parameters (Popovskaya, 2000). The recurrent pattern of a picoplankton bloom, dominated by cyanobacteria during summer can be triggered by a stable stratification and N-depletion, which hampers phytoplankton growth, but favours a self-sustaining N-fixing community during this time. The vertical migration of zooplankton, which could help to increase the concentration of ammonia-N is obviously not sufficient to force a phytoplankton bloom. Later, after a break of this stratification by turbulence, some ammonia-N probably returns to

the photic zone and the autumn bloom can take place, again we find diatoms and green algae.

Role of the Benthos

A pelagic-benthic coupling can be assumed for these river mouths, where nutrients can be regenerated from microbes or resuspended and thus given back to the pelagic environment (Sapota et al., 2006). The deeper parts receive particulate matter via sedimentation process. However, much of the particulate organic material can be regenerated and particulate inorganic material, e.g., diatom shells, redissolved on the way through the water column. A recycling of Si in sediments, as well in the water column is regarded as an important process in geochemical cycling and has been proposed by Callender and Granina (1997).

An indication for a strong decomposition in the water column is the fact that only 28 % of surface pigments reach the bottom in the south basin (Fietz et al., 2005b), but nearly 90 % of these pigments could be related to Bacillariophyceae and Chrysophyceae. Ryves et al. (2003) and Batterbee et al. (2005) even assume that only 1 % of the diatoms accumulate in the sediments and many species dissolve (e.g., *Nitzschia acicularis*) in the water column. Hence, the organic matter is set free for microbial attack and mineralization and thus nutrients, e.g., nitrogen in the form of ammonia, may have a chance to be recirculated to the euphotic zone and to stimulate a regenerated production.

The dominant spring diatoms (*A. baicalensis*, *A. skvortzowii*), on the other hand, show high sinking rates with 60-100 m d⁻¹ (Ryves et al., 2003), which is in the same order of marine species, which accelerate their sinking rates by aggregate formation (Eppley et al., 1967; Smetacek, 1985). In this case, however, organic material (and recycled nutrients) are lost for the euphotic zone. As *A. baicalensis* is capable to

produce large free-floating macro-aggregations grown in this state, it serves as a preferred food source for bottom invertebrates (Bondarenko et al., 2006), and thus serves in these areas for a link between sediment and water.

Sediments, however, do not show an even seasonal signal. The taxa found can be related well to environmental variables, i.e., ice conditions, radiation etc. (Mackay et al., 2003). Only few data are available about benthic remineralization processes and a process, which might bring back remineralized nutrients to the euphotic zone. Maerki et al. (2006) showed that mineralization occurs in deep water sediments mainly by oxidative processes. But the return of inorganic matter to the euphotic layer is difficult. Deep ventilation has been described only as an episodic event (Killworth et al., 1996) or is due to local thermal bars (Shimaraev et al., 1993). Hence, significant amounts of nutrients from benthic processes are probably restricted to coastal areas such as river mouths.

Remineralisation in the water column

Total C-production can be assumed to be about 20 g C m⁻¹ yr⁻¹ in the south basin, and 14 g C m⁻¹ yr⁻¹ in the north basin, respectively (Müller et al., 2005, ILEC). These figures underpin the oligotrophic character of the lake which is assumed to be due to a lack of available phosphate (Müller et al., 2005) and have been confirmed by Straskrabova et al. (2005). Low concentrations of phosphate (< 15-20 mg L⁻¹ PO₄-P) have also been described as sporulation threshold for *Aulacoseira skvortzowii* (Jewson et al., 2008). Such figures have to be related to the occurring secondary production either by direct feeding of herbivorous zooplankton or via heterotrophic uptake of exudates by bacteria which then are consumed by protozooplankton which enters the food chain by carnivorous or

omnivorous zooplankton. This latter link, known as the microbial loop, was under investigation by Straskrbova et al. (2005) and presents the only intensive view on the abundance view on these critical items of the microbial loop. High amounts of dissolved organic carbon have been reported by Yoshioka et al. (2002), but not clearly related to its sources.

Due to these patterns (Silow, 1999, Moore et al., 2009) and, in more detail, Yoshii et al. (1999) describe different but straight – „simple“ – food webs from phytoplankton to top consumers for the pelagic and the benthic system, the latter underpins this finding from studies with stable isotopes. Yoshii et al. (1999) just present five steps, expressed by five ecological groups, i.e., phytoplankton (*A. baicalensis*), mesozooplankton (*Epichura baicalensis*), macrozooplankton (*Macrohectopus branickii*), fish (*Coregonus autumnalis*), and the seal (*Phoca sibirica*). There is much evidence that limnoecology of Lake Baikal works basically at these levels, as this sustains an empiric observation of the food web. Nevertheless, the bypass by the microbial loop cannot be ignored, as we see high amounts of dissolved organic matter and – at least for some time – the occurrence of protozooplankton. Figures of production rates show a decrease from low primary production ($2100 \text{ mg m}^{-2} \text{ yr}^{-1}$) to bacterial production ($748 \text{ mg m}^{-2} \text{ yr}^{-1}$), herbivorous zooplankton ($178 \text{ mg m}^{-2} \text{ yr}^{-1}$), carnivorous zooplankton ($10 \text{ mg m}^{-2} \text{ yr}^{-1}$) and fish ($4 \text{ mg m}^{-2} \text{ yr}^{-1}$) (ILEC).

External impacts

The impact of global warming has also reached Lake Baikal with effects on mean annual temperature of air and water with consequences on ice duration and biological features (Moore et al., 2009). These authors also describe the subsequent steps in physical and biological oceanographic patterns, like the shift to earlier

dates of the spring and summer bloom onsets of phytoplankton. An increase in radiation is followed by an increase in water temperature and thus water stratification and water mixing in the lake's basins. Longer periods have positive effects on primary production, phytoplankton growth and succession. Such increase in average water temperature by $1.21 \text{ }^{\circ}\text{C}$ since 1946 is reported by Hampton et al. (2008) with consequences on chlorophyll *a* contents and different zooplankton grazers. A negative influence can be expected on the growth of the spring bloom diatom *Aulacoseira skvotzowii* which is cold adapted and its mortality will increase at temperature above $6.5 \text{ }^{\circ}\text{C}$ (Jewson et al., 2008). Autotrophic picoplankton has proposed as indicators for ecosystem health in general (Munawar et al., 1994), hence, survey studies should keep an eye on this group of organisms.

Summary

This review showed a strong evidence for a strong local diversity in Lake Baikal's pelagic and benthic biology. The location of the lake and the different seasonal and local effects make it difficult to analyse the available data with respect to a comprehensive biological view. The concern is especially true for the shifting phytoplankton spring blooms from south to north as well as for the widely uncoupled benthic-pelagic systems, i.e., the pelagic system in the photic zone. The decoupling can be regarded as a main factor for the nutritional oligotrophic regime of Lake Baikal. In order to analyse the pelagic food web with respect to an active microbial loop and the nutrient recovery from deep lake environments, new approaches in research are needed. This is especially necessary, when coping the new environmental problems of global warming and increasing anthropological inputs into the lake. Studies on sedimentation, nutrient and pollution

recovery from the deep layers might become a serious problem in near future when the mixing zone might shift to deeper layers due to strong impacts from atmospheric events.

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Существует ли микробная петля в озере Байкал?

М. Болтер^а, Л.Р. Изместьева^б

^а *Институт полярной экологии,
Университет Христиана-Альбрехта,
Германия 24148, Киль, Вишхоф штр. 1-3*

^б *НИИ биологии,
Иркутский государственный университет,
Россия 664003, Иркутск-3, а/я 24*

Обсуждается существование микробной петли в пелагиали в связи как с гидрологическими и метеорологическими факторами, так и с состоянием планктона в разные сезоны в оз. Байкал. Условия, в которых происходит таяние льда и ход весеннего развития планктона, указывают на наличие сильной связи между фитопланктоном и бактериями. Тем не менее отсутствие данных по микрозоопланктону и появляющиеся сообщения о роли разных групп, вовлеченных в микробную петлю, затрудняют получение общей картины потоков вещества в озере. Кроме того, скорость погружения диатомовых водорослей не дает возможности реминерализации планктонных углерода и азота в фотическом слое. Таким образом, минерализованные бактериями биогенные вещества долгое время пребывают в абиссали озера, что и может приводить к олиготрофности верхних слоев.

Ключевые слова: оз.Байкал, лимнология, микробная петля.
