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ORIGINAL PAPER

Marine Lake Mogilnoe (Kildin Island, the Barents Sea): one hundred years of solitude

Petr Strelkov · Natalia Shunatova · Mikhail Fokin · Nikolay Usov · Mikhail Fedyuk · Sergey Malavenda · Olga Lubina · Alexey Poloskin · Sergei Korsun

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Abstract Lake Mogilnoe (Kildin Island, the Barents Sea) is a marine stratified lake, a refuge for landlocked populations of marine organisms. Unlike other known marine lakes from polar areas, which communicate with the sea by water percolation at the surface, Mogilnoe has a subterranean connection with the sea like tropical and subtropical anchialine lakes. Similarly to some other marine lakes, Mogilnoe has traditionally been considered to be biologically isolated from the sea and subject to little change. We review the current status of the physical features, zooplankton and benthos of Mogilnoe and trace changes that have occurred in the lake since the start of observations in 1894. The anaerobic bottom water layer has expanded by 100 %, while the upper freshwater layer has diminished by 40 %. The species diversity of zooplankton and macrobenthos has halved. The occurrence of Atlantic cod likens Mogilnoe to some other Arctic marine lakes while the presence of large flocks of sea anemones, scyphomedusae and suberitid sponges makes it similar to tropical anchialine lakes. Lake Mogilnoe is not entirely biologically isolated; accidental introduction of species from the sea does occur. We argue that the idealised model of an isolated steady-state ecosystem can be applied to a marine lake with caution. A model of fluctuating abiotic environment and partial biological isolation portrays the real situation better.

Keywords Anchialine lake · Meromictic lake · Isolation · Benthos · Zooplankton · Stratification

Introduction

Marine lakes are natural coastal lakes, saline or brackish, containing marine biodiversity. Since marine lakes are usually influenced both by the sea and by run-off from the local watershed, their physical features depend on water density due to salinity stratification. Therefore, they are often meromictic, with the upper mixed layer, mixolimnion, overlying the anoxic monimolimnion (Strøm 1936; Hamner and Hamner 1998).

Marine lakes, though not numerous, occur all over the world. The list of prominent examples includes tropical lakes of Palau (Micronesia), Ha Long (Vietnam), Berau (East Kalimantan) and Raja Ampat (West Papua), communicating with the sea through underground tunnels and fissures in the limestone (Hamner and Hamner 1998; Cerrano et al. 2006; Tomascik and Mah 1994; Becking

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P. Strelkov (✉) · N. Shunatova · M. Fedyuk · A. Poloskin · S. Korsun
Faculty of Biology and Soil Science, St. Petersburg State University, Universitetskaya Emb., 7-9, Saint Petersburg 199034, Russia
e-mail: p_strelkov@yahoo.com

M. Fokin · N. Usov
Zoological Institute, Russian Academy of Sciences, Universitetskaya Emb., 1, Saint Petersburg 199034, Russia

S. Malavenda
Faculty of Biology, Murmansk State Technical University, Sportivnaya Str., 13, Murmansk 183010, Russia

O. Lubina
Murmansk Marine Biological Institute, Russian Academy of Sciences, Vladimirskaya Str., 17, Murmansk 183010, Russia

S. Korsun
Shirshov Institute of Oceanology, Nakhimovsky Pr. 36, Moscow 117997, Russia

et al. 2011); Mediterranean karst lakes Vouliagmeni (Greece), Rogoznica and the lakes of Mljet island (Croatia), with surface (Mljet) or underground (Vouliagmeni and Rogoznica) connection with the sea (Benović et al. 2000; Kršinić et al. 2000; Chintiroglou et al. 2008); the unique lake Motitoi in the crater of an erupted volcano on Satonda Island in Indonesia, which is suspected to be completely isolated from the sea (Kempe and Kaz'mierczak 1993; Pisera et al. 2010); and high-latitude lakes on the coasts affected by glacial isostatic uplift, communicating with the sea through shallow straights, such as Lake Ogac on Baffin Island in Canada (McLaren 1961), lakes in Vestfold Hills in Antarctica (Bayly 1986; Gibson 1999) and lakes along the Norwegian coast (Klaveness 1990; Hognestad 1995; Ström and Klaveness 2003).

Although the term "marine lake" as defined above is in common use (e.g. Dawson et al. 2009), these water bodies are also sometimes treated in the literature under two formally non-overlapping categories of marine systems, or habitats. One category is "landlocked waters" defined as "shallow basins that have a communication with the sea through a channel which is of less depth than the basin itself and possess the combined density stratification arising from temperature and salinity differences" (Strøm 1936, p. 9). The other is "anchialine habitats" defined as "bodies of haline waters, usually with a restricted exposure to open air, always with more or less extensive subterranean connections to the sea, and showing noticeable marine and terrestrial influences" (Stock et al. 1986). Lakes with surface connection to the sea (e.g. Ogac) fall into the "landlocked waters" category together with silled fjords and inlets, but not lakes with subterranean connection to the sea. Marine lakes with subterranean connection (e.g. lakes of Palau) are classified into the "anchialine systems" category together with the exotic phenomena of inland marine caves and blue holes but not with landlocked waters sensu Strøm (1936). This terminological discrepancy partly has a geographical nature: while landlocked waters are common in subpolar regions (Strøm 1936), anchialine systems are almost exclusively a tropical and subtropical phenomenon (but see below). Since anchialine systems are popular research objects, the term "marine lakes" tends to be mentioned mostly in tropical and subtropical context. It is indicative that on the most comprehensive map of global distribution of marine lakes (Dawson et al. 2009), no high-latitude lakes are shown.

Being affected by isostatic uplift as well as eustatic regressions and transgressions, individual marine lakes should be ephemeral on a multimillennial timescale though theoretically this could be untrue for complexes of interconnected marine lakes in dynamic karst landscapes. Frequently, their physical features are also unstable at the interannual timescale. Their dynamics is governed by climatic and meteorological factors affecting stratification patterns (e.g. lakes of Palau, Dawson et al. 2001; Martin et al. 2006; and of Norway, Ström and Klaveness 2003), as well by anthropogenic ones. Common types of anthropogenic impact are eutrophication, which provokes anoxia, and activities that alter the lakes' water balance, e.g. excavation of a channel between the lake and the sea (Sorokin and Donato 1975; Ström and Klaveness 2003). Curiously, the notion that marine lakes are unstable somehow coexists in the literature with the hypothesis about their strong temporal stability (Massin and Tomascik 1996; Hamner and Hamner 1998; Benović et al. 2000; Chintiroglou et al. 2008), logically linked to that about biological isolation and incipient speciation.

The most impressive biological feature of marine lakes is a recurrent phenomenon of occurrence and thriving in them of particular macrofauna taxa, first of all the Atlantic cod *Gadus morhua* L. in Arctic lakes (Hardie et al. 2008) and scyphomedusae in tropical and subtropical lakes (Hamner et al. 1982; Tomascik and Mah 1994; Benović et al. 2000; Cerrano et al. 2006; Becking et al. 2011). Another intriguing feature of marine lakes is the presence in their fauna of morphologically diverging forms of marine animals, which is usually interpreted as a result of in situ evolution. Endemic species or subspecies have been described from many marine lakes (e.g. Vouliagmeni, lakes of Palau, Vietnam, Indonesia and Mljet, see references above).

Marine lakes contain communities with a low number of species (all the cited examples), probably due to unfavourable abiotic environment and low habitat diversity. Another factor presumably influencing their biota is biological isolation, a side effect of hydrographic isolation. The significance of this factor is evident when lakes serve as refugia for species absent in the adjacent sea; good examples are populations of cod in Lake Ogac and two recently discovered "cod lakes" on Baffin Island (Hardie et al. 2008). Since isolation is generally considered as a prerequisite for speciation, the presence of divergent animal forms in marine lakes is assumed to indicate biological isolation. The hypothesis of isolation was sometimes even applied to communities and entire ecosystems as in the case of some lakes in Palau (Hamner and Hamner 1998), Indonesia (Massin and Tomascik 1996) and Mediterranean (Benović et al. 2000; Chintiroglou et al. 2008). As some level of stability is needed for the persistence of isolated populations and communities, these lakes were supposed to be temporally stable. Because of their unusual biological and physical features, marine lakes have been always regarded as unique ecosystems of high conservation value (all cited tropical and subtropical examples, see references above).

Lake Mogilnoe (Kildin Island, the Barents Sea) is the only known anchialine lake in the Arctic. First drawn on a geographical map in 1594 (Linschoten Van 1601) and first described scientifically in 1804 (Ozereckovsky 1804), Mogilnoe must be the oldest anchialine lake in the scientific record. Derjugin (1925) put forward two principal ideas concerning the way the lake ecosystem is organised and functions: (1) that it is temporally stable, i.e. there are no long-term trends in the environment and the composition of the biota, and (2) that the lake is completely biologically isolated from the sea. He also concluded that incipient speciation took place in the lake. As far as we know, it was the first time when the model of isolated steady-state ecosystem, a hot spot for evolution, was applied to a marine lake.

In this paper, we (1) present contemporary data on physical features, benthos and zooplankton of Lake Mogilnoe, (2) compare our findings with the corresponding earlier data and assess the changes that have occurred in the lake since the beginning of the twentieth century and (3) critically review the hypotheses that the lake persists in a stable state and that it is biologically isolated from the sea.

Materials and methods

Study area

Kildin Island (17.6 km length, 7 km width) is a tundra-covered plateau, up to 280 m in elevation, built of shale and sandstone. The island drops sharply to the sea in the north and forms wide terraces in the south. A 1.5-km-wide marine Kildin Strait separates the island from the mainland. Lake Mogilnoe (literally "grave lake" in Russian) is situated in the south-eastern end of the island, on the lowermost terrace, and is separated from the strait by a natural dam 60 m wide and 3 m above the spring tide (Derjugin 1925; Figs. 1, 2a). The sea-water filtration occurs through the dam, which consists of boulders, pebble and sand, at the depth of 5–8 m below the lake surface (see Table 1 for basic information about the lake). This water exchange, combined with the freshwater supply from the catchment area and precipitation, results in a permanent stratification of the lake. Its upper water layer is nearly fresh, the bottom layer is saline and sulphidic, while the intermediate layer is saline and oxic. The anoxic monimolimnion is capped by a thin (0.5 m) distinctive red water layer. Its colour is due to a high density of purple sulphur bacteria oxidising the hydrogen sulphide formed by sulphate-reducing bacteria in the deep water layer and the bottom sediments. Unlike the strait, which never freezes, the lake is covered with ice from November until June (Derjugin 1925). The main hypothesis is that the lake developed in Late Holocene from a marine inlet, due to the tectonic and/or isostatic land rebound.

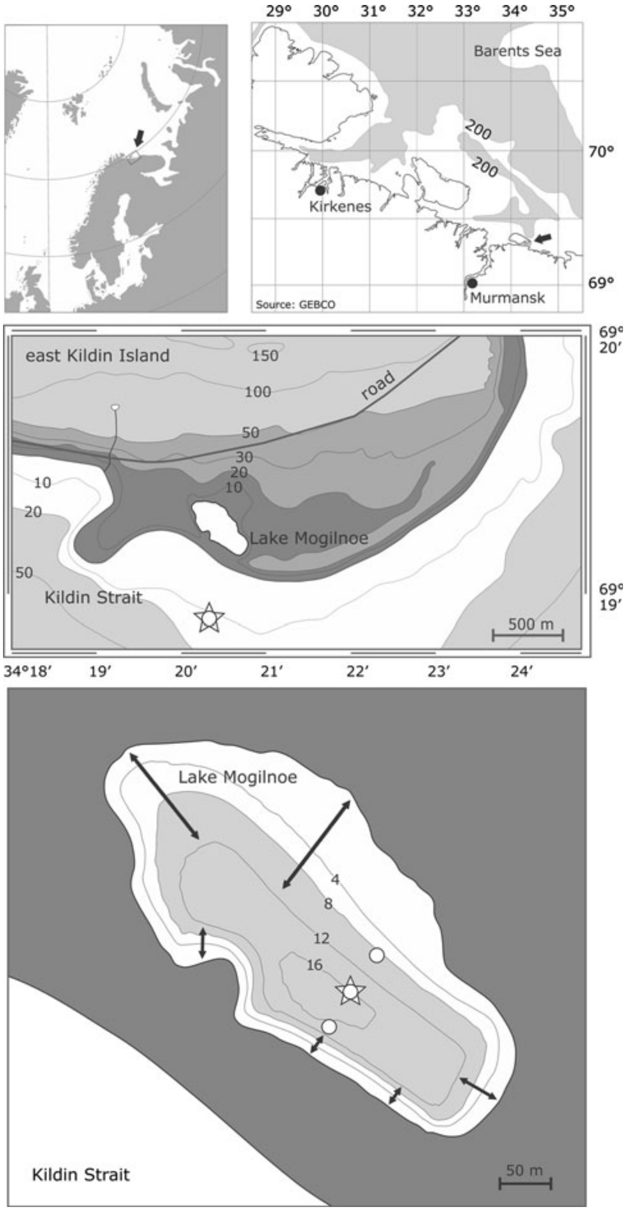

Fig. 1 Map of study area. *Upper panels* Northern Europe, *arrow*—Kildin Island. *Bottom panels* Lake Mogilnoe and surroundings. Bathymetry of the lake is after Titov et al. (2002). Points of hydrological sampling are indicated by *asterisks*, of plankton sampling—by *open dots*. Benthos transects are indicated by *two-sided arrows*

The dam was formed as an intertidal accumulation of shore drift (Mityaev et al. 2008). From the seventeenth to the twentieth century, SE Kildin was a local centre of fisheries (Derjugin 1925; Lajus et al. 2005). During the second half of the twentieth century, the island was a militarised zone. Military installations, one of which used to be on the very shore of the lake, were shut down by the end of the century. Nowadays, Kildin is an idle land, with almost no human activities around the lake (Strelkov and Fedyuk 2006).

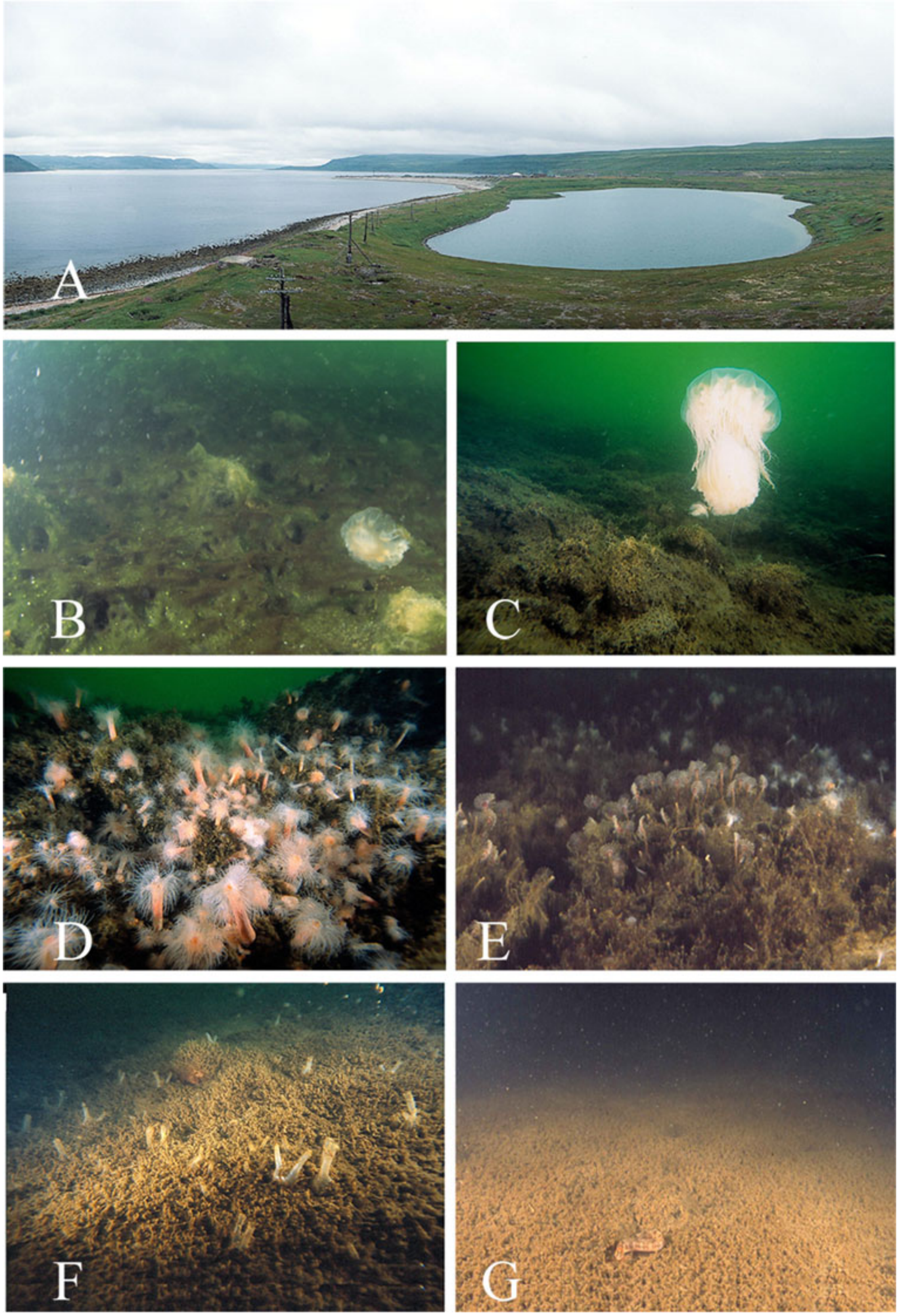

Fig. 2 Lake Mogilnoe and its inhabitants. **a** View on the lake from the East. Maximum length of the Lake is 562 м, width—275 m. **b** Mats of green algae and cyanobacteria, water depth 3–4 m. **c** *Cyanea arctica* medusae, debris of green algae and tubes of spionid polychaetes, 4–5 m. **d** Actinia *Metridium senile*, 6–7 m. **e** Cluster of polychaete *Pseudopotamilla reniformis*, 6–7 m. **f** Ascidians *Molgula citrina*, tubes of spionid polychaetes, 7–8 m. **g** Butterfish *Pholis gunellus*, tubes of spionid polychaetes, 7–8 m

Data set and sampling design

We visited Lake Mogilnoe in late August 2003, early August 2004, late September 2005 and early July 2007. Earlier, the lake has been studied in the 1894–1921, in the late 1960s and early 1970s, and in the late 1990s (Derjugin 1925; Gurevich 1975a; Titov et al. 2002, and references therein). However, the lake's benthic biota, the basis of its

Table 1 Morphometric and hydrographic characters of Lake Mogilnoe, after Gurevich (1975b)

Maximum length of the lake, m	562
Average (maximum) width of the lake, m	190 (275)
Surface area of the lake, km^2	0.11
Average (maximum) depth of the lake, m	7.4 (16.3)
Total volume of the lake, m^3	794
Elevation of the lake, m	0.30–0.45
Catchment area of the lake, km^2	3.30[a]
Minimum width of the dam, m	63
Minimum height of the dam above the average lake level, m	3.4
Depth of saline water filtration horizon, m	5–8
Average (maximum) tide range in the lake, m	0.04 (0.08)
Average (maximum) tide range in the sea, m	2.4 (4)
Average delay of tide in the lake against the sea, h	3.2
Estimated daily average influx of sea water into the lake, m^3	45
Estimated daily average influx of fresh water into the lake, m^3	400

[a] Our unpublished data

biodiversity, has not been studied since the beginning of the twentieth century. The data used for comparison are from these studies. We also included hydrological data from the recent study of Emelyanov et al. (2010), performed in 2006.

We measured temperature and salinity along the water column at the station located in the deepest point of the lake (N 69°19.09′, E 34°21.01′, Fig. 1), with an increment of 2.5 m in 2003 and with an increment of 1 m in 2004, 2005 and 2007. In 2004, oxygen content was also measured, in the same samples as the temperature and the salinity. Water samples were taken with a Nansen bottle. Temperature was measured by reversing thermometers attached to the bathometer, salinity by a refractometer (S/Mill-E, Atago, Japan) and oxygen content by an oxygen meter (OXY-320, WTW, Germany). During each survey, the colour of the water samples was visually recorded in order to determine the position of the red water layer. In 2004, we also measured temperature, salinity and oxygen content at one station in the Kildin Strait (N 69°18.97′, E 34°20.44′, depth 16 m, Fig. 1). The samples from the sea were taken and processed in the same way as those from the lake.

Salinity vertical profiles (in July and August) are available from 1894, 1900, 1901, 1906, 1909, 1921 (reviewed by Derjugin 1925), 1968, 1969 (Gurevich and Shirokolobov 1975, graphs on p. 41) and 2006 (Emelyanov et al. 2010). We compared these measurements with our July and August data. In different surveys, water samples were taken with a different depth increment, so in order to remove this noise from the comparison, we pooled all data points for each year for the water layers 0–3, 4–6, 7–9, 10–12 and 12–15 m. The depth of the red water layer was recorded in 1909, 1921 (Derjugin 1925), 1968, 1969 (Gurevich et al. 1975b: p. 46, fig. 14) and 2006 (Emelyanov et al. 2010). We compared these data with those from our observations in order to trace the changes in the position of the top of the anoxic layer. We did not compare the data on oxygen content and temperature, since our oxygen content data are scarce and probably biased (see “Results”), while temperature profiles of the lake are characterised by considerable intra- and interseasonal variability (Gurevich and Shirokolobov 1975).

We sampled zooplankton at three stations (N 69°19.09′, E 34°21.01′; N 69°19.07′, E 34°21.03′; N 69°19.164′, E 34°21.052′; Fig. 1) in 2003, 2004 and 2007 and at one station in 2005; the station of hydrological sampling was always included. The sampling was performed with the Juday net (mesh size 0.2 mm; mouth diameter 26 cm), hauled vertically at three water layers (5–0 m, 10–5 m and 15–10 m), one haul per layer. In 2004 and 2007, zooplankton samples were also taken at the station of hydrological sampling in the Kildin Strait. The samples were fixed with 4 % formaldehyde for subsequent identification and counting of the zooplankton using standard methods (Harris et al. 2000). In the previous studies, trawls and dredges were used for benthic sampling, but we dismissed them as traumatic for benthic communities and instead worked with SCUBA divers. After examining the bottom and mapping the underwater landscapes and communities, the divers collected macrobenthos. Most samples were collected along the southern shore of the lake, where the sea-water infiltrates and where the previous benthic studies were made (Derjugin 1925). Altogether, 62 samples were collected along the southern shore. Amongst them, 14 samples were taken in 2003–2005 using cores (0.005 m^2) so as to describe typical landscapes and communities, and 48 samples were taken in 2007 at three vertical transects evenly placed along the southern shore (N 69°19.13′, E 34°20.73′; N 69°19.07′, E 34°20.96′; N 69°19.02′, E 34°21.1′; Fig. 1). At each transect, samples were taken at depths 0.3–0.5, 3.5–4.0, 6.0–6.5 and 8.5–9 m, with four samples for each depth interval: one hand-grab sample (area 0.04 m^2 at 0.3–0.5 m or 0.025 m^2 at a greater depth) and three core samples (0.005 m^2). The rest of the lake was covered in 2007 by three similar vertical sections in different parts of the lake (N 69°19.24′, E 34°20.63′; N 69°19.21′, E 34°21.05′; N 69°19.07′, E 34°21.27′; Fig. 1). Samples were washed through a 0.5-mm mesh sieve, and the macrobenthos organisms were identified to the lowest taxonomic category possible, generally to the species level, and weighted (wet weight).

In the course of previous studies, zooplankton was sampled, from July to September, in 1898, 1900, 1901, 1906, 1909, 1915 (Derjugin 1925), 1967 (Fomin 1975) and 1997–98 (Drobysheva 2002). Information about sampling details is limited. In 1898–1915, sampling was most extensive in 1915; in 1967, only the 5–0-m water layer was sampled using Juday net (0.06 mm mesh size) hauled horizontally, while in 1997–98, the 9–0-m water layer was sampled using Bongo net hauled horizontally (see references above). Since we suspect that sampling effort and methods were different during different expeditions, we shall base our temporal comparisons on the pooled data from the most intensively studied time period, 1898–1915. In this way, the analyses of the changes in the zooplankton and the benthos diversity will also be comparable.

Qualitative data on zoobenthos had been obtained by several expeditions in 1887–1921 and were compiled by Konstantin Derjugin (1925). The total number of the benthic samples studied is unknown, but it is documented that 27 dredge samples were taken from the lake during the expedition of 1898, to be studied personally by Derjugin. Therefore, we have good reasons to believe that Derjugin's account of the benthic fauna is accurate. The same cannot be said, however, of phytobenthos. The list of algae used by Derjugin was compiled by E. Zinova, but it is unclear what material she studied. We made comparisons after adapting the cited lists to modern taxonomies (see the Online Resources for details of synonymisation procedures). In order to compare ecological groupings, we, following the earlier researchers (Derjugin 1925; Fomin 1975), classified lacustrine planktonic invertebrates into inherently freshwater, brackish and marine.

Calculations and statistics

This study is based on qualitative comparisons; therefore, we basically avoid the use of quantitative statistics. To characterise a sample, the arithmetic mean and the standard error or the 95 % confidence interval of mean were used, while to emphasise the magnitude of variable change with time, the Pearson product–moment correlation coefficient r was used.

Results

Physical features, stratification and oxygen content in the water column

Depth profiles of salinity, temperature and oxygen recorded in the lake in July 2004 are shown in Fig. 3a. In the 0–3-m depth interval, the salinity was 3–5 ppt and the temperature, 17–18 °C. In the 3–9-m depth range, the salinity increased abruptly to 28 ppt, while the temperature dropped to 11 °C. At greater depths, the salinity was 28–30 ppt and the temperature, 10–12 °C. The oxygen concentration was 8–9 mg l^{-1} (>90 %) above 7 m, dropped to 2 mg l^{-1} (20 %) by 10 m and decreased up to 0.9 mg l^{-1} at greater depths. In the Kildin Strait, the salinity was invariably 33 ppt and the oxygen concentration, 9 mg l^{-1} ($\approx$100 %), while the temperature decreased from 13 °C on the surface to 10 °C below 10 m. The vertical distribution of salinity, temperature and oxygen in the lake in our following summer surveys was essentially similar to that in July 2004. In autumn (late September 2005), however, the situation was different: the salinity in the surface layer was higher (6–7 ppt), while the maximal temperatures were observed at 4–8 m (11.2–12.4 °C vs. 6.4–8.1 °C at 0–3 m and 7.0–9.0 °C at the deep water). In every survey, the red water layer was registered at 9–10 m, indicating anoxia in a stable system.

The long-term changes in stratification are schematically shown in Fig. 3c. Comparison with the earlier data revealed a considerable change in the position of the red water layer and in the salinity of the subsurface water layer (4–6 m). The red water layer was situated at a depth of 13 m in 1909 (Derjugin (1925) also mentioned that an earlier expedition had recorded the same position, p. 43) and at 12 m in 1921. Half a century later, in 1968–1969, the red water layer was already at the depth registered in the 2004–2007 surveys, 9–10 m. Thus, from the early twentieth century to the 1960s, the thickness of the anoxic layer increased by about 3 m. The average salinity of the subsurface water layer (4–6 m) increased from 2 to 8 ppt (mean ± 95 % confidence interval 4.8 ± 2.89) in 1894–1921 to 15–20 ppt (17 ± 2.94) in 2003–2007 (Pearson's $r = 0.84$ between year of sampling and salinity, $p < 0.01$, $N = 10$). In other words, on the average the 5 ppt isohaline was at 5 m in 1900–1921 and at 3 m in 2003–2007. The situation in 1968–1969 was close to that in 1900–1921, which means that the change in the salinity of the subsurface layer has occurred after the 1960s. A small but significant downtrend in the salinity of the bottom layer (13–15 m) was also recorded (Pearson's $r = -0.80$, $p < 0.01$, $N = 10$) (Fig. 3b).

Zooplankton

Taxonomic structure of zooplankton in 2003–2007 in comparison with that from previous surveys is given in Table 2, while the total lists of zooplankton species recorded in every survey are presented in Online Resource 1. Zooplankton was most numerous in the intermediate water layer (10–5 m) and the least abundant in the near-bottom layer (15–10 m). Zooplankton density in the intermediate ("marine") water layer was an order of magnitude higher than in the sea (53.5 vs. 5.8 ind m^{-3} in 2004, 19.7 vs. 1.1 ind m^{-3} in 2007). Four taxa (the marine copepod *Pseudocalanus* sp., the marine spionid polychaete

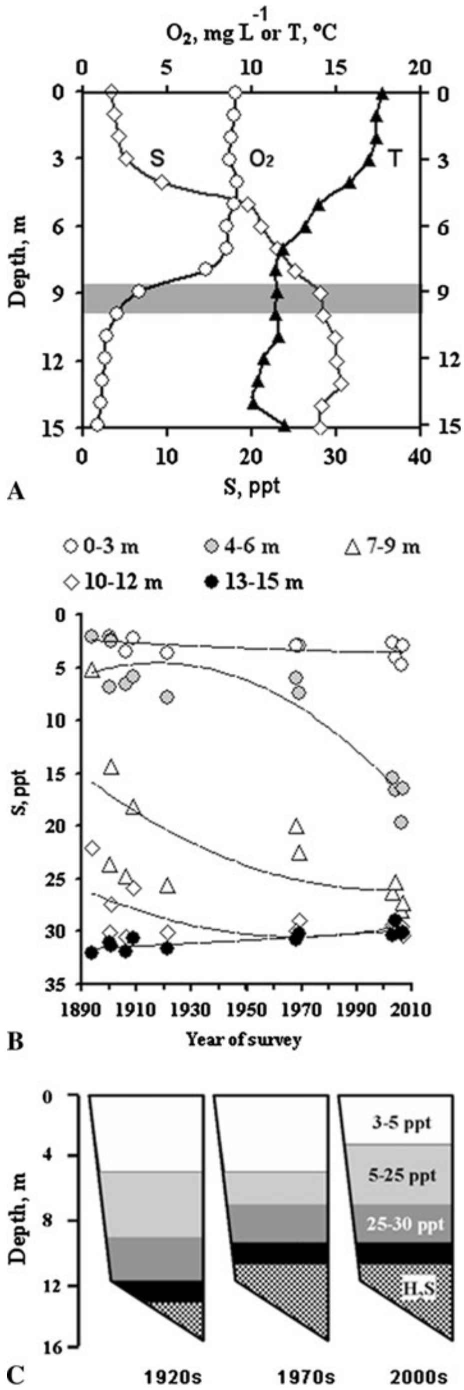

Fig. 3 Physical characteristics of Lake Mogilnoe. **a** Salinity (*S*, ppt, *diamonds*), dissolved oxygen (O_2, mg l^{-1}, *circles*) and temperature (*T* °C, *triangles*) (29.07.2004). The horizontal strip denotes the red water layer. **b** Salinity change over decades. All casts are made in July or August. Each *point* in the *plot* averages all measurements from a certain year of survey for a 3-m interval of water depth. Data signs differ between the five water depth intervals. Each of the five time series is approximated by a cubic polynomial fit. **c** Diagrammatic representation of the stratification during different decades. The section of the lake adjacent to the dam is shown schematically after Emelyanov et al. (2010)

Table 2 Taxonomic spectrum of zooplankton in Lake Mogilnoe

	1898–1915	1967	1997–1998	2003–2007	Total
Rotifera	11	2	2	1	12
Cladocera	5	0	2	4 (1)	6
Copepoda	12	1	4	4	14
Cnidaria	2	1	2	2	3
Benthic larvae	3	1	2	3 (1)	5
Total	33	5	9	14 (2)	39

The number of species registered in different periods is indicated. The number of new species registered in 2003–2007 is given in parentheses. The data for 1898–1915 are from Derjugin (1925), those for 1967 from Fomin (1975), those for 1997–98 from Drobysheva (2002), those for 2003–2007 ours

larvae, the brackish cladoceran *Pleopis polyphaemoides* Leuckart and the freshwater rotifer *Keratella quadrata* Müller) dominated the zooplankton of the lake, accounting for more than 95 % of zooplankton numbers in any sample. The structure of the zooplankton community in the lake was rather dynamic in space and, particularly, in time (Fig. 4a). The zooplankton of the Kildin Strait was much more diverse than that of the lake (22 taxa vs. 12 in 2004 and 24 vs. 9 in 2007) and dominated by forms entirely absent from the lake (e.g. copepod *Oithona similis* Claus, cirriped and echinoderm larvae).

Besides the mesoplankton, two macroplanktonic species were recorded in the lake: the medusae *Rathkea octopunctata* Sars (Hydrozoa) and *Cyanea arctica* Péron et Lesueur (Scyphozoa) (Fig. 2c). The hydrozoan medusa was rare (only several specimens were collected) and occurred in the intermediate layer (5–10 m). The scyphozoan medusa was small, with the umbrella diameter not exceeding 5 cm; its yellow colour differed distinctly from the orange–purple of its conspecifics from the Barents Sea. It was mainly confined to the intermediate layer. The *Cyanea* jellies were not repelled by the red water; they even descended to the monimolimnion then returning to the oxygenated layer (underwater observations). These jellies were rather numerous. For instance, in late August of 2003, the SCUBA divers observed dozens of them within a visibility zone three to five metres wide.

Each year of study, we recorded from nine to 11 forms of zooplankton in our samples, while in previous studies, from three to 20 forms were recorded seasonally. In total, 14 forms of meso- and macrozooplankton were registered in the lake in 2003–2007, while in all the previous summer studies, 36 forms were mentioned. A total of 24 previously recorded species were missing from the lake during the 2003–2007 surveys; 16 of them had been mentioned only once, and 11 from 24 were freshwater. At the same time,

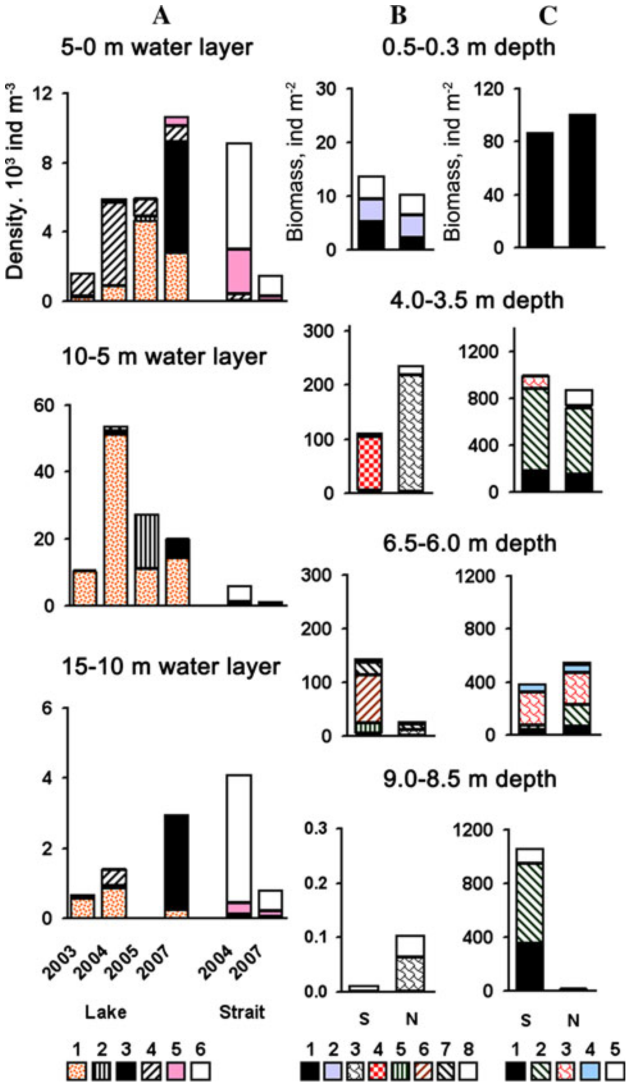

Fig. 4 Vertical distribution of zooplankton density (10^3 ind m^{-3}) and benthos biomass (g m^{-2}) in Lake Mogilnoe. Note that the Y-axis scale changes between graphs. **a** Zooplankton in Lake and Kildin Strait in 2003–2007. 1—*Pseudocalanus* sp., 2—polychaete larvae, 3—*Keratella quadrata*, 4—*Pleopis polyphaemoides*, 5—other lake forms, 6—other strait forms. **b** Zoobenthos along southern (S) and other (N) shores of the lake in 2007. 1—*Gammarus duebeni*, 2—*Cricotopus* sp., 3—*Polydora ciliata*, 4—*Macoma balthica*, 5—*Astarte montagui*, 6—*Metridium senile*, 7—*Molgula citrina*, 8—others. **c** Phytobenthos along southern (S) and other (N) shores of the lake in 2007. 1—cyanobacteria, 2—filamentous green algae, 3—*Polysiphonia urceolata*, 4—*Phyllophora brodiae*, 5—others

the freshwater cladoceran *Macrothrix hirsuticornis* Norman et Brady and the bivalve larvae, which we noted in the lake, were not registered by the earlier authors. In Fig. 5a we show changes that have occurred between the two time periods, 1898–1915 and 2003–2007: total diversity decreased by about 60 %, and, in particular, the number of non-freshwater species decreased by one-third and that of the freshwater ones, by a factor of seven.

Benthos

Information on taxonomic structure of macrobenthos in 2003–2007 in comparison with such from previous surveys is given in Table 3, while the total lists of benthic species recorded in 1887–1921 and in 2003–2007 are presented in Online Resource 2. The underwater southern slope of the lake has an angle of 20–60°; the bottom is composed of boulders and covered with the fluffy sediment 1–5 cm thick. The downslope distribution of the benthos demonstrates a well-defined zonality. In brief, the distribution of the dominant taxa was as follows. Within the depth range 0–3 m (salinity range 3–5 ppt), the phytobenthos was represented by algal mats, mainly composed of *Rivularia* sp. (Fig. 2b), while zoobenthos contained the amphipod *Gammarus duebeni* Liljeborg, oligochaetes and chironomid *Cricotopus sp.* Within the depth range 3–5 m (5–15 ppt), the phytobenthos was represented by filamentous cyanobacteria and green algae, the epifauna by the bryozoan *Electra crustulenta* Pallas and the sponge *Protosuberites epiphytum* Lamark, and the infauna by the tube-dwelling polychaete *Pygospio elegans* Claparède and the clam *Macoma balthica* L. (Fig. 2c). At a depth of 5 m, aggregations of the mussels *Mytilus edulis* L. were found. This species has not been previously recorded in the lake. The mussels in aggregations were rather large, up to 80 mm in length. Within the depth range 5–7 m (19–23 ppt), the phytobenthos was dominated by the red algae *Phyllophora brodiae* Turner and *Polysiphonia urceolata* Lightfoot, the epifauna by the ascidian *Molgula citrina* Alder et Hancock and the sea anemone *Metridium senile* L. (Fig. 2d) and the infauna by the bivalve *Astarte montagui* Dillwyn and the two polychaetes *Nainereis quadricuspida* Fabricius and *Fabriciola baltica* Friedrich. The latter polychaete had not been previously recorded in the lake. A sole large cluster of the sabellid polychaete *Pseudopotamilla reniformis* Müller was found at a depth of 7–8 m (Fig. 2e). The lower boundary of this community was marked by a white belt of bacterial mat. Within the depth range 7–9 m (23–28 ppt), no algae were present. The tubes of the annelids Tubificidae gen. sp. and *Polydora ciliata* served as reinforcement for the loose sediment, and the stones were crowned with the ascidians *M. citrina* (Fig. 2f, g). No macrobenthos was found below 9 m. Extensive shallow areas elsewhere in the lake were occupied by the same shallow-water community as in the southern shore area in the 0–3 m depth range and by soft-bottom communities dominated by filamentous algae, oligochaetes and *P. ciliata* at greater depths. All species found here we also present along the southern shore. In qualitative terms, zonality of benthos in Lake Mogilnoe is illustrated in Fig. 4b, c by data of regular sampling undertaken in 2007. In that survey, the mean biomass of all benthic organisms (± standard error) was

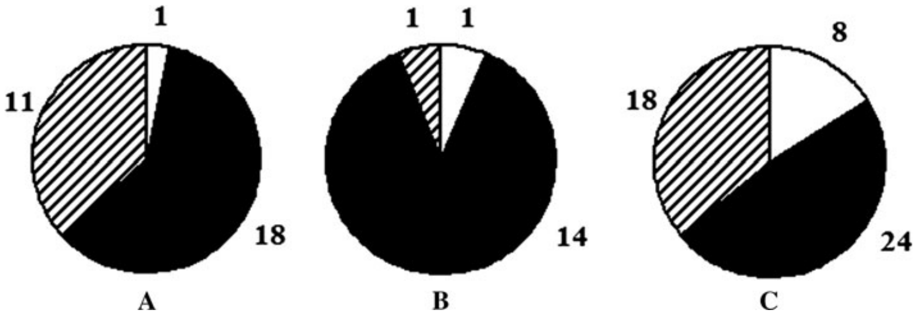

Fig. 5 Number of zooplanktonic and macrobenthic taxa registered in Lake Mogilnoe in different time periods. White sector, the taxa found in 2003–07 but not in earlier surveys, striped sector, found both in 2003–07 and in earlier surveys, black sector, found in earlier surveys but not in 2003–07. **a** Zooplankton taxa of marine and brackish origin. **b** Zooplankton taxa of freshwater origin. **c.** Zoobenthos. See online resources for source data

Table 3 Taxonomic spectrum of macrobenthos of Lake Mogilnoe

	1898–1921	2003–2007	Total		1898–1921	2003–2007	Total
Zoobenthos	42	26 (8)	50	Bryozoa	1	2 (1)	2
Porifera	3	1	3	Echinodermata	1	0	1
Cnidaria	7	4 (2)	9	Tunicata	8	2	8
Nemertini	1	1	1	Phytobenthos	18	16 (7)	25
Annelida	7	8 (3)	10	Phaeophyta	4	6 (4)	8
Pantopoda	1	0	1	Rhodophyta	5	2	5
Mollusca	10	4 (1)	11	Chlorophyta	3	5 (3)	6
Arthropoda	3	4 (1)	4	Cyanobacteria	6	3	6

The number of species registered during different periods is indicated. The number of new species registered in 2003–2007 is given in parentheses. The data for 1898–1921 are from Derjugin (1925), and those for 2003–07 are ours

573 ± 182.4 g m^{-2}, of zoobenthos 67 ± 24.3 g m^{-2} and of phytobenthos 506 ± 181 g m^{-2}.

Out of the 42 invertebrate taxa mentioned in 1887–1921, we found 18 (Fig. 5c; though we did not identify Oligochaeta to the species level as Derjugin did). Specifically, we found four out of ten molluscs, two out of eight ascidians, two out of seven cnidarians and five out of seven annelids (Table 3). Some of the invertebrates that have disappeared from the lake are trivial and conspicuous, such as periwinkles, sea spiders, sea slugs and chitons. On the other hand, we found eight previously unrecorded invertebrate species in the lake (see Online Resource 2). Most of them are small and hardly noticeable, but one species, *M. edulis*, is large and conspicuous. The algal diversity has not changed much: a total of 16 species today versus 18 in the beginning of the twentieth century. However, the correspondence between the two lists is poor. Nine algae from Derjugin's (1925) list are missing today, and seven new taxa are present (Table 3).

To complete the biological description of the lake, we note that all the three fish species registered earlier in the lake (Derjugin 1925; Titov et al. 2002)—the Atlantic cod *G. morhua* L., the butterfish *Pholis gunellus* L. (Fig. 2g) and the three-spine stickleback *Gasterosteus aculeatus* L.—are still present there (underwater observations and observations from the shore).

Discussion

The comparative analysis of the hydrological and biological data collected in our survey and the corresponding data from the preceding ones made it possible to assess the state of Lake Mogilnoe over the period of almost 100 years. The analysis revealed that certain features of the lake have remained more or less the same over this time period, while the others have undergone considerable changes.

Specific features of Lake Mogilnoe and similarities with other marine lakes

Our data illustrate very well the following basic and well-recognised features of Lake Mogilnoe.

(1) A strong stratification of the water column by temperature, salinity and oxygen content. In midsummer, the upper layer is almost fresh and warm, and the bottom layer is saline and cold. Sharp halo- and thermoclines separate the two layers. The bottom

layer (monimolimnion) is oxygen-depleted. The monimolimnion is capped by a red water layer (Derjugin 1925; Gurevich et al. 1975a; Gurevich and Shirokolobov 1975). Strangely, the oxygen content in our water samples taken from the sulphidic layer (below 9 m) was 2.0–1.0 mg l^{-1}. One would not expect any oxygenation at the bottom. All the previous surveys had reported instrumental-zero oxygen in samples below the red water layer (see references above). Our non-zero values must have been an artefact, probably arising from the use of polarographic electrodes that have been shown not to be precise in water containing dissolved hydrogen sulphide (Hale 1983).

(2) Species-poor but abundant zooplankton. According to Drobysheva (2002), the zooplankton is many times more abundant in the "living" zone of the lake (the upper 10 m of the water column) than in the corresponding depth range of the Kildin Strait. We confirmed this estimate for the intermediate, "marine" layer (5–10 m). The differences between the abundance of zooplankton in the 0–5 water layer in the lake and in the strait were not so striking. It is noteworthy that in our survey as well as in the previous ones (Derjugin 1925; Fomin 1975), the hauling of the anoxic layer yielded a few zooplankters. We suppose that these specimens were actually carcasses sinking from the upper layers.

(3) A rather rich marine benthos, which is arranged into distinct subhorizontal girdles. Early researchers considered the existence of diverse marine benthos as an amazing feature of Lake Mogilnoe (Derjugin 1925 and references therein). The zonality has not been demonstrated previously, though Derjugin (1925) predicted its existence judging by the known salinity preferences of the taxa.

Some of the features described above are common for marine lakes on the whole (Table 4). Stratification is their common feature, while in the most isolated ones meromixis is observed. The red water layer is always formed in meromictic basins when chemocline is exposed to sunlight intensities sufficient for the growth of purple bacteria (Sorokin and Donato 1975). Simplification of the pelagic community against the background of the very high abundance of particular species also is a general feature of marine lakes. A notable fact is that the fauna of Mogilnoe includes the whole "top list" of macroscopic taxa (species or taxonomic groups) known to prosper in marine lakes, however, usually not concurrently. These taxa are the Atlantic cod, scyphozoan jellyfishes, sea anemones and suberitid sponges (see Table 4 and references therein). The prosperity of suberitid sponges in marine lakes is related to their general ability to tolerate stressful habitat conditions facilitated by the production of gemmules (resting bodies) (Pisera et al. 2010). Similarly, the advantage of scyphozoan jellyfishes, particularly *Cyanea* in marine lakes, could be their high ability to thrive in low-oxygen environments facilitated by the physiological mechanism of oxygen storage in the mesoglea, with the gel working literally as a scuba (Thuesen et al. 2005). What adaptations underlie persistence and thriving of cod and sea anemones in marine lakes is unclear. The simultaneous presence in Mogilnoe of abundant jellyfishes, suberitid sponges and sea anemones makes it surprisingly similar to tropical anchialine lakes. One more common feature of many marine lakes is the presence in their fauna of regionally or globally endemic species (Table 4). In Lake Mogilnoe, there is one generally recognised endemic subspecies, the Kildin cod *G. morhua kildinensis* (Derjugin 1925; Hardie et al. 2008 and references therein).

Long-term changes and temporal stability of Lake Mogilnoe

Derjugin (1925) put forward two principal ideas concerning the way the lake ecosystem is organised and functions: that it is temporally stable and that the lake is completely biologically isolated from the sea. While the first statement was questioned already in the 1970s when the expanding of the anoxic zone was recorded (Gurevich and Shirokolobov 1975; Gurevich et al. 1975b), the second Derjugin's statement was accepted without reservation by all the recent researchers (Gurevich 1975a; Titov et al. 2002). In the following paragraphs, we argue that both statements need to be amended.

Derjugin assumed that the lake became isolated in the Early Holocene and thus persisted as a refugium for marine organisms for thousands of years. However, studies of sediment cores from the lake bottom, including radiocarbon dating of sapropel, dated the lake back to 1,000 years only (Gurevich and Liiva 1975). The estimate of 1,500–1,000 years was confirmed in a recent geomorphological study (Mityaev et al. 2008). To note, the incorrect information that Lake Mogilnoe is ten thousand years old is presented, by mistake, in the recent review of the "cod lakes" (Hardie et al. 2008). Thus, the period of scientific observations of the lake amounts to about one-tenth of its history. During this period, considerable changes in the species diversity of the lake and in its vertical stratification have occurred. The bottom anoxic layer has expanded, while the upper freshwater layer has become thinner. These changes date back to different time periods (between the 1920s and the 1960s, and between the 1960s and the Noughties, respectively) and thus were probably due to different causes.

Usually, temporal changes in physical features of marine lakes are related to meteorological and climatic factors

Table 4 Some common physical and biological features of Lake Mogilnoe and the best-studied other marine lakes

Region	Arctic			Antarctic	Mediterranean			Tropics			
Lake	1	2*	3*	4*	5	6	7	8*	9*	10*	11
Underground communication with a Sea	+	−	−	−	−	+	+	+	+	+	−
Stratification by salinity and oxygen	+	+	+	+	+	+	+	+	+	+	+
Meromixis	+	+	+	+	−	−	+	+	−	−	+
Red water layer	+	?	?	−	−	−	+	+	−	−	−
Reduced biodiversity	+	+	+	?	?	+	+	+	?	+	+
Numerically abandoned zooplankton	+	?	+	+	−	?	+	+	+	?	−
Atlantic cod	+	+	+	−	−	−	−	−	−	−	−
Scyphozoan jellyfishes	+	?	−	−	+	−	−	+	+	+	−
Sea anemones	+	?	?	−	−	+	−	+	+	+	−
Suberitid sponges	+	?	?	−	?	−	−	+	+	+	+
Endemic and (or) relict species	+	+	+	−	+	+	+	+	+	+	?

Question marks indicate that the data are absent or inconclusive. Lakes: 1. Mogilnoe, after Derjugin (1925) and present study; 2. Rossfjord, Norway, Hognestad (1995); 3. Ogac, Baffin Island, McLaren (1961); 4. Burton, Vestfolld Hills, Bayly (1986); 5. Veliko Jezero, Mljet Island, Croatia, Benović et al. (2000); 6. Vouliagmeni, Greece, Chintiroglou et al. (2008); 7. Zmajevo oko (=Rogoznica), Croatia, Kršinić et al. (2000); 8. Ongeim'l Tketau (=Jellifish), Palau, Hamner et al. (1982) and Hamner and Hamner (1998); 9. Hang Du I, Vietnam, Cerrano et al. (2006); 10. Kakaban (=Halimeda lagoon), Indonesia, Tomascik and Mah (1994) and Becking et al. (2011); 11. Motitoi (=Satonda Crater lake), Indonesia, Kempe and Kaz'mierczak (1993) and Pisera et al. (2010). Lakes marked by an asterisk represent clusters of similar lakes

that influence the stratification, or to anthropogenic influence. For example, a long-term change in salinity and depth of monimolimnion in the brackish meromictic Lake Abashiri in Japan, similar to that in Mogilnoe, was related to the long-term downtrend in precipitation coupled with the sea-level rise (Kuwabara 2001). For Ongeim'l Tketau (Jellyfish Lake) on Palau, an abnormal increase in temperature and salinity of mixolimnion in 1997–98, which caused disappearance of jellyfish swarms, was related to a severe El Niño–La Niña episode (Dawson et al. 2001; Martin et al. 2006). In retrospect, a change of views on the stability of the Jellyfish Lake can be seen. The initial hypothesis that the Lake was remarkably stable on timescales of months to millennia was challenged after the 1997–98 El-Nino event (Dawson et al. 2001).

Gurevich (1975c) speculated that the drastic expansion of the anoxic layer in Lake Mogilnoe between the 1920s and the 1960s was due to anthropogenic eutrophication caused by the activities of the settlement situated west of the lake. However, little is known of the impact, and this hypothesis cannot be either corroborated or refuted. Noteworthy, 8 years after the cessation of human activities on Kildin, the depth of the anaerobic layer stayed unchanged. We relate the fact that the chemocline has stabilised at the depth of 9–10 m to the position of the water filtration horizon at 5–8 m (Gurevich 1975b). The anoxic level has probably reached its uppermost level and cannot rise above the present-day depth of 9–10 m.

Kildin Island experiences land uplift at a rate that exceeds that of the sea-level rise (Mityaev et al. 2008). As the isolation progresses, the surface salinity of the land-locked waters should decrease (Strøm 1936). Yet, the salinity of Lake Mogilnoe does not decrease; on the contrary, the opposite trend is observed. We present two mutually non-exclusive hypotheses explaining the salinity change in the lake. The first is climate-driven change. The water temperature in the Barents Sea changes substantially at the timescale of years and decades (Levitus et al. 2009). The Noughties when we recorded the highest salinities in the lake were the warmest decade in the Barents Sea since the start of observations in 1900, while most of the earlier observations were performed during cold periods (e.g. 1910–1920, 1970s, see Levitus et al. 2009 and data on Kola oceanographic transect at www.pinro.ru). We suspect a link between the sea-water temperature and the lake stratification. For instance, an increased water-surface and air temperature could cause higher evaporation and the reduction in freshwater influx to the lake. Our other hypothesis is that the thinning of the upper (freshwater) layer, which occurred between the 1960s and the Noughties, was due to a macadam road that was built in the mid-1970s several hundred metres inland from the lake, across the lake's catchment area. The road probably redistributed the flow of the precipitation collected uphill, sending some of it west, into the stream discharging to the sea ca. 1 km west of the lake (see Fig. 1 for location of the road and the stream). Thus, the road must have hampered the freshwater inflow to the lake.

The number of species in the zooplankton of marine origin and in zoobenthos has halved since the beginning of the twentieth century; the diversity loss in freshwater zooplankton was even greater. Some of the diversity loss may in fact be illusory and associated with the discrepancies in the research methods. The comparison of the species lists can be blurred by seasonal development of certain species, unrepresentative sampling and misidentification. In our case, the least reliable is the comparison of the algal taxonomies, because common taxa comprise only 30 % of the two species lists compared. This discrepancy probably results from insufficient sampling in the beginning of the twentieth century. The zooplankton species lists obtained by different expeditions also differ substantially. Fomin (1975) explained these disagreements, firstly, by the great interannual variability in the abundance of some taxa and, secondly, by the differences in approaches to sampling. A good illustration of the latter is the list of freshwater rotifers. Seven out of the ten species found in the lake were recorded only in 1915, in the samples taken from the near-bottom waters in the freshwater layer (Derjugin 1925, see also Online Resource 1). Since we did not sample this biotope (and neither did, probably, most of the other researchers), we simply do not know whether these rotifers are still present in the lake. In any case, the observed decrease in the diversity of zooplankton is primarily at the expense of freshwater species, which is in line with the salinity changes occurred in the lake: the freshwater layer has thinned. For this reason, the lake can no longer be described as a freshwater marine following Derjugin (1925); it is now brackish marine. The most reliable comparison can be drawn from the taxonomical lists of the zoobenthos. Firstly, all the surveys carried out comprehensive benthic sampling. Secondly, the density of macrobenthic taxa usually does not fluctuate much on the seasonal or interannual scale. Finally, the absence of several trivial and conspicuous species recorded in the lake earlier undoubtedly indicates the biodiversity loss.

One would anticipate a shift in physical settings to govern the species composition change in the lake biota. Literature on marine lakes and landlocked waters contains examples of benthic extinctions caused by incidents of sulphide poisoning of the upper water layers (e.g. Skei 1988; Fallesen et al. 2000; Barić et al. 2003). Since neither we nor our predecessors recorded any incidents of hydrogen sulphide poisoning of the mixolimnion of the lake, we regard this mechanism as improbable and will turn to the decadal changes recorded. The lens of fresh water has thinned over decades, whereas the bottom anoxic layer has expanded. As a result, the intermediate oxic saline layer, which hosts most of the marine plants and animals, has shifted upwards and thinned. In the 1960s, when the anoxic layer had already expanded and the freshwater lid had not yet thinned, the “marine” layer was only 4 m thick as compared to 7 m in the 1890–1920s and 6 m in the Noughties (Fig. 3c). Considerable fluctuations in the abiotic factors and the temporal shrinkage of the inhabitable volume most probably had a negative effect on the marine biota of the lake.

Degeneration of the environment is not the only possible cause of species loss if one assumes that the lake has no influx of marine taxa. According to the hypothesis of complete biological isolation, the lake is a sort of an aquarium: after introduction of marine plants and animals only the water is changed. Apparently, the biodiversity of such a system, especially a small one, cannot but decrease: taxa are lost even in stable abiotic conditions due to stochastic factors governing the dynamics and extinction of small isolated populations.

So far, the main argument in favour of the isolation hypothesis has been the microporous structure of the filtering dam (Derjugin 1925). This argument was examined by direct observations for the first time in our study, and indeed, the scuba divers found no visible reach-through holes in the dam. On the other hand, the dam structure should be indeed very fine to detain small holoplanktonic organisms as well as propagules and larvae of benthic species.

The data accumulated to date strongly indicate that the hypothesis of lake’s complete biological isolation should be challenged. We found a number of benthic species unseen previously in the lake. One of them is the mussel, a large, conspicuous species, which could hardly have been missed during the extensive studies in the early twentieth century. The previous surveys have recorded similar “unexpected” findings. A single starfish identified as *Stichaster albulus* Stimpson was found in 1889 (Derjugin 1925). A single specimen of the moon jelly *Aurelia aurita* L was observed in 1967 (Fomin 1975). Numerous ophioplutei were recorded in the plankton in 1900 (Derjugin 1925), whereas nobody has seen either adults in the benthos or larvae in the plankton before or after 1900. The most credible explanation of these findings is that some organisms do occasionally arrive from the sea. The general route should be through the pinholes in the dam. Sea birds, fishermen and scientists occasionally visiting the lake could also be responsible for the introduction of some marine organisms, transported as a prey, in microdroplets of water on the plumage or with the fishing gear and the research equipment.

Apart from Mogilnoe, the hypothesis of strict biological isolation has been applied to lakes Ogac (McLaren 1961), Ongeim’l Tketau (Hamner and Hamner 1998), Motitoi (Kempe and Kaz’mierczak 1993), Kakaban (Massin and Tomascik 1996) and Vouliagmeni (Chintiroglou et al. 2008). Except Motitoi, which probably does not communicate with the sea at present, the other lakes directly communicate with the sea either by water percolation at surface (Ogac) or through tunnels and fissures in the limestone rock. These lakes should be hypothetically even less protected from the penetration of organisms from the sea than Mogilnoe. As stated by McLaren (1961), zooplankton from the sea does penetrate into Lake Ogac, but nevertheless contributes almost nothing to its faunal composition, probably because "the residents of the lake may be genetically or ontogenetically adapted to conditions of the lake, for the allochthonous zooplankton brought by the tides is soon eliminated" (p. 154). In line with these ideas, Dawson et al. (2009) suggested treating marine lakes as habitat islands, that is, entities circumscribed not so much geographically as ecologically (cf. common theory of island biogeography, MacArthur and Wilson 1967). This is probably also true for Mogilnoe. Genetic studies are needed to assess the degree of isolation of the lake populations and, in the long run, of the entire lake ecosystem. For the present, we conclude that the lake is not completely isolated physically and thus can be prone not only to extinction but also to colonisation.

Conclusions

According to the scientific as well as the popular tradition established by Derjugin (1925), Lake Mogilnoe is considered unusual, even unique for the following reasons. It is multilayered: freshwater at the surface, marine at intermediate depths and anoxic at the bottom. Its depths are seething with an unexpectedly rich marine life including abundant populations of cod, jellyfishes, actinia and sponges. The consequences of evolution can be observed in the lake at first hand: it is inhabited by animal forms that have evolved there. The lake is a "lost world" that has been developing, according to its own laws, in complete isolation for centuries. Our review reveals that nearly the same set of features, either proved or assumed, was independently attributed to a number of other marine lakes in different parts of the world. Amongst these lakes, Mogilnoe boasts the longest history of scientific studies. Our data demonstrate that, contrary to the traditional views, the lake is rather dynamic: during the period of observations, the stratification has changed and the biodiversity decreased. The temporal changes in biodiversity also cannot be explained without admitting that animals are occasionally introduced from the sea. Thus, an idealised model of an isolated steady-state ecosystem cannot be applied to a marine lake without reservations: a model of fluctuating abiotic environment and partial biological isolation would portray the actual situation more adequately.

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