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HYDROCHEMISTRY, HYDROBIOLOGY: ENVIRONMENTAL ASPECTS

The Ecology of Meromictic Lakes in Russia. 2. Continental Water Bodies

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Abstract—Meromictic water bodies (water bodies with stable vertical water stratification, which forms because of a difference between the density of its layers) is a rare phenomenon, which deserves protection. On the territory of Russia the territory of Russia in its boundaries of 2020, 53 meromictic lakes were identified, including 30 coastal water bodies of marine origin, 10 karst lakes, 5 glacial lakes, and 4 drainless salt meromictic water bodies in arid zone. A review is given for the main ecological features of continental meromictic lakes and for original methods used to study stratified water bodies.

Keywords: meromictic water bodies, stratification, chemocline, anoxia, relic water bodies, salt lakes

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INTRODUCTION

Meromictic water bodies were found in many regions of Russia and became the focus of many studies. However, until recently, there have been no generalizing survey of such lakes. The review of Walker K.F., Likens G.E. of 1975, where they give one of the first inventories of meromictic lakes of the world, mentioned 11 lakes in USSR territory, 6 of which are in Russia [64]. Two more lakes were added to these in 2009 in the *Encyclopedia of Inland Waters* [63]. The recent review *Encyclopedia of Lakes and Reservoirs*, published in 2012, mentions 28 meromictic lakes for the entire Europe and 9 lakes for Asia [55], which is much less than their actual number, because not all Russian water bodies were taken into account.

The scientific literature presents data on 52 meromictic water bodies (with the Black Sea, the largest meromictic water body in the world, taken into account, there are 53) and their main features relating to stable stratification. The Vinogradsky Institute of Microbiology, Russian Academy of Sciences has contributed much to studying such water bodies [12, 14, 36, 51]. Integrated studies of meromictic lakes were launched in Khakassia on the basis of the Institute of Biophysics, Siberian Branch, Russian Academy of Sciences (Krasnoyarsk) in Lake Shira and two other lakes. The inventory and studies of meromictic water bodies in the Middle Volga region is carried out by the Institute of Ecology of the Volga Basin, Russian Academy of Sciences [7, 8, 24, 48, 49], and in Arkhangelsk oblast, by the Institute of Environmental Problems of the North, N. Laverov Federal Center for Integrated Arctic Research of the Ural Branch of the Russian Academy of Sciences [21, 22, 43, 61]; in the recent 10 years, integrated studies of coastal meromictic water bodies have been carried out on the basis of the White Sea Biological Station, Lomonosov Moscow State University [23, 40]. The first part of the review focuses on the coastal meromictic water bodies. This second part considers continental meromictic lakes (Table 1).

In accordance with the generally accepted definition, by meromictic water bodies the author implies those in which water layers with different chemical composition do not mix in the period of seasonal circulation or mix incompletely. The top layer is called mixolimnion, while the bottom layer, in which the density is higher and there is no circulation, is called monimolimnion; these layers are separated by pycnocline, i.e., a zone of dencity gradient. In many water bodies, the zone not involved in circulation is divided into aerobic and anaerobic parts, separated by a redox zone or chemocline. In most cases, chemocline coincides with pycnocline and the vertical structure of the water body simplifies to two layers with a transitional zone between them. Meromictic water bodies are divided into ectogenous and endogenous [64]. The formers include three types: (I) water bodies with surface inflow of fresh or mineralized water, including a continental variant Ia and a coastal marine variant Ib; (II) water bodies with surface inflow of turbid water; (III) crenogene, i.e., with inflow of mineralized groundwater. The endogenic water bodies are divided into two types: (IV) small deep water bodies, where water mixing is hampered by the shape of lake hollow and the surrounding relief; (V) water bodies with accumulation of salts in the bottom layer because of internal processes, including freezing-out during ice formation. Russian meromictic water layers are of all types except for II; in most cases, the difference between water densities is caused by more than more than one factor .

KARST AND GLACIER MEROMICTIC LAKES

The most common among continental meromictic lakes is karst type; the list presented here contains 10 such lakes. They represent a mixed type of meromixis III–IV. Many such water bodies are located in the Middle Volga Region [7, 13, 37, 53]. Lake Belovod in Vladimir oblast has been studied since before 1917 [25]; in the 1950s, it served as a model object for microbiological studies [17, 20, 29]; however, since that time, it fell beyond the focus of scientists. Lake Sakovo in Vologda oblast was studied in 1972 [14]; the meromictic character of the near-Moscow Lake Bezdonnoe can be supposed only based on the opinions of divers, because it has not been studied yet.

The type ranking third in terms of occurrence includes the lakes of glacial origin in the northwestern Russia (5 water bodies) with mixed type of meromixis III–IV.

MEROMICTIC LAKES WITH FERRUGINOUS ANOXIA

Of particular interest among karst and glacial meromictic water bodies are lakes with ferruginous anoxia. Unlike water bodies with sulfide anaerobic zone (euxinic), their monimolimnion contains few sulfates, but it is rich in bivalent iron and manganese. There are few water bodies of this type in the world, while in Russia, 7 such lakes are known. The first was the lake Urozero (Uzornoe of Okha-Lampi) in Karelia, mentioned in the list of K.F. Walker and G.E. Likens [64] with a reference to the article by V.F. Piotrovskii and B.P. Ditmar [31]. This is a relatively small lake 37 m in depth with a funnel-shaped profile. In 1964–1969, G.A. Dubinina and Z.P. Deryugina studied the microbiological processes in this water body and found, in the zone of temperature jump, several classes of iron bacteria, which accounted for 50–75% of the bacterial community [16]. Iron bacteria oxidize ferrous iron to ferric and convert it from a soluble into an insoluble state. The ferruginized envelopes of bacterial cells and the free iron hydroxide settle into a zone with reduction conditions and acid environment (low pH), where they gradually dissolve and become again available for such bacteria. Such circulation maintains the mineralization difference between the layers. The best known and studied lake with iron meromixia is Kuznechikha Lake in the Zvenigovskii raion, the Republic of Marii El. The meromictic character of this lake was first identified by researchers from the Institute of Microbiology, Russian Academy of Sciences [13, 53]. In the 2000s, a group of researchers from the Institute of Ecology of the Volga Basin (Tolyatti) continued studies and gave a detail description of the specific features of this water body [7, 37]. As iron is not toxic for living organisms, phytoplankton can exist in the anaerobic zone same time with anaerobic bacteria and produce oxygen, making the gradient between aerobic and reducing conditions smooth and chemocline, very wide. A vertical series of layers with different phototroph eukaryotes and bacteria appears in the chemocline. The very fine green algae of picoplankton size, concentrated in the upper part, are followed by the layer of purple layer of purple sulfur bacteria—anoxic phototrophs, which use hydrogen sulfide for photosynthesis, underlain by a layer with green filamentous bacteria Chloronema giganteum, typical of lakes with iron-containing monimolimnion. Lying below is a layer with mixotrophic eukaryotes (which can pass from photosynthesis to the consumption of available organic matter), which in Lake Kuznechikha are represented by euglena algae; these are underlain by green sulfur bacteria, which are tolerant to the lack of illumination. Unlike water bodies with sulfide zone, the ferruginous water bodies never contain layers with blooming cyanobacteria and cryptophytic algae, because there is no niche for them, i.e., a microsulfide layer, where other oxygenic photosynthetics cannot exist [37].

The same type of meromixis was found in Lake Zelenoe 40 km to the southeast. Lakes Konon”er and Bol’shoi Mushan-Er have been mentioned as meromictic with a high iron content [50, 52]; however, according to the data of the recent studies, these lakes became irregularly mixing [49].

An iron-manganese type of meromixis was also found in some lakes of glacial origin. A chain of five water bodies, which are studied by the Institute of Environmental Problems of the North, FECIAR UrB RAS (Arkhangelsk) exists in Kholmogorskii raion, Arkhangelsk oblast, near the source of the Svetlaya R. [22]. One of these lakes (Lake Svetloe-1), which is known better than other lakes, was classified as meromictic [38]. Two other lakes were found to have density stratification; however, the estimation of its stability requires additional observations.

Lake Svetloe-1 is transparent enough for photosynthesizing organisms—cyanobacteria Synechococcus sp., tolerant to hydrogen sulfide—to live in its chemocline between 20 and 24 m [18]. They contain a red pigment phycoerythrin and impart pinky color to the water. The same horizon contains some purple sulfur bacteria. In winter, when the lake is covered by ice, the amount of cyanobacteria is greater than in summer; however, the rate of the phososynthesis they provide is half that of anoxygenic bacteria [61].

One more lake of this type, Temnoe, is located 70 km from this group; its water, unlike that of clear Svetlye Lakes, is dark because of the humic substances. The chemocline at a depth of 22–25 m is

Table 1. Meromictic water bodies in Russia and the coverage by territorial protection measures

Water body name	Geographic coordinates	Origin of water body bed	Area, ha	Maximal depth, m	Depth to thermocline, m	Meromixis type*	Anoxia type	Specially protected natural areas
Arkhangelsk oblast								
Lake Svetloe-1	65°4′59″ N, 41°6′29″ E	Glacial	13.2	39	20–24	III–IV	Fe	No
Lake Temnoe	64°28′36″ N, 41°44′43″ E	″	9.4	37	22–25	III–IV	Fe	No
Vladimir oblast								
Lake Belovod	55°58′4″ N, 40°3′09″ E	Karst	2.0	24.5	14.5	III, IV	H_2S	Regional hydrological natural monument Belovod'e Karst Lake
Vologda oblast								
Lake Sakovo	60°31′11″ N, 38°42′22″ E	″	53	16	3.0–4.5	III, IV	H_2S	No
Zabaikal'skii territory								
Lake Doroninskoe	51°14′8″ N, 112°13′59″ E	Tectonic	450	5.4	3.0–4.5	Ia, V	H_2S	Regional hydrological natural monument Doroninskoe Soda Lake
Moscow oblast								
Lake Bezdonnoe (its meromictic character needs verification)	56°14′31″ N, 36°58′25″ E	Karst	2.4	6.3	5.0	III, IV	??	State Natural Wildlife Reserve of Oblast Significance Lake Vertlino and its Bed
Samara oblast								
Pond Nizhnii in the Botanic Garden at the Samara University	53°12′59″ N, 50°10′43″ E	Artificial, dam	0.55	5.8	1.5–3.5	III, V	H_2S	Botanic Gardens of Samara SU
Republic of Karelia								
Lake Urozero (Uzornoe or Okha-Lampi)	60°35′23″ N, 29°58′8″ E	Glacial	15.4	37	7–13	III, IV	Fe	Regional hydrological natural monument as a part of Urozero Wildlife Reserve
Lake Igumenskoe (on Valaam Isl.)	61°22′41″ N, 30°54′16″ E	″	2.2	8.0	3.0–4.0	III, IV	Fe	Natural Park Valaamskii Archipelago
Lake Chernoe (on Valaam Isl.)	61°22′45″ N, 30°54′28″ E	″	0.8	8.5	3.0–4.0	III, IV	Fe	

Table 1. (Contd.)

Water body name	Geographic coordinates	Origin of water body bed	Area, ha	Maximal depth, m	Depth to thermocline, m	Meromixis type*	Anoxia type	Specially protected natural areas
Republic of Mariy-El								
Lake Chernyi Kichier	56°4′34″ N, 48°20′26″ E	Karst	5.0	10.5	3.5	III–IV	H_2S	The territory of the National Park Mari Chodra
Lake Nonon"er (according to recent studies, it is not meromictic)	56°7′49″ N, 48°28′42″ E	″	8.3	22	10	III–IV	Fe	The same
Lake Shungadalan	56°8′56″ N, 48°26′31″ E	″	2.5	13.5	3.5	III–IV	H_2S	″
Lake Zelenoe	55°58′34″ N, 48°19′52″ E	″	5.0	19	5.5	III–IV	Fe	″
Lake Golubaya Staritsa (its meromictic character needs verification)	56°9′18″ N, 48°24′32″ E	″	0.8	8.5	4.0–4.5	III–IV	H_2S	″
Lake Kuznechikha	56°11′45″ N, 47°46′25″ E	″	9.3	20	11	III–IV	Fe	Part of the extended projected variant of Lebedan' Republican Forest-Melioration Natural Reserve
Lake Solenoe	56°33′46″ N, 47°21′47″ E	″	10.0	18	1.8	III–IV	H_2S	Integrated Republican Wildlife Reserve Lake Solenoe
Lake Palenoe	56°32′46″ N, 47°15′36″ E	″	1.1	7.5	1.5	III–IV	H_2S	Anticipated regional natural monument Lake Palenoe
Republic of Khakassia								
Lake Shira	54°30′27″ N, 90°12′19″ E	Tectonic	3600	24	6.0–8.0	Ia, V	H_2S	Part of the water area and coast enters the area Lake Shira, Khakassian State Natural Reserve
Lake Shunet	54°25′9″ N, 90°13′39″ E	″	50	6.2	4.3–5.3	Ia, V	H_2S	No
Lake Uchum	55°5′37″ N, 89°42′59″ E	″	400	7.9	4.4–5.6	Ia, V	H_2S	Resort Lake Uchum

* According to classification of Walker and Lickers, 1975.

deeply submerged into aphotic zone [39, 43]. The difference in mineralization between mixolimnion and bottom water is <20 μS/cm; however, it is sufficient for meromixis [30]. The water masses differ considerably in chemistry, and the temperature at the bed is always the same (3.9°C).

The list of the few lakes with ferruginous anoxia has been supplemented by two such lakes on Valaam Island: Igumenskoe and Chernoe. Their meromictic character was determined in the course of study at the Valaam Educational–Research Station of the Russian State University for Humanities (St. Petersburg) [5]. These lakes are small in area and protected from wind by a forest. The higher salinity of bottom water is due to the geological features of the underlying rocks, represented by ferro-gabbro-diabase with high iron content.

WATER BODIES WITH TEMPORARY MEROMIXIS

In the Middle Volga region, in addition to lakes with distinct meromixis, there are many water bodies that are similar to them by stratification, which appears for one season, but can persist over a longer time. The author of the term *meromictic* [46] considered these to be reservoirs that are mixed not more than once a year. With this definition, the lakes that do not mix at least in one circulation cycle fall into this class. Finnish researcher A. Hakala also considers them meromictic, as can be seen from her classification of meromictic water bodies [54]. Usually, these are small eutrophic and mesotrophic lakes, including karst lakes (e.g., Bezdonnoe, Maloe Karstovoe, Serebryanka in the territory of the national park Samarskaya Luka, Goluboe in the valley of the Sok R., Takhtarka in the neighborhood of Pavlovsk Town in Voronezh oblast), oxbow lakes (Bol'shoe Shelekhmetskoe in the same national park, Zereklikul and Novyi Karazerik in the middle reaches of the Ik R. in Tatarstan), humanmade ponds ponds (including lakes Podgorskoe and Gudronnoe in Samarskaya Luka national park) from ultrafresh to brackish (1.5 g/L), mostly of carbonate and some of sulfate type [7–9, 24, 48]. These water bodies show a distinct vertical gradient of mineralization, the presence of an anaerobic zone and a layer of anoxygenic phototrophic bacteria in chemocline. Maybe, there are also real meromictic lakes in the region, but they have not been adequately studied.

DRAINLESS MEROMICTIC LAKES OF ARID ZONE

Another group of meromictic water bodies includes drainless salt lakes in arid zone, where evaporation is in excess of precipitation. Freshened layer in them forms mostly due to freshwater inflow from the drainage basin (type Ia) and freezing out of salts during freeze-up period (type V). Three such lakes lie in Minusinskaya depression in the Republic of Khakassiya (Shira, Shunet, and Uchum) and one in Zabaikal'skii krai (Doroninskoe). More lakes may also be found in the future.

Lake Shira is known all over the world and has been described in a huge number of publications [32, 33, 35, 44, 45, 67]. Studies covered all components of its ecosystem and made it possible to construct a model of the water body, which adequately describes the vertical thermohaline structure and can be used to predict the position of the thermo- and halocline, as well as the layers of the concentration of zoo- and phytoplankton [42, 44, 47]. A version of the model was used to calculate the effect of changes in water level in this lake in 1910–1930, when the level dropped by 7 m [33]. Calculations confirmed that the salinity could flatten out and the lake could loose meromixis. The developed models are also applicable to other meromictic water bodies [41, 56].

The second well-studied lake—Shunet—is worth mentioning as the saltiest among the lakes of the Khakassian group with water mineralization at the bed of 90–100 g/L. This is attributed to the salt crust, which existed on the bed in the early XX century, when the lake was shallow, and which has not yet dissolved completely. Lake Shunet features the strongest density gradient (the salinity in mixolimnion is 17–20 g/L), higest among such lakes hydrogen-sulfide concentration (up to 300 mg/L), and extremely high abundance of bacteria in chemocline—up to 10^8 cell/mL [60]. The same abundance was recorded in Lake Mahoney in Canada [58] and in the meromictic Lake Trekhtzvetnoe on the White Sea coast [28]. The microbial layer in Lake Shunet sometimes consists of two sublayers: a red one with purple sulfur bacteria and cryptophyte phytoflagellates on the top and a green one with green sulfur bacteria [34].

One more lake, the meromictic status of which was detected in 2015–2016, is situated 70 km north of this lake group [33]. It occupies an intermediate position between Lake Shira with its smooth and unstable chemocline, and the strongly stratified Lake Shunet.

Lake Doroninskoe in Transbaikalia is unique in many respects. First, this is the only soda meromictic water body in Russia [12] with pH 9.6–10.5 [3]; sulfate-reducing bacteria, which use sulfates and shift the equilibrium of ions toward carbonates, contribute to an increase in alkalinity. Second, the formation of meromixis includes one more mechanism in addition to freshening due to freshwater springs, mostly in the coastal zone, and realize of salt by freezing of salts water; this mechanism is hydrogenic mineral formation [2]. It is due to the formation of crystals of calcite $CaCO_3$ in winter at the cooling of mixolimnion to temperature below zero, with subsequent settling into monimolimnion. Third, the hydrogen sulfide, which is produced by sulfate-reducing bacteria and which exists in the water body mostly in the form of hydrosulphide HS^-, is recorded all over the depth, including the oxygen zone, and its concentration has a local peak near lake surface [66]. Fourth, the purple non sulfur bacteria, which dominate in the high-density microbial community of chemocline, can change their metabolism from photosynthesis to chemotrophic type [57].

MEROMICTIC WATER BODIES OF ARTIFICIAL ORIGIN

No data on meromictic water bodies of artificial origin in in Russia have been found in the scientific literature. Such water bodies form in flooded mines, as, for example, lakes Cueva de la Mora in Spain and Goitsche in Germany [45], flooded quarries in Lvov oblast in Ukraine [6], including Pomyaretskoe Lake, studied by microbiologists in the 1970s [15], or Lake Atomnoe on Semipalatinsk test ground, which formed because of a nuclear explosion [1].

The only artificial continental meromictic water body is the Nizhnii Pond in the Botanic Gardens at the Samara State University. Systematic integrated studies of this water body have been carried out since 2004 by the Institute of Ecology of the Volga Basin, Russian Academy of Sciences [11]. The water body was formed by a dam, and the difference between the densities of its layers has a double origin. It is partly biological, because of precipitation of calcium carbonate during active photosynthesis, followed by dissolution in the bottom layer, and, partly, crenogene due to mineralized springs. Ice cover also plays a significant role. Ice melting leads to a decrease in the TDS in the surface layer, and the density difference that forms in this case is sufficient to prevent total spring circulation. The monolimnion contains hydrogen sulfide in concentration up to 180 mg/L. As is the case with many other meromictic water bodies, the upper stage within chemocline here is occupied by cyanobacteria, followed in lower layers by purple sulfur bacteria, and deeper, by green sulfur bacteria [10]. Bacteria do not form a dense population with a high color, maybe because of their grazing by infusoria, for which the zone of maximal abundance coincides with the layer of anoxic phototrophs. The Nizhnii Pond of the Samara Botanic Gardens is among the few Russian meromictic water bodies where infusoria are well studied; a peak of their diversity lies in the chemocline [4]. Within it, three communities coexist: the top stage is occupied by a community with aerobic benthic migrants; the middle stage, by mixotrophs, which are well adapted to the life under oxygen deficiency, because they use the oxygen released by their symbionts; and the bottom stage is occupied by sapropel infusoria, which feed on bacteria bacteria in the anaerobic part of chemocline.

ORIGINAL METHODS FOR STUDYING MEROMICTIC WATER BODIES STOP

Studying the meromictic water bodies with their contrast layers and gradient zones requires special means and methods other than those commonly used to investigate continental water bodies and seas. The main problem is related with the zone with strong vertical gradients, where the result of measurements depends on the accuracy of positioning a probe or a sampler. Water samples can be taken with a step of several centimeters along the vertical with the use of multisyringe samplers. Researchers from the Institute of Biophysics, Siberian Branch, Russian Academy of Sciences, have patented a sampler with syringes spaced 5 cm apart [59]. An analogous sampler with a different principle of opening was designed at the White Sea Biological Station, Moscow State University; this sampler has a sampling interval ≤2.5 cm, and the syringe can be extracted from it unopened. To avoid the contact of sample with oxygen, the syringes can be transported in a vessel prefilled by argon. Researchers from the Institute of Natural Resources, Ecology, and Cryology, Siberian Branch, Russian Academy of Sciences (Chita), in their work at Lake Doroninskoe, used a vacuum water sampler with an intake tube fixed on a vertical mast [26].

The vertical distribution of amphipods in lakes Shira and Shunet was studied with the use of a high-resolution camera-recorder with a leakproof box [65]. An especially directed laser beam was used to form an illuminated plain in front of the camera, and the particles flashed when crossing this plane. A frame was mounted in front of the objective to indicate the counting area.

Layers with different physicochemical properties are sometimes not horizontal, and their mapping requires many profiles with many parameters to be analyzed in different parts of the water body. A special autonomous sounding measurement system EKO-ZOND was designed in the Special Design Engineering Bureau for Automation Equipment for Marine Studies, Far East Branch, Russian Academy of Sciences (Yuzhno-Sakhalinsk C.). This system moves the the probe in the vertical direction and performs measurements at specified depths; the collected data are transferred via radio or satellite channel in automatic mode to a computer on the shore or a ship [19].

In stratified water bodies with turbid interlayers, special devices are required to measure the amount of light energy reaching different depths. Probes for determining photosynthetically active radiation (PAR) are sensitive in the part of the light spectrum that excites chlorophyll *a*, while photosynthetics with other pigments, for example, anoxygenic phototrophic bacteria, are sensitive to other parts of the spectrum. A sensor, consisting of a silicon photodiode and a combination of glass optical filters for light absorption in UV and IR bands and the registration of photon flux in the visible part of the spectrum was designed in the Institute of Ecology of the Volga Basin, Russian Academy of Sciences (Togliatti C.) [37]. Researchers from the White Sea Biological Station, Moscow State University, solve this problem with the use of a modified lux meter with a water-tight submersible sensor. It can be used to measure the illumination in the blue-green part of the spectrum, which penetrates deep into water, and to which human eye is sensitive. A illumination meters in different bands with appropriate light filters are also used to study heat exchange in Lake Doroninskoe [56].

For determining the taxonomic composition of phototrophic microorganisms, researchers from the Faculty of Physics, Lomonosov Moscow State University, developed several for identifying the dominating group of anoxic phototrophs, evaluating the contributions of various taxa to the total bacterial pool by fluorescence spectra and light absorption spectra, determining the concentrations of bacteriochlorophylls *d* and *e* by the area of the long-wave absorption band without extraction of pigments. The formulas for calculating bacteriochlorophyll concentrations, proposed by the authors [27], can be used, in particular, in automated monitoring systems, which can be developed in the future.

Molecular-genetic methods are very promising for studying the microbial community. The abundance of green sulfur bacteria in Lake Shunet chemocline was successfully evaluated in the Institute of Biophysics, Siberian Branch, Russian Academy of Sciences, by fluorescent in-situ hybridization (FISH) with probes specific to sulfate-reducing, green sulfur, and purple sulfur bacteria [33]. The method allows to avoid cultivating microorganisms and count of the cells on filters and excludes errors in their determination.

CONCLUSIONS

The analysis of the scientific literature on Russian territory in the boundaries of 2020 revealed 20 continental meromictic water bodies, including 10 karst, 5 glacial, and 4 drainless salt lakes in the arid zone, one pond of human-made origin, as well as two karst water bodies, which in recent years have lost their long-existing meromixis. Their number is far in excess of those given in the summaries published before. In the opinion of experts taking part in inventory of this type of lakes in various regions, the intensive search will, no doubt, give new cases. This is true, primarily, for karst lakes, which already include three potential members of this list, requiring only the confirmation that the stratification persists all year round. It is also reasonable to search for new objects among salt lakes in the arid zone. Among the lakes of glacial origin, two lakes from the lake system of the Svetlaya River in Arkhangelsk oblast are also candidates to the list of meromictic lakes. A large number of lakes have never been examined for possible meromixis. All the known meromictic water bodies are concentrated in nine regions, where there are scientific groups focused on their study; however, the major portion of the vast Russian territory still remains a blank spot.

Compared with the meromictic water bodies of marine origin, the continental ones are more diverse either in terms of their origin (karst, glacial, drainless salt) or in their salt composition and the mechanism of anoxia formation (euxinic or iron–manganese). Nevertheless, they have much in common, especially in what regards the functional organization of chemocline and the anaerobic zone, where microorganism communities, which perform the same geochemical functions, are formed. Regrettably, meromictic water bodies have been studied very unevenly; therefore, they cannot be compared in terms of some characteristics. Each group of lakes contains those subjected to long-term integrated studies; however, most lakes have been studied not fully, and some even have no scientific publications describing their annual hydrological cycles. The authors hope that this review will stimulate the search for new meromictic water bodies and more detail studies of those already known.

Though the number of meromictic water bodies was found to be greater than expected, they are still rather rare and are to be taken under territorial protection as unique hydrological objects. Compared to the coastal marine meromictic water bodies, among which territorial protection measures have been taken for less than a half, the situation with continental ones is better. Out of the 22 water bodies included in the presented list, 15 are under protection and 2 more are included in the list of specially protected areas. However, it is of importance to provide such measures for all meromictic water bodies together with the surrounding landscapes.

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