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Ecology of Meromictic Lakes of Russia. 1. Coastal Marine Waterbodies[1]

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Abstract—Based on the analysis of scientific literature for the period from the end of the XIX century to the present, as well as the author's own research, the information about meromictic waterbodies in Russia has been collected. The list includes 54 water bodies, 31 coastal water bodies of marine origin and 22 inland waterbodies, as well as the Black Sea, the world largest meromictic waterbody. An overview of the main ecological features of the most numerous categories of Russian meromictic waterbodies, the coastal waterbodies of marine origin, is presented.

Keywords: meromictic waterbodies, stratification, chemocline, anoxia, relict waterbodies, salt lakes

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INTRODUCTION

Meromictic waterbodies are rare and scattered throughout the world. The author of the term Austrian limnologist Ingo Findenegg [49] introduced it in contrast to holomictic, fully mixed waterbodies, and called it water bodies with stable vertical stratification, which arises due to the difference in the density of water layers and persists for at least several years, and in many cases, hundreds and even thousands of years.

A huge array of data on meromictic waterbodies has been accumulated abroad, where an inventory is carried out and a classification has been developed [51, 54, 57, 61]; it is generally accepted that they all deserve protection. In Russia, meromictic waterbodies have not yet been cataloged. In the first list of meromictic lakes published by Walker and Lickens in 1975 [64] 11 waterbodies are mentioned on the USSR territory. Six of them are located in Russia: three karst lakes in the Republic of Mari-El, one each in the Vladimir Oblast and in Karelia, and Lake Mogil'noye on Kildin Island in the Barents Sea. In the "Encyclopedia of Inland Waterbodies" published in 2009 [61], two of the most famous waterbodies of Khakassia, lakes Shira and Shunet were added to this list. In 2012, the "Encyclopedia of Lakes and Reservoirs" [52] lists 28 meromictic lakes throughout Europe and nine in Asia. These numbers are clearly underestimated due to the lack of information about Russian territory.

In the present review, the information on all meromictic waterbodies available in the scientific literature is collected. Within the borders of the territory of Russia for 2020, 53 meromictic waterbodies have been identified (the 54th one, the Black Sea, the largest meromictic waterbody in the world, part of which is under the jurisdiction of Russia should be added). Among them there are 31 coastal waterbodies of marine origin, 12 karst lakes, five glacial, four landlocked salt meromictic waterbodies in the arid zone and an artificial pond. Due to the large number of waterbodies and publications about them, the review is divided into two parts: the first is devoted to coastal marine meromictic waterbodies; the second, to continental ones.

MAIN FEATURES OF MEROMYKTIC WATERBODIES AND TERMINOLOGY

Depending on the factors that determine the differences in water layers, meromictic waterbodies are divided into ectogenic and endogenous types [51, 61, 64]. In ectogenic waterbodies the meromixia arises from the influx of water with a different salinity from the outside – either fresh water into a salty body of water, or salty water into an initially fresh one. They are divided into three types: type I – the waterbodies with surface inflow of fresh or mineralized waters, including the continental variant Ia and the coastal sea variant Ib; type II is for cases with the inflow of waters enriched in organic substances or nutrients, which leads to the deposition of organic matter and an increase in mineralization in the bottom layer due to

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its decomposition; type III – crenogenic, where meromixia appears due to the influx of underground mineralized waters. In the endogenic waterbodies stratification of the water mass by density occurs due to effect of internal factors. These are either small deep waterbodies, where mixing is impeded by the shape of the lake basin and the surrounding relief (type IV), or waterbodies with accumulation of salts in the bottom layer due to freezing during ice cover period or other similar processes (type V).

In Russia, the most common variant of meromictic waterbodies is coastal marine (Table 1). Density stratification in them is formed as a result of the overlap of seawater by fresh runoff, which corresponds to ectogenic waterbodies of the coastal marine type (Ib).

The stable heterogeneity of the distribution of physical and chemical factors creates a vertical sequence of ecological niches. For the upper water mass subject to seasonal circulation, the name "mixolimnion" is adopted; the lower layer with a higher density, not subject to circulation, is called monimolimnion. The aquatic communities of the mixolimnion are formed under the same conditions as the communities of holomictic waterbodies of the same region, and are similar to them in composition (at the same level of mineralization, trophic state, and morphology of the waterbody). In the bottom zone, an anoxic (i.e., devoid of oxygen) zone is often formed, where conditions from the distant past of our planet are reproduced and microorganisms with ancient variants of metabolism develop *en masse*. The vertical structure of layers with a predominance of oxidizing and reducing conditions is universal not only for different historical eras, but even for other planets. According to NASA data obtained from the Curiosity rover, Martian Gale Crater was once a meromictic lake, which had two layers: the upper aerobic layer with oxidized metal compounds and the lower one with reduced forms [53].

The anaerobic part of monimolimnion may be either euxinic (this term is applied to the hydrogen sulfate variant of anoxia arising from sulfate-reducing bacteria that carry out sulfate respiration: they oxidize organic matter with sulfate to form reduced sulfur compounds, including hydrogen sulfide), or ferruginous (which is maintained by cyclic redox transformations of iron). In the coastal meromictic waterbodies, sulfate reduction is predominant.

The variability of physicochemical parameters decreases from the surface to the bottom up to the constancy of thermohaline characteristics in the lower part of the monimolimnion. An example is Lake Trehtsvetnoye in the Kandalaksha Bay of the White Sea (Fig. 1). Seasonal temperature fluctuations (from 0 to 25.1°C) in its fresh surface layer correspond to climatic conditions, while in the salty monimolimnion the temperature (6.1–6.3°C) is practically constant and remains unchanged even during the freeze-up period.

The transition zone between mixolimnion and monimolimnion is usually called chemocline [54], which in the classical version serves as a pycnocline (density jump zone) due to the difference in the concentration of mineral salts (halocline), and often also the redox zone (transition from the aerobic zone to the anaerobic one). However, in many meromictic waterbodies, especially in coastal ones (with which this article deals), there is another layer between the halocline and the redox zone, protected from thermal circulation by a jump in density, but at the same time aerated due to the vigorous activity of phytoplankton releasing oxygen during photosynthesis (Fig. 2). Therefore, the term "chemocline" should be used with a certain caution. This article uses this term synonymously with the redox zone, whether it is the same as a halocline or not.

In the chemocline, the conditions are often favor the development of anoxygenic phototrophic bacteria. These microorganisms use reduced compounds, for example, hydrogen sulfide, for the most ancient variant of photosynthesis, during which not oxygen, but sulfur is released.

OVERVIEW OF KNOWN COASTAL MEROMYCTIC WATERBODIES IN RUSSIA

The majority of coastal meromictic lakes are concentrated in the areas of coasts uplifts. On the shores of the Barents and White seas, the waterbodies at any stage of isolation from the sea may be found. K.M. Deryugin, L.A. Zenkevich and E.M. Kreps found many such waterbodies at the beginning of the 20th century on Novaya Zemlya Archipelago [10, 12, 18], including Chernaya Guba (bay), where nuclear tests were later carried out. Access to these areas is prohibited, but all the waterbodies they described have survived.

Lake Mogil'noye

The best known coastal meromictic waterbody is the relict Lake Mogil'noye on Kildin Island. This is the only anchiolin lake (i.e. having an underground connection with the sea; it is carried out in depth through a filtering rocky bulkhead) in Russia., Lake Mogil'noye has the longest history of study of all the meromictic lakes in Russia. This history goes back to 1887, when Atlantic cod was caught in this lake, that at first was thought as freshwater. Later it was found that under the fresh water layer there is a salty one, where the cod lives. The Kildin cod (*Gadus morhua kildinensis*) is a subspecies of Atlantic cod, endemic to the Lake Mogil'noye, and listed in the Red Data Book of Russia. During its isolation, it acquired morphological and genetic differences from the Barents Sea population [32, 48, 65].

In the late XIX to early XX centuries, the lake was studied by the expedition of K. M. Deryugin, which

Table 1. Coastal meromictic waterbodies of Russia (hal. – halocline, chem. – chemocline)

Waterbody name	Geographic coordinates	Area, ha	Maximal depth, m	Depth of halocline/ chemocline, m	Specially Protected Natural Territory
			Black Sea		
Black Sea	44° N 35° E	43640200	2210	150–200	No
			Barents Sea coast		
Lake Mogil'noye	69°19′9″ N 34°20′60″ E	9.6	16.5	2.0 (hal.), 8.0–9.0 (chem.)	Federal hydrological nature monument "Lake Mogil'noye"
Ivanovskaya Guba, upper trough	68°14′26″ N 38°47′26″ E	98	20	2.0–6.0 (hal.), 12 (chem.)	State complex nature monument "Guba Ivanovskaya" on the coast
Lake Sisjajarvi	69°38′16″ N 31°31′54″ E	67	41	Needs specification	No
Kislaya Guba	69°21′58″ N 33°4′23″ E	117	36	5.0 (hal.), 15 (chem.)	No
Chernaya Guba on Novaya Zemlya. Lake 4	70°40′57″ N 54°34′4″ E	0.8	3.0	2.0	Novaya Zemlya nuclear test area, closed access
Chernaya Guba on Novaya Zemlya. Lake 9	70°43′29″ N 54°26′42″ E	0.8	3.0	2.0	Same
Chernaya Guba on Novaya Zemlya. Second trough of first stop	70°40′49″ N 54°36′16″ E	208	38	25	″
			White Sea coast		
Lake Mertvoye in Dolgaya Guba (Bolshoy Solovetskiy Island)	65°2′52″ N 35°45′43″ E	1.0	7.0	2.0	No
Kanda Guba, Fedoseyevskiy Reach	67°5′50″ N 32°10′34″ E	157	14	9–10 m	No
Lake Savino-Kanozero	67°9′35″ N 32°22′32″ E	4.7	4.4	1.0 (hal.), 3.0–4.0 (chem.)	No
Laguna 1 on Lake Telyach'ye	67°6′56″ N 32°18′51″ E	1.0	3.0	1.0–2.0 (hal.)	Kandalaksha State Natural Reserve
Laguna 2 on Lake Telyach'ye	67°6′54″ N 32°19′15″ E	1.8	3.4	1.0–2.0 (hal.)	Same
Lake Bol'shoye Khruslomeny	66°43′1″ N 32°51′34″ E	75	21	1.5–2.0 (hal.), 2.75 (chem.)	No
Lake Kislo-Sladkoye	66°32′54″ N 33°8′5″ E	1.78	4.5	1.0 (hal.), 2.0–3.5 (chem.)	State Regional Complex wildlife sanctuary "Polyarnyi Krug"
Lagoon Cape Zelenyi	66°31′50″ N 33°5′42″ E	2.0	6.5	1.0 (hal.), 4.5–5.5 (chem.)	Same
Lake Elovoye (Elovyi Navolok, 1st Kumyazh'ye)	66°28′55″ N 33°16′49″ E	5.0	5.5	1.0 (hal.), 3.0 (chem.)	″
Lake Nizhneye Ershovskoye	66°28′55″ N 33°16′49″ E	8.9	2.7	2.2–2.5	″
Lake Trehtsvetnoye	66°35′33″ N 32°58′43″ E	3.5	7.5	2.0	No

Table 1. (Contd.)

Waterbody name	Geographic coordinates	Area, ha	Maximal depth, m	Depth of halocline/ chemocline, m	Specially Protected Natural Territory
Lake Vpnyuck'e in Chupa Guba	66°17′23″ N 33°19′52″ E	15	2.2	1.0 (hal.), 1.9–2.0 (chem.)	No
Lake of Tonisoar Island	66°9′39″ N 34°13′33″ E	2.5	10	1.0 (hal.), 8.0–9.0 м (chem.)	No
Lake Merolambina	66°10′1″ N 34°10′56″ E	20.5	8.0	1.0 (hal.)	No
Glubokaya Guba near Sonostrov Island	66°10′3″ N 34°9′8″ E	5.0	7.7	6.0 (chem.)	No
Bering Sea coast					
Gladkovskaya Lagoon	54°44′3″ N 167°43′26″ E	16.2	8.3	3.0–6.0	S. V. Marakov Komandor Natural Biosphere Reserve
Pacific Ocean coast, Kamchatka Bay					
Lake Kultuchnoye	56°29′31″ N 163°0′42″ E	9900	12	4.0–8.0 m	No
Lake Bol'shoy Vilyuy	52°49′41″ N 158°32′53″ E	8100	7.0	4.0	Base waterbody of Vilyuysk salmon hatchery
Sea of Japan coast					
Lake Dukhovskoye	44°38′54″ N 136°12′40″ E	147	4.5		Regional nature monument "Dukhovskiye Ozyora "
Lake Mramornoye	44°38′0″ N 136°12′27″ E	37	4.0		Same
Lake Krugloye	44°36′45″ N 136°12′43″ E	27	7.8	5.0	″
Sea of Okhotsk coast					
Lake Tunaycha	46°46′25″ N 143°10′29″ E	17400	34	15	Regional complex nature monument "Ozero Tunaycha"
Lake Izmenchivoye	46°52′17″ N 143°6′59″ E	820	6.0	Varying	No
Lake Ptich'ye	46°24′7″ N 143°33′28″ E	3200	10	0.5–2.0 at open and 5.0 at closed channel	No

resulted in the publication of a monograph about this lake [11]. The second monograph was devoted to studies of the bacterial community of Lake Mogil'noye, carried out by the founder of marine microbiology B.L. Isachenko [13]. He discovered a pink interlayer at the border of the aerobic and hydrogen sulfide zones and explained it by the massive development of photosynthetic purple sulfur bacteria that use hydrogen sulfide incoming from below. Two more monographs summarized the combined studies by the Murmansk Marine Biological Institute (MMBI), Russian Academy of Sciences [35] and the Polar Institute of Fisheries and Oceanography (PINRO) [34]. They pointed to a gradual change in the vertical structure of the lake: in the surface layer, previously fresh, salinity increased and, in addition, the boundary of the spread of hydrogen sulfide rose up. These changes did not stop even after the termination of economic activities in the catchment [62]. By the end of the second decade of the XXI century,.the depth of the freshened layer decreased from 5 (as at the beginning of the 20th century) to 2 m, the salinity in it increased to 5.3–10.7‰, and the freshwater plankton community was replaced by a brackish water type [63]. The border of the anaerobic zone, which at the end of the XIX century was at a depth of 14 m, rose to 7.9–8.5 m. Now hydrogen sulfide fills half of the lake's depth, and its concentration in the bottom layer has reached 122–227 mg/L. Catastrophic changes have occurred in benthic communities: the zone of benthos habitat has decreased, bivalve mollusks *Astarte montagui* and colonies of sessile polychaete worms *Pseudopotamilla reniformis* have disap-

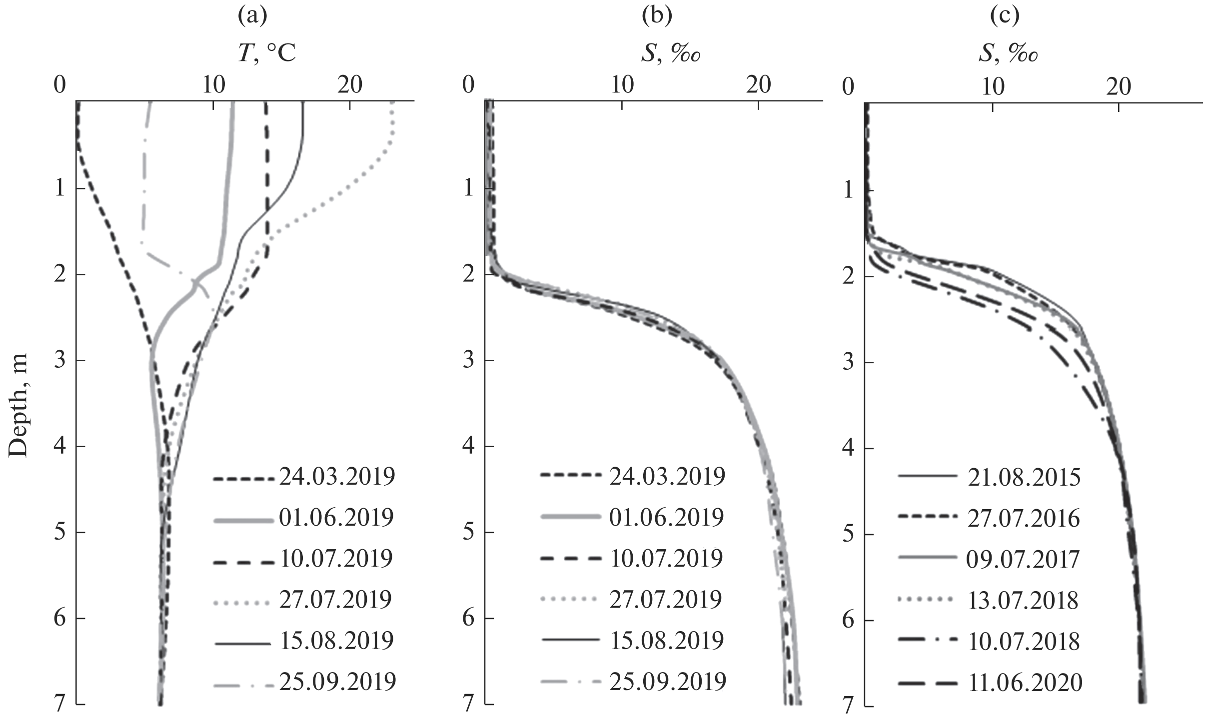

Fig. 1. Variability of thermohaline characteristics in the coastal meromictic Lake Trehtsvetnoye (Kandalaksha Bay of the White Sea); vertical profiles of temperature (a) and salinity (b) in different seasons of 2019 and in the summer period of different years (c).

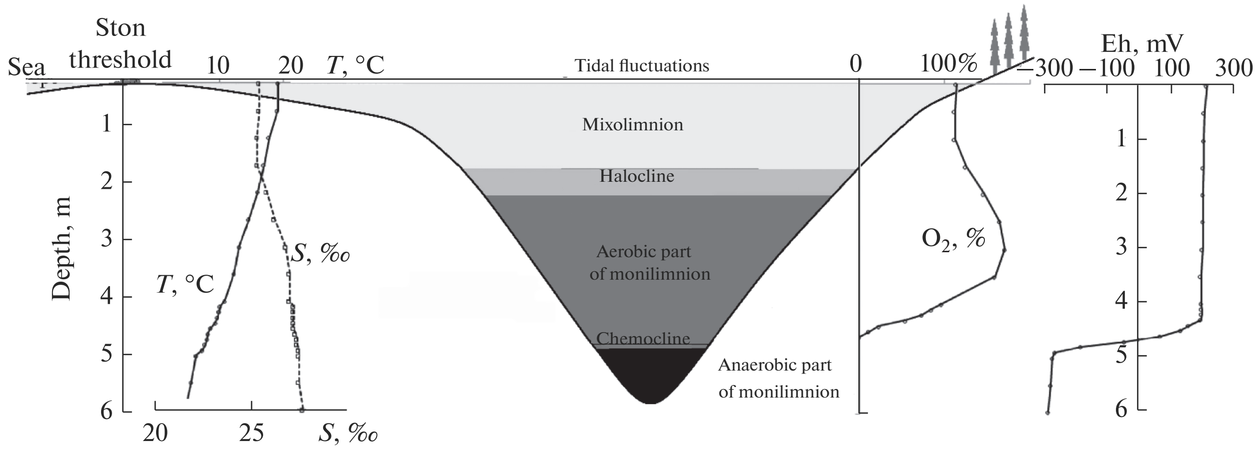

Fig. 2. Vertical zoning of meromictic lagoon of Cape Zelenyi Kandalaksha Bay of the White Sea, July 8, 2018).

peared. A change in the dominant species of bacteria in the colored layer is also associated with progressive hydrogen sulfide contamination. Already in the 1970th not purple, but more severe anaerobes—green sulfur bacteria *Ch. phaeovibrioides* brown in color [50]. Comparison of the photosynthesis intensity of phytoplankton in the aerobic zone and anoxygenic phototrophic bacteria at the border of the distribution of hydrogen sulfide revealed that in the latter it is fourfold higher. Later, such pattern was confirmed in other meromictic waterbodies. In 2018–2019 colored layer in the Lake Mogil'noye rose to 8.5–9 m and is still formed by green sulfur bacteria.

It is believed that salinization of the upper layer in the Lake Mogil'noye relates to the climate change. Analysis of data from the nearest "Teriberka" meteorological station over the past 130 years showed that summer temperatures are gradually increasing, winters have become milder and little snow, which leads to a decrease in freshwater runoff [3]. However, it is likely that the progressive hydrogen sulfide contamination is driven by another factors: the weakening of water exchange with the sea due to a decrease in the permeability of the dam.

Fjord Lagoons in the Ivanovskaya and Ambarnaya Bays

The upper trough of the Ivanovskaya Guba (bay) on the coast of the Kola Peninsula is considered as an analogue of Lake Mogil'noye. The Ivanovskaya Guba is a fjord-like bay, separated from the sea by a narrow shallow canal and divided by transverse rapids into three reaches. A stable vertical stratification is observed in the upper one [1]: the surface layer is desalinated to 10–14‰, the middle layer is salty and saturated with oxygen, the lower water mass with a salinity of 24‰ contains hydrogen sulfide. Unlike the Lake Mogil'noye, the border of the spread of hydrogen sulfide here has not changed over the past decade.

According to V. N. Semenov [41], who studied the marginal waterbodies of the Kola Peninsula, there are no other analogues of Lake Mogil'noye in Murman. However, another potential analogue which is still poorly studied in hydrological aspect, is known: Lake Sisiajärvi in the Ambarnaya Guba head [9]. There are two isolated reaches at the head of this bay: the lower one, Lake. Linjalamppi, connected to the sea and aerobic to the bottom, and the upper, Lake Sisiajärvi, where circulation is weakened and stable temperature stratification is recorded. In its near-bottom layer there are signs of hydrogen sulfide contamination, at least periodically. Hydrochemical studies have not been carried out there, but the high abundance of saprobic polychaetes *Scalibregma inflatum* and the low abundance of echinoderms, which are common in the open part of the bay, serve as an indirect indicator of anoxia.

Marine trough Bays

The marine trough bays is one another variant of the waterbodies with stable vertical stratification. The examples of such waterbodies are Lake Linjalamppi and the first two reaches of the Ivanovskaya Guba. G.S. Gurvich [8] called as “troughs” the bays bounded by shallows with deep holes and the same amplitude of tides as in the outer areas. The first studied was the Dolgaya (Glubokaya) Guba on the Bol'shoy Solovetskiy Island, connected by two narrow straits with the Onega Bay of the White Sea. At the end of the XIX century, N. M. Knipovich discovered in this bay the Arctic benthic fauna dominated by the bivalve mollusks *Portlandia arctica* (previously known as *Joldia arctica*) at an unusually shallow depth for them [14]. He suggested that this bay is a refugium of relict Arctic fauna. Later, similar communities were found in other White Sea bays: Bab'e More, Lov, Kolvitsa, and Palkina [5, 8, 27, 29].

Psychrophylic forms may exist there due to the structure of two immiscible layers: the upper one, which is freshened to varying degrees and warms up in summer, and the lower salty with temperatures below zero often occurring even in summer. In the White Sea the negative temperature starts from a depth of 100 m while in the trough bays, from 15–20 m. The lower layer is renewed more slowly than the upper one and is replenished only in winter [30]. However, as a rule, there is no anaerobic zone in the White Sea trough bays; the oxygen concentration in the lower water mass is often even higher than in the surface one [28]. The troughs may become euxinic under the influence of anthropogenic factors, e. g. during the installation of mussel plantations, and very rarely, naturally.

Lakes and lagoons on the White Sea coast

Another variant of marginal waterbodies with stable stratification, among which there are many euxinic ones, are the coastal lagoons and lakes, separated from the White Sea as a result of the prostglacial rise of the coast. Their isolation progresses as the rise continues at a rate of 1–4 mm per year [36, 42]. In the Kandalaksha Bay, the combined studies organized by the White Sea Biological Station of Moscow State University revealed more than two dozen waterbodies at different stages of isolation [16, 46]. The typological series drawn on their base reflects the chronology of the transformation of ecological communities and makes it possible to reconstruct the evolution of the waterbody [17, 24]. According to the data of paleolimnologists who studied the bottom sediments of lakes on the Solovetsky Islands [42], in this area a sea bay transforms into a freshwater lake during the period of several centuries.When the threshold separating the bay from the sea rises above the low water level, the tidal fluctuations in the waterbody weaken and become asymmetrical with a short high tide and a long low tide. Among such waterbodies are the lagoon at Zelenyi Cape, the lake at Tonisoar Island and the head of Glubokaya Guba bay near Sonostrov Island [15]. When the threshold rises above the average tide level, seawater will only inflow during syzygy (for example, in Lake Kislo-Sladkoye), at the further rise, their frequency decreases to one to two times a year (in Lake Nizhneye Ershovskoye), then they occur at multi-year intervals (in lakes Elovyi Navolok and Trehtsvetnoye).

Within the wind mixing zone, limited to a depth of 1–2 m, the surface layer is diluted and becomes more and more freshwater. The composition of the fauna in it changes according to the changing water salinity [17, 24]. Sea water remains under the desalinated layer for a long time. As long as there is water exchange with the sea, the upper part of the saline zone remains aerobic and serves as a habitat for marine benthos. The less the sea water inflows, the narrower becomes the saline aerobic layer and the habitat of marine organisms shrinks. The biomass of benthos and the number of species decrease. Eventually, the salty aerobic layer and its inhabitants disappear.

Simultaneously, bacterial sulfate reduction is activated in the bottom depression of the waterbody [58]. The stronger the isolation, the higher the concentration of hydrogen sulfide and the sulfate-chloride ratio shifts towards chlorides [4].

Colored interlayers with anoxygenic phototrophic bacteria usually appear in the chemocline of the White Sea coastal waterbodies. The water in them is colored green if the green-colored form of *Ch. phaeovibrioides* dominates; the color becomes reddish if the brownish colored form dominates [55, 56, 59]. In the White Sea waterbodies, the purple sulfur bacteria responsible for the pink layer in Lake Mogil'noye a hundred years ago, are usually innumerous. Chemocline is the most productive zone in the separating waterbodies due to the fact that the rate of anoxygenic photosynthesis in it is several times higher than that of oxygenic photosynthesis of phytoplankton in the aerobic zone of the same lake [39]. Chemocline accounts for the highest intensity of dark fixation of CO_2 and chemosynthesis, as well as of sulfate reduction (which in the waterbodies lacking stratification occurs most actively in the surface layer of the bottom sediments). Subtle biogeochemical processes at the border of the aerobic and anaerobic zones and the participation of microorganisms in them are of particular interest for science but are still poorly studied. For example, a bacterial process new to salt waterbodies – the photodependent oxidation of methane, was recently revealed in the chemocline of one of the White Sea lakes [38].

Presence of sharp vertical gradients is a characteristic of the chemocline. This is why, a small-scale series of ecological niches is formed in it. This series, in addition to the colored bacterial layer, also includes a layer of mixotrophic protozoans adjacent to it from above. These protozoans are capable of switching from photosynthesis to consumption of ready-made organic substances and vice versa. Among these organisms may ciliates with phototrophic endosymbionts, dinoflagellates with kleptoplastids (chloroplasts borrowed from other microalgae) or cryptophytic flagellates, which may reach the number causing "hyper-blooming" there and form a colored layer themselves [55]. It seems very likely, that they are exploiting bacterial production. The layer with a high density of unicellular organisms provides food for zooplankton, and, thus, the production of anoxygenic photosynthesis is transmitted through them to higher trophic levels, to fish and invertebrates, i. e. to the community of the overlying aerobic zone of the reservoir.

Coastal Water Bodies with Anthropogenic Isolation

Stable vertical stratification and the related anoxia in the waterbodies separated from the sea may occur naturally, but more quickly with human intervention. At Lake Bolshie Khruslomeny on Olen'iy Island in Kovda Bay, a natural threshold was built up at the end of the 20th century aimed in the desalination of the waterbody for refilling with water of the steam machines of the sawmill [23]. Instead of the fresh waterbody, it turned to a meromictic waterbod with brackish water at the surface, salt water below 1.5 m, and a sulfide zone starting from 3–5 m. In the Solovets Dolgaya Guba, the erection of a dam in 1854, which blocked water exchange through one of the straits, led to bottom anoxia. Hydrogen sulfide was noticed already at the beginning of the 20th century [45], and by the end of XX century it was found that compared to the middle of the XIX–early XX centuries the species composition of benthos has changed. Several previously numerous species have disappeared: the sea urchins *Strongilocentrotus pallidus*, the ophiura *Ophiopholis aculeata*, and the brachiopod *Hemithyris psittacea* [31, 43]. Fractal separation of small waterbodies also occurs within this bay, and euxinic meromixia is also observed in them, as, e. g. in Lake Mertvoye [40].

The Kanda Guba in the head of the Kandalaksha Bay is a striking example of anthropogenic isolation. This bay was blocked off in two places: in 1916 by a railway dam and in the late 1960s, by automobile route dam. The waters of the Kanda River have freshened most of the bay, but in the bottom depressions, the salt water processed by sulfate-reducing bacteria has been preserved in some places. Hydrogen sulfide and methane accumulate there, and the composition of anions has also changed: the proportion of chlorides and carbonates has increased, while the proportion of sulfates has decreased. In the Fedoseevsky Reach, which is completely isolated from the sea and is adjacent only to freshwater areas, the bottom layer of salt water, most likely, has been stored for more than a hundred years [37].

The Barents Sea Kislaya Guba, a 3.5 km long fjord, became natural-technogenic meromictic system appeared as a result of building in 1968 the first (and so far the only) tidal power electric plant (TPEP) in Russia. Immediately after isolation, signs of stagnation appeared at the bay head: the upper 5–7 m became freshwater and hydrogen sulfide appeared deeper than 15 m. Previously, the waterbody did not freeze, but now every winter it covered with thick ice. All these factors led to the degradation of littoral fauna and flora, depletion of plankton and fish fauna.

After the putting in action of TPEP, water exchange improved; however, further changes in the operating mode led either to a complete cessation of water exchange and repeated sharp depletion of oxygen, or to a temporary improvement in the ecological situation [25]. Observations of the dynamics of benthic communities in this bay made it possible to develop a model scale for assessing the state of macrozoobenthos during isolation of a waterbody [47]. The first to die out are the filter-feeding mollusks, then, the burrowing organisms; further, only chironomid larvae and oligochaete worms, resistant to oxygen deficiency, remain in the mass. Later, these groups also disappear, giving way to amphipod crustaceans that do not burrow into the ground. Finally, in a catastrophic situation, the macrobenthos completely disappears. Already today these data enable reasonable forecasting for projects related to the separation of regional waterbodies during the anthropogenic development of the Arctic coast.

Far-Eastern Sea Lagoons

Numerous semi-isolated lagoons with varying degrees of desalination, including meromictic ones, were found on the eastern coast of Kamchatka, on Sakhalin Island and on the eastern coast of the Sikhote-Alin mountain range [22, 26, 44].

One of the effects associated with meromixia—a deepened temperature maximum, which falls on the density jump zone was studied on the example of Lake Bolshoy Vilyui on the southeastern coast of Kamchatka [60]. This large in area lake (8.1 km^2, with maximal depth of 7 m) is a part of the estuarine system of the Bolshoy Vilyui and Maly Vilyui rivers,. In summer, a heated layer appears under the pycnocline. Using the one-dimensional hydrological model "LAKE", the main conditions for the appearance of this phenomenon were determined: the presence of a salinity jump with a gradient sufficient to prevent mixing during the night cooling of the surface, the thickness of the mixolimnion should not exceed 2 m, it should be transparent, the weather during the day should be sunny, without strong winds at night.

The dynamism is an important feature of the Far-Eastern lagoons. The shapes of the spit built of marine sediments, which separate the lagoons from the sea, periodically, up to several times a year, change during storms, and the lagoons either open or completely isolate. During a closed period or with a strongly weakened water exchange with the sea, a meromictic regime may be established in them. These lagoons are a convenient object for observing the dynamics of biota under changes in hydrological conditions.

The Lake Kultuchnoye, an estuarine lagoon in the mouth of the Kamchatka River, became meromictic a little over a hundred years ago after the sea water was thrown into a fresh waterbody during the tsunami in 1923. The evolution of the ecosystem of this lake was tracked thanks to the materials of the expedition of F.P. Ryabushinsky at the beginning of the 20th century, who studied the waterbody that was in a freshwater state [6], according to I. I. Kurenkov data for 1951-1962 and data of combined research in 2009–2010 [7]. These studies documented rapid changes in the ecosystem of Lake Kultuchnoye and neighboring Lake Nerpich'ye, the progressing of hydrogen sulfide contamination, and the disappearance of benthos from vast area of the bottom.

Another waterbody that has undergone dramatic changes after isolation (they are well tracked) is Lake Tunaicha, the second largest lake in Sakhalin, and Lake Izmenchivoye, separated from Tunaicha. Initially freshwater in the Middle Holocene, Lake Tunaicha merged with the Sea of Okhotsk, and about a thousand years ago, after the formation of the spit that separated it from the sea, it turned into a deep lagoon [22]. The regular supply of seawater ceased in the mid-1970s after the construction of the road bridge, and now the seawater inflows only during storms. As a result, the surface layer began to desalinate. Salinity decreased from 6.6 to 2.4–2.6‰, summer warming intensified, and the seasonal temperature fluctuations reached the bottom layer. At present, the waterbody has a two-layer structure with a chemocline at a depth of 15 m and hydrogen sulfide below it in a concentration of up to 300–320 μg/L.

All components of the Lake Tunaicha aquatic ecosystem have been studied in detail in the course of long-term combined hydrobiological research organized by SakhNIRO. Because of desalination, the predators—marine cladocerans *Podon leuckarti* and *Evadne nordmani* disappeared from its zooplankton, and the large species were replaced by small ones. Although the structure of the community has become simpler, the total biomass of zooplankton has not decreased [18]. In benthos, the total biomass increased threefold due to the spread of the brackish-water mollusk *Corbicula japonica*, while the marine species *Potamocorbula amurensis* and *Macoma balthica* are at the brink of extinction [19].

Lake Izmenchivoye, separated from Lake Tunaicha 400–150 years ago, has its own connection with the sea through a channel that is often blocked by sediments and then opens again. When the channel is closed, the surface layer is desalinated by several units of salinity and the lagoon acquires a meromictic character. At the same time, the number of benthos species decreases several times and increased warming leads to the replacement of cold-water species with brackish warm-water species. When communication with the Sea of Okhotsk is restored, psychrophylic forms enter the lake again and a reverse change of communities occurs. Observations of the dynamics of benthos during the closure and opening of a channel made it possible to establish two fundamental principles of the change of communities in lagoon waterbodies: the identity of the final result during long-term and rapid (catastrophic) changes and the reversibility of the processes [20].

The lagoon with a variable regime, the Gladkovskaya lagoon, also exists on the northeastern shore of Bering Island. The difference in salinity between the surface and near-bottom water layers provides a meromictic regime in it, regardless of the degree of openness of the channel. A deepened temperature maximum often occurs under the halocline, and at a depth of 6–7 m, where oxygen disappears and hydrogen sulfide appears, a layer with increased turbidity due to bacterial suspension is recorded. In 1981–1987 this lagoon became the subject of research of the joint expedition of VNIRO, the Kamchatka Department of Nature Management of TINRO and the Institute of Oceanology of the Russian Academy of Sciences.

This lagoon is of special interest because of presence of commercially valuable stock of Pacific mussel *Mytilus trossulus*, the biomass of which is very high here (3–4 kg/m^2), and the mollusks are twice as large in linear size than in the sea [33]. The meromictic nature of the lagoon and the annual cyclicity of the oxygen regime turned out to be an obstacle for collector mariculture: due to the spring deficiency of oxygen in the lagoon, mass death of adult mussels occurs [2]. When the channel is completely blocked, the surface layer is totally desalinated, and hydrogen sulfide may spread throughout the salty zone. After one such event, the benthic fauna did not recover even after five years.

CONCLUSIONS

It was found that the number of meromictic waterbodies on the territory of Russia is much larger than indicated in the previously. The number of only coastal waterbodies of marine origin described is 31. For this type of meromictic waterbodies, the concept of meromixia as a stage in the evolution of a water body [51] is fully valid both in the paleolimnological aspect concerning slow changes and in short periods of time.

In the dynamic Far-Eastern lagoons, meromixia is a frequently recurring state; in each cycle of changes in the coastal sediment line, the vertical stratification is formed anew with a different ratio of the layer thickness and the degree of desalination of the mixolimnion. In the areas with coastal uplift, the meromictic stage is an intermediate stage on the way of the waterbody from the sea bay to the final freshwater state. Even the most stable meromictic waterbodies of water, such as Lake Mogil'noye are also in dynamics, albeit slow.

Meromictic reservoirs are one of the natural treasures of our country. On the sea coast of Russia there are any variants of stratified waterbodies: the trough bays aerated from top to bottom, bays at different stages of isolation from the sea, lagoons with a variable hydrological regime, and the coastal lakes with a hydrogen sulfide zone of natural or anthropogenic origin. The analysis of scientific publications carried out during the preparation of the present review showed that most of them are still poorly studied. Of the 31 waterbodies, only one third is covered by multi-year combined research.

The ecological studies are especially focused on the aerobic biota of the mixolimnion, which may be of economic interest. The microbial communities of the anaerobic zone and chemocline, which, in essence, determine the specificity of meromictic waterbodies, in most cases remain outside the scope of attention. Not only hydrochemical research, but also measurements of thermohaline characteristics along the entire vertical profile, even in the warm season, have yet been performed only in a few waterbodies.

All meromictic waterbodies deserve protection as a rare phenomenon, but only six of coastal marine ones received the status of hydrological reserves and natural monuments, and other ten are located within specially protected natural areas and restricted access zones. The remaining 15 waterbodies lack the legislative protection. There is no doubt that this list is far not full and will continue to grow. We hope that the present review will serve as a starting point for new studies of meromictic waterbodies of marine origin, aimed at a comprehensive description of this phenomenon as a single and unique ecological system, and will contribute to their preservation.

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