

EXPERIMENTAL
ARTICLES

Cryptomonad Alga *Rhodomonas* sp. (Cryptophyta, Pyrenomonadaceae) Bloom in the Redox Zone of the Basins Separating from the White Sea

E. D. Krasnova^{a, 1}, A. N. Pantyulin^b, D. N. Matorin^a, D. A. Todorenko^a,
T. A. Belevich^a, I. A. Milyutina^c, and D. A. Voronov^{c, d}

^a Biological Faculty, Moscow State University, Russia

^b Faculty of Geography, Moscow State University, Russia

^c Belozersky Institute of Physico-Chemical Biology, Moscow State University, Russia

^d Kharkevich Institute for Information Transmission Problems, Russian Academy of Sciences, Moscow, Russia

Received August 6, 2013

Abstract—Bloom of a cryptomonad alga *Rhodomonas* sp. (Cryptophyta, Pyrenomonadaceae) was observed in the chemocline of saline basins separating from the White Sea, resulting in red coloration of the relevant water layer. According to the sequence of the 18S nuclear rRNA gene, this species was identical to *Rhodomonas* sp. RCC2020 (GenBank accession no. JN934672) from the Beaufort Sea. The presence of the red layer formed by mass development of *Rhodomonas* sp. is considered an indicator of a certain stage of separation of a basin from the sea.

Keywords: *Rhodomonas* sp., red water layer, basins separating from the sea, redox zone, chlorophyll fluorescence, 18S RNA, White Sea

DOI: 10.1134/S0026261714030102

A layer of red water is sometimes formed in some meromictic basins at the boundary between the mixolimnion (the layer susceptible to wave and convective mixing) and the monimolimnion (stable lower water mass where mixing does not occur). As a rule, it turns red due to the presence of phototrophic prokaryotes: purple or green sulfur bacteria [1–5]. This phenomenon was recorded in both continental and marine meromictic basins, e.g., in Lake Mogil'noe on Kil'din Island in the Barents Sea [6–8]. In recent years, numerous bodies of water with the signs of meromixis were found at the Karelian coastline of the White Sea [9–11]. They were formed as a result of postglacial isostatic uplift of the shore, which in the area of the White Sea Biological Station, Moscow State University (WSBS MSU) occurs at a rate of 4 mm per year [12], via the bay separating from the main waters of the sea. These basins are at different stages of isolation from the sea: in some of them, the tides are still observed, albeit at a lower amplitude than at the sea; in others, inflow of seawater is limited to irregular flows of an especially high tide inwards. Some basins have a freshwater or brackish surface layer and saline bottom water, including one real meromictic lake. These water bodies have been monitored by researchers of the WSBS MSU since 2010, and cases of the development

of the red water layer were recorded in some of them [13]. In this work, we studied the biological objects in the red water layer and the conditions under which this layer appears.

MATERIALS AND METHODS

The work was performed using the facilities of the White Sea Biological Station, Moscow State University. In 2010–2013, 16 basins at different stages of separation from the sea were studied in the vicinity of the biological station. The deepest point in basin was determined using a Fishfinder 90/140 echo sounder; water temperature and salinity were measured in situ with a 0.5-m step from surface to bottom using a ProfiLine Cond 197i conductometer. The samples were taken from the same depths with a Mini Purger WP 4012 submerged pump equipped with a silicon rubber tube.

The algal chlorophyll fluorescence parameters (F_0 , F_v/F_m) were determined by pulse fluorometry using a Water-PAM device (Walz GmbH, Germany) in the red-layer water sampled in lagoon at Cape Zeleny on September 3, 2012. Since the F_0 value depends on the amount of chlorophyll in the cells, this can be used to determine its concentration, as well as to assess the amount of the phytoplankton biomass [14]. After calibration, it is possible to quickly assess the concentra-

¹ Corresponding author; e-mail: e_d_krasnova@wsbs-msu.ru

Table 1. Basins with a layer of red water and conditions under which it appeared

Basin	Dates of the red water layer appearance	Water temperature in the red layer, °C	Water salinity in the red layer, ‰	Depth, m
Lake Kislo-Sladkoe	18.10.12	10.7–10.9	25.8	3.5
Lagoon at Cape Zeleny	03.09.12	11.1	28.8	5
	18.10.12	11.3–12.7	28.6–28.8	4–5
	08.01.13	4.0	27.4	4.5
Lake Elovoe	19.06.12	7.8–9.1	23.4–23.5	2.5–3
	23.07.12	6.6–9.5	23.8–23.9	3–4
Lake Bol'shie Khruslomeny	12.08.12	7.9–10.1	17.5–18.7	4–4.5
Total	Recorded in January, June, July, August, September, and October	Temperature range: 4°C; 6.6–12.7°C	Salinity range: 17.5–28.8‰	Depth range: 2.5–5 m

tion of algal pigments in the water sample. Based on the chlorophyll fluorescence data, it is possible to obtain information not only on the relative abundance of phytoplankton (F_o) but also on its photosynthetic activity (F_v/F_m). The F_v/F_m parameter indicates the efficiency of accumulation of light energy at the initial stages of photosynthesis [14]. The light absorption spectrum in the samples from the red water layer was determined on a HITACHI-557 spectrophotometer. The algal chlorophyll fluorescence parameters (F_o , F_v/F_m) in the lagoon at Cape Zeleny were determined in September and October 2012 when a clearly seen red layer was present in this basin.

The presence of microalgae in the samples and their taxonomic identity were determined under a Leica fluorescence microscope with a set of N2.1 filters (excitation/transmission 515–560/580 nm). For more exact genus and species identification of the microalgae, the sequence of the fragment of the nuclear 18S rRNA gene (about 1500 bp) was determined; it was deposited in GenBank under accession no. KF039722. The DNA was obtained using the Nucleospin Plant Extraction Kit (Macherey-Nagel, Germany). PCR was performed using the Dialat LTD (Moscow, Russia) kit of reagents under the following conditions: initial denaturation at 94°C for 3 min; 30 cycles: 94°C, 30 s; 58°C, 30 s; 72°C, 30 s; in the final cycle, the elongation time was 5 min. The primers Q5 (forward) 5'-TCTGGTTGATCCTGCCAGT-3' (complementary at the gene 5'-end) and r71 (reverse) -5'-GGGCGGTGTGTACAAAGGGCAGGGAC-3' were used. DNA sequencing was carried out using the ABI PRISM® BigDye™ Terminator v. 3.1 reagent kit

with the subsequent analysis of the reaction products on an Applied Biosystems 3730 DNA Analyzer at the Genom Collective Use Center (Institute of Molecular Biology, Russian Academy of Sciences). In order to determine the taxonomic position of the organism studied, the 18S rRNA nucleotide sequence obtained was compared to the nucleotide sequences from the GenBank (<http://www.ncbi.nlm.nih.gov>).

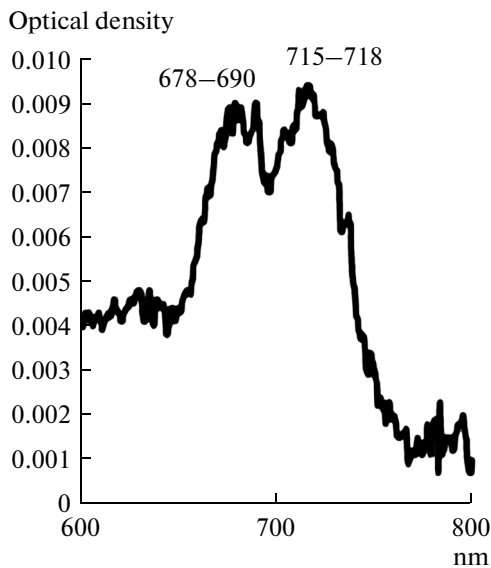
RESULTS

Layers of red water were registered in four basins: Lake Kislo-Sladkoe, lagoon at Cape Zeleny, Lake Elovoe, and Lake B. Khruslomeny (Table 1). This phenomenon was not revealed in the other 12 basins.

These basins are at different stages of separation from the sea: seawater flows into Lake Khruslomeny and lagoon at Cape Zeleny during high tides, while the entrance of seawater into the lakes Kislo-Sladkoe and Elovoe is limited to irregular high tides blown up by very strong wind surges, which do not occur every year. The latter three basins are small-sized: from 5 to 15 ha with a maximum depth of 4.5 to 6.5 m; the area of Lake Bol'shie Khruslomeny is 157 ha, and the depth is 21 m.

While the red water layer occurred, vertical stratification with sharp gradients of the hydrophysical parameters was observed in all basins. Their temperature and salinity ranges substantially differed.

In Lake Kislo-Sladkoe (Lagoon Polupresnaya; 66°32.87' N, 33°08.14' E), the surface water layer is often diluted: its salinity normally varies between 7 and 17‰; the bottom water mass is saline throughout a



Light absorption spectrum in the red layer of water sampled on September 3, 2012 in Cape Zeleny lagoon.

year (22.6–27.8‰). The red layer was recorded in October 2012. At this moment, the halocline was at a depth of 1.5 m, and reverse temperature stratification was observed: the water was colder near the surface (3.5°C) than at the bottom (10.7–10.9°C). The red layer coincided with the warmest deep layer containing hydrogen sulfide, below 3.5 m.

In Lake Elovoye (66°28.7' N, 33°16.9' E), practically fresh water (0–0.4‰) is near the surface down to 0.5-m depth, and the bottom depression is filled with saline water (23.2–24.5‰). The bottom water temperature does not increase above 6°C even in summer. The red layer was recorded in June and July 2012. In this period of its existence, the halocline was at a depth of 1 m. The thermocline was below the halocline, at a depth of 2–2.5 m; the difference between the temperatures near the bottom (5.5 m) and at the surface was 12.6–13.1°C. The layer of red water was directly below the thermocline: at depths of 2.5–3 and 3–4 m in June and July, respectively. Below 3.5 m (in June) and 4 m (in July), the water had a distinct hydrogen sulfide odor; however, in the red layer itself, the odor was absent.

In Lake Bol'shie Khruslomeny on Island Olenii in Bay Kovda (66°43' N, 32°51' E), the upper 2 m are diluted to 4–7‰; below is saline water; towards the bottom, its salinity gradually increases to that of seawater (22.8–23.9‰). The temperature of the bottom water mass is 8–9°C; the overlying layers may be heated to over 20°C. The red layer was observed in the thermocline at a depth of 4–4.5 m in August 2012. The vertical temperature gradient was 8.6°C for a 1 m depth. The hydrogen sulfide odor in the red-water layer was absent and appeared at a depth of 5.5 m.

The lagoon at Cape Zeleny (66°31.80' N, 33°05.55' E), unlike the previous three basins, has no signs of desali-

nation; on the contrary, the salinity in the bulk of the water column is higher than in the White Sea—up to 29‰. The bottom water temperature varies between 3 and 7.6°C throughout a year; near the surface the water is warmed up according to the season. In this basin, the red layer was observed at a depth of 4–5 m in the zone with increased salinity. In September, the middle layer of water (2.5–4 m; 15.1–15.9°C) was the warmest, the water above and below it was relatively cold. The red layer was below the lower thermocline. In October, the middle layer (3–4.5 m) was also the warmest, and the red layer was also slightly lower than the warm zone. There was no hydrogen sulfide odor in the autumn red-water samples. In January, reverse temperature stratification was observed: the red layer was at the same depth as in autumn, but now the hydrogen sulfide-containing layer rose higher (to a depth of 3.5 m), and the red layer appeared to be submerged in the hydrogen sulfide column.

With all the variety of thermohaline conditions in these stratified water bodies, the red layer appeared only within saline water masses (17.5–28.8‰) and was almost always in the 9–10°C zone incorporating the adjacent layers with temperatures varying between 6.6 and 12.7°C (Table 1). Only once, in January, it coincided with the 4°C layer; at that time it was the warmest in this basin.

In the lagoon at Cape Zeleny, the algal chlorophyll fluorescence parameters (F_o , F_v/F_m) were determined in different layers at the time when a clearly seen red layer was present. They are shown in Table 2. In the upper layers (to a depth of 1.5–2 m), the chlorophyll a content calculated by the F_o value was 5.5–5.6 µg/L in September and 2.3–3.0 µg/L in October at a low photosynthetic activity F_v/F_m (0.47–0.60 in September and 0.17–0.58 in August), which corresponded to the values observed at this time in the sea. In September, the fluorescence values increased with depth and attained the maximal values in the red layer (at a depth of 4.5–5 m). The chlorophyll a content calculated according to F_o in this layer attained very high values. The photosynthetic activity was also high (0.71), which is characteristic of algae during the period of intense blooming. In October, the layer of red water was higher, the chlorophyll a content in it was the highest for the water column (82.2 µg/L), but the photosynthetic activity was significantly lower than in the previous month, indicating a decrease in the number and activity of algae in autumn. In both cases, the water below the red layer contained hydrogen sulfide in the presence of which algal photosynthesis is impossible.

The spectrum of light absorption by the water sampled from the red layer in September had two maxima: in the 678–690 and in the 715–718-nm range (figure). The bacteriochlorophyll of green sulfur bacteria is most likely responsible for absorption in the long-wave part of the spectrum. The peak at 678–690-nm prob-

Table 2. Characteristics of different layers of water in lagoon at Cape Zeleny in September and in October 2012

Depth, m	September 3, 2012						October 18, 2012					
	S, ‰	T, °C	pH	properties of water	photosynthetic activity (F_v/F_m)	chlorophyll concentration calculated with the F_o value ($\mu\text{g/L}$)	S, ‰	T, °C	properties of water	photosynthetic activity (F_v/F_m)	chlorophyll concentration calculated with the F_o value ($\mu\text{g/L}$)	
0	24.5	12.7		Clear, odorless	0.47	5.6	22.6	4.7	Clear, odorless	0.17	2.5	
0.5	24.6	12.7	9	»			23.1	6.1	»			
1	24.6	12.7	8.9	»			23.9	7.6	»	0.23	2.3	
1.5	24.6	12.6	8.9	»	0.52	5.5	25.2	9.3	»			
2	25	13	8.8	»			25.2	9.6	»	0.55	3.0	
2.5	28.6	15.9	8.8	»			27.2	11	»			
3	28.7	16.7	8.7	»	0.60	18.4	28.4	12.1	»	0.58	8.8	
3.5	28.9	16.6	8.5	»			28.4	12.5	»			
4	28.8	15.1	8.2	»			28.6	12.7	Red	0.53	82.2	
4.5	28.8	13	8	»			28.8	12.4	Pinkish, H ₂ S			
5	28.8	11.1	8.1	Red	0.71	281.3	28.8	11.3	»	0	—	
5.5	28.8	10	8	H ₂ S			28.8	9.7	Green, H ₂ S	0	—	
6	28.8	8.2	7.6	H ₂ S, green	0.06	—						
6.4	28.8	7.6	7.7	Green	0.042	—						

ably corresponded to the chlorophyll of the algae, which abounded in the red water layer from lagoon at Cape Zeleny.

Red color of the water samples was due to the blooming of a cryptophytic alga of the genus *Rhodomonas*. The nuclear 18S rRNA gene was sequenced for more exact genus and species identification. A search for the homology between the sequence obtained and the GenBank 18S rRNA sequences with the BLAST software showed 100% homology of the 18S rRNA gene fragment of the microalga from the red layer with the nucleotide sequence of *Rhodomonas* sp. RCCC2020 (GenBank no. JN934672).

During the survey of four more basins that are in the process of separation from the sea (October 2012), *Rhodomonas* sp. cells were also found in Lake Kislo-Sladkoe and Lake Elovoe, but were absent in Lake Nizhnee Ershovskoe (66°32.28' N, 33°3.48' E) and Lake Trekhtsvetnoe in the Pekkelinskaya Bay of (66°35.53' N, 32°59.97' E). In the first two basins, they were concentrated directly above the upper boundary of hydrogen sulfide occurrence: in Lake Kislo-Sladkoe, at a depth of 2 m at $T = 8.9^{\circ}\text{C}$ and $S = 24.6\text{‰}$; in Lake Elovoe at a depth of 3 m at $T = 12.7^{\circ}\text{C}$ and $S = 24.0\text{‰}$. The number of *Rhodomonas* sp. cells was insufficient for the red layer formation. Nevertheless, in the fluorescence intensity profile of Lake Elovoe, the layer with a high number of these flagellates accounted for the maximum chlorophyll fluorescence; chlorophyll concentration calculated using the F_0 value was 82.2 $\mu\text{g/L}$, which was an order of magnitude higher than in the overlying layers. The variable fluorescence output (F_v/F_m) value was 0.529, indicating a moderate photosynthetic activity in this layer in autumn.

The layer of red water in different basins formed in different seasons: in two of them, in summer; in two others, in autumn; in one, in January. Some basins have been under observation for more than one year, and the occurrence of this phenomenon may be assessed. For example, in Lake Kislo-Sladkoe and in lagoon at Cape Zeleny, the red layer was recorded only once over three years of observations, when they were studied in autumn. In Lake Elovoe, it appeared in July 2011, but was absent in the same month of the previous year, and, similarly, in Lake B. Khruslomeny, the red layer was recorded in August 2012, but not in August 2010.

DISCUSSION

The red layer of water associated with mass development of phototrophic bacteria was recorded in many meromictic lakes, including freshwater ones, e.g., Lake Mahoni in Canada [15], Lake Cadagno in the Swiss Alps [5], and Lake Buchensee in West Germany [4]; alkaline Lake Shira and Lake Shunet in Khakassia [1–3]; and marine ones, for example,

Lake Mogil'noe on Kil'din Island in the Barents Sea [6, 7]. This layer always occurs near the redox horizon (the horizon where the redox potential changes from positive to negative), where the surface mass of oxygen-containing water contacts with the bottom reduced hydrogen sulfide-containing water mass, provided this horizon is in the photic zone. Investigation of the basins separated from the White Sea showed that in some of them a red interlayer of water also occurred. In particular, previous researchers [16] noted a high number of anoxygenic phototrophic bacteria in the red water layer in Lake Kislo-Sladkoe located not far from the WSBS MSU. However, in some bodies of water the red layer might develop not due to bacteria but algae. The presence of eukaryotic cells in the redox zone was noted by Lunina [16], who revealed them among bacterial cells in the photographs taken under a transmission electron microscope. We revealed the presence of living algal cells in the layer of red water in the course of the studies of fluorescence, when a high chlorophyll concentration was discovered in it, and confirmed this finding by light microscopy of the freshly taken samples.

The high variable fluorescence output values gave evidence of an active state of the photosynthetic apparatus of the algae present there. Analysis of absorption spectra confirmed that, apart from bacteria, certain organisms containing chlorophyll a are also responsible for the optical characteristics of the water. Those were the cryptophytic algae of the genus *Rhodomonas*. As far as we know, it is the first observation of the red water layer in meromictic basins formed due to the development of cryptophyte algae.

Determination of the species and even generic identity of cryptophytic algae is difficult due to the insufficiently developed taxonomy [17]. The optimal approach to this problem is the application of molecular genetic methods [18]. Comparison between the nucleotide sequences of the nuclear 18S rRNA gene fragment with those published in GenBank showed that the *Rhodomonas* sp. that created the red layer in Cape Zeleny lagoon was identical to the cultures of *Rhodomonas* sp. RCC 2020 from the Beaufort Sea (GenBank, JN93467). The species identity of the strain *Rhodomonas* sp. RCC 2020 was not determined. The *Rhodomonas* species from the White Sea and from the Beaufort Sea formed a single group, which differed from the nucleotide sequence of the nuclear 18S rRNA gene of all the rest representatives of this genus available in the GenBank database.

Cryptophytic flagellates are one of the typical variants of "stratified" algae [19]. Owing to their pigment composition and capacity for phagotrophy, they are well adapted to habitation in stagnant basins with clear water and a stable density gradient. The conditions suitable for their mass development occur in certain tropical lakes, in the polar regions, in mountainous regions, as well as in small bodies of water, where the organic-enriched effluents flow from agricultural ter-

ritories [19]. In marine basins, these organisms are widespread; however, their mass development is observed extremely rarely. In the White Sea, blooming of cryptomonads was recorded in two biotopes, and both were connected with the basins that were in the process of separation from the sea: in the ice [20] and, as we know now, above the boundary of the hydrogen sulfide water mass.

The red layer, as well the zone of concentration of *Rhodomonas* sp. cells outside the period of their blooming, is topographically associated with the redox zone and is located directly above it. In the surface waters above the red layer, chlorophyll concentration is significantly lower; therefore, the red layer may be regarded as a deep chlorophyll maximum.

Our findings concerning the conditions under which the red layer occurs in those basins separated from the White Sea make it possible to characterize, in general, the ecological preferences of the algae.

Rhodomonas sp. RCC2020 revealed by us in the White Sea separating basins and isolated from seawater samples in the Beaufort Sea was in both cases found at high latitudes in the Arctic [21] between 66° N and 69° N; one, in the western hemisphere; the other, in the eastern hemisphere. *Rhodomonas* sp. from the Beaufort Sea was found at the depths of 4 and 40 m at 8.33 and -1.17°C, respectively, where the deep chlorophyll maximum was observed. The range of salinity at which this species occurred in the North American Arctic sector (14.7 and 31.3‰) was slightly wider than in the White Sea (17.5–28.8‰). Since *Rhodomonas* sp. did not bloom at the time of sampling in the Beaufort Sea (the deep chlorophyll maximum was represented exclusively by the diatom *Chaetoceros*), it is difficult to judge the ecological preferences of this strain in the Beaufort Sea. Our data on the conditions of mass development of *Rhodomonas* sp. in the White Sea, including the cases when it forms the red layer, provide for a better characteristic of its requirements for the environmental conditions.

The White Sea basins where we registered mass development of *Rhodomonas* sp. all still retain their connection with the sea, and they all have a layer of salty oxygen-containing water as a result of the entrance of sea water with high tides or splash water. In other lakes (Nizhnee Ershovskoe and Trekhtsvetnoe) further advanced in separation from the sea, all the saline water mass is contaminated with hydrogen sulfide and this alga has not been revealed there. The position of the red layer did not depend on either the size of the lake or its depth. The range of depths at which the red layer occurred was 2.5 to 5 m with a median at 4–4.5 m. Its thickness did not exceed 1 m and not infrequently was less than 50 cm. The water in these basins is clear, and the corresponding depths are in the photic zone. According to the impressions of the divers who explored some of these basins, the water below the redox zone is turbid due to the finely dis-

persed white suspension likely to be created by bacterial cells and sulfur crystals.

The 17.5–28.8‰ salinity range in the red water layer of the basins separating from the White Sea agrees with the values characteristic of saline bodies of water, and *Rhodomonas* sp. inhabiting this layer may be attributed to the category of mesohalobic species according to the Kolbe halobity scale and the Proshkina-Lavrenko specifications [22].

The constant temperature of the red layer (9–10°C) merits attention. There is a high probability that this range corresponds to the optimum temperature for this species. Remarkably, the temperature preferences in two freshwater species of this genus from Lake Bodensee in the Alpine piedmont were similar: *Rhodomonas lens* were concentrated in the layer with a temperature in the 9.2–9.9°C range; *Rhodomonas minuta* v. *planctonica*, in the 9.6–10.2°C range [23].

The attitude of *Rhodomonas* sp. to hydrogen sulfide is of special interest. The highest cell concentration in all basins was noted above the boundary between the oxidized and reduced layers. The samples from the layer with the most intense red color did not smell of hydrogen sulfide; however, at its lower boundary, sulfide did appear. Other researchers [24, 25] also noted that cryptophytic algae could tolerate low small sulfide concentrations in the chemocline of meromictic lakes. As a rule, under such conditions one of the *Cryptophyta* species forms a monoculture with a high number of cells that is many times higher than that of the phytoplankton in the overlying mixolimnion. According to the data of Camacho [26], up to 60% of the biomass of lacustrine phytoplankton in Lake Ciso (Spain) was concentrated in the deep chlorophyll maximum at the upper boundary of occurrence of hydrogen sulfide predominantly consisting of the cryptomonad *Cryptomonas phaseolus* cells.

What attracts cryptophytic algae to the redox-zone? The conditions favorable for their development are possibly linked to suitable thermohaline conditions, illumination, and the flow of biogenic elements from the bottom water mass. It is possible that the attractants to the hydrogen sulfide layer are bacteria as a possible source of food or biogenic elements. The position of the cryptophyte red layer between the oxidized and reduced water masses, together with the known capacity of certain species of cryptophyte algae to phagocytize bacterial cells [27, 28], and their high nutritional value for higher level consumers of [29, 30] indicate the role of the red cryptophyte layer as a possible link between the bacterial community of the hydrogen sulfide layer and the metalimnion community of oxyphiles, which are spatially separated due to stratification and meromixis.

Since blooming of *Rhodomonas* sp. was observed only in the basins which retained their connection with the sea, the presence of the red cryptophytic layer may be regarded as an indicator of a certain stage of their separation. It is noteworthy that the red crypto-

phytic layer has been observed both in the bodies of water which evolve by decreasing their salinity and in those where salinity was higher than in the maternal water body. The sporadic nature and irregularity of formation of the red layer is likely to be explained by the fact that the position of the redox zone does not always coincide with the temperature optimum zone.

ACKNOWLEDGMENTS

We are grateful to E.P. Lukashov, a researcher from the Department of Biophysics, Biological Faculty, Moscow State University, for help in determining the light absorption spectra.

REFERENCES

- Pimenov, N.V., Rusanov, I.I., Karnachuk, O.V., Rogozin, D.Yu., Bryantseva, I.A., Lunina, O.N., Yusupov, S.K., Parnachev, V.P., and Ivanov, M.V., Microbial processes of the carbon and sulfur cycles in Lake Shira (Khakasia), *Microbiology* (Moscow), 2003, vol. 72, no. 2, pp. 221–229.
- Lunina, O.N., Bryantseva, I.A., Akimov, V.N., Rusanov, I.I., Rogozin, D.Yu., Barinova, E.S., Lysenko, A.M., and Pimenov, N.V., Seasonal changes in the structure of the anoxygenic photosynthetic bacterial community in Lake Shunet, Khakassia, *Microbiology* (Moscow), 2007, vol. 76, no. 3, pp. 386–379.
- Rogozin, D.Yu., Trusova, M.Yu., Khromechek, E.B., and Degermendzhi, A.G., Microbial community of the chemocline of the meromictic Lake Shunet (Khakassia, Russia) during summer stratification, *Microbiology* (Moscow), 2010, vol. 79, no. 2, pp. 253–261.
- Overmann, J. and Tilzer, M.M., Control of primary productivity and the significance of photosynthetic bacteria in a meromictic kettle lake Mittlerer Buchensee, West-Germany, *Aquatic Sci.*, 1989, vol. 51, pp. 261–278.
- Storelli, N., Peduzzi, S., Saad, M.M., Frigaard, N.-U., Perret, X., and Tonolla, M., CO₂ assimilation in the chemocline of Lake Cadagno is dominated by a few types of phototrophic purple sulfur bacteria, *FEMS Microbiol. Ecol.*, 2013, vol. 84, pp. 421–432.
- Isachenko, B.L., Investigation of bacteria of the Arctic Ocean, in *Tr. Murmanskoi nauchnoi promyslovoi ekspeditsii 1906 g.* (Proc. Murmansk Sci. Commer. Expedition), St. Petersburg, 1914. Cited from: Gurevich, V.I., *Reliktovoe ozero Mogil'noe* (The Relic Lake Mogil'noe), Leningrad: Nauka, 1975.
- Gorlenko, V.M., Vainshtein, M.B., and Kachalkin, V.I., *Reliktovoe ozero Mogil'noe* (The Relic Lake Mogil'noe), Gurevich, V.I., Ed., Leningrad: Nauka, 1975, pp. 188–197.
- Lunina, O.N., Gorlenko, V.M., Popova, O.A., Akimov, V.N., Rusanov, I.I., and Pimenov, N.V., Seasonal changes in the structure of the anoxygenic phototrophic bacterial community in Lake Mogil'noe, a relict lake on Kil'din Island in the Barents Sea, *Microbiology* (Moscow), 2005, vol. 74, no. 5, pp. 588–596.
- Shaporenko, S.I., Korneeva, G.A., Pantyulin, A.N., and Pertsova, N.M., Characteristics of the ecosystems of water bodies separating from Kandalaksha Bay of the White Sea, *Water Res.*, 2005, vol. 32, no. 5, pp. 469–483.
- Pantyulin, A.N. and Krasnova, E.D., Separating water bodies of the White Sea: a new object for interdisciplinary research, in *Geologiya morei i okeanov* (Geology of Seas and Oceans), Proc. 19th Int. Conf. (School) Marine Geol., 2011, vol. 3, pp. 241–245.
- Krasnova, E.D., Pantyulin, A.N., Belevich, T.A., Voronov, D.A., Demidenko, N.A., Zhitina, L.S., Il'yash, L.V., Kokryatskaya, N.M., Lunina, O.N., Mardashova, M.V., Prudkovskii, A.A., Savvichev, A.S., Filippov, A.S., and Shevchenko, V.P., Multidisciplinary Studies of the separating lakes at different stage of isolation from the White Sea performed in March 2012, *Oceanology*, 2013, vol. 53, no. 5, pp. 714–717.
- Olyunina, O.S., Romanenko, F.A., and Golovkina, E.A., Postglacial uplift of the Karelian shore of the White Sea: preliminary results of investigation of coastal peat bogs, in *Geologiya morei i okeanov* (Geology of Seas and Oceans), Proc. 19th Int. Conf. (School) Marine Geol., 2011, vol. 1, pp. 91–92.
- Krasnova, E.D., Pantyulin, A.N., Matorin, D.N., Todorenko, D.A., Belevich, T.A., Milyutina, I.A., and Voronov, D.A., Nature of red layers in the lakes separating from the White Sea, in *Morskaya biologiya, geologiya, okeanologiya—mezhdistsiplinarnye issledovaniya na morskikh statsionarakh* (Marine Biology, Geology, Oceanology—Interdisciplinary Studies at Marine Stations), Proc. Sci. Conf., Moscow: KMK, 2013, pp. 151–156.
- Matorin, D.N. and Rubin, A.B., *Fluorestsentsiya khlorofilla vysshikh rastenii i vodoroslei* (Chlorophyll Fluorescence of Higher Plants and Algae), Izhevsk—Moscow: Izhevsk. Inst. Comput. Res., 2012.
- Overmann, J., Beatty, J.T., Hall, K.J., Pfennig, N., and Northcote, T.G., Characterization of a dense, purple sulfur bacterial layer in a meromictic salt lake, *Limnol. Oceanogr.*, 1991, vol. 36, no. 5, pp. 846–859.
- Lunina, O.N., Savvichev, A.S., Kuznetsov, B.B., Pimenov, N.V., and Gorlenko, V.M., Anoxygenic phototrophic bacteria of the Kislo-Sladkoe Stratified Lake (White Sea, Kandalaksha Bay), *Microbiology* (Moscow), 2014, vol. 83, nos. 1–2, pp.
- Novarino, G.A., Companion to the identification of cryptomonad flagellates (Cryptophyceae = Cryptomonadea), *Hydrobiologia*, 2003, vol. 502, pp. 225–270.
- Cavalier-Smith, I.T., Couch, A.J., Thorsteinsen, K.E., Gilson, P., Deane, J.A., Hill, D.R.A., and Mcfadden, G.I., Cryptomonad nuclear and nucleomorph 18S rRNA phylogeny, *J. Phycol.*, 1996, vol. 31, pp. 315–328.
- Reynolds, C.S., Huszar, V., Kruk, C., Naselli-Flores, L., and Melo, S., Towards a functional classification of the freshwater phytoplankton, *J. Plankton Res.*, 2002, vol. 24, pp. 418–428.
- Il'yash, L.V., Belevich, T.A., Zhitina, L.S., Kolosova, E.G., and Kudryavtseva, V.A. First data on ice biota of the lakes separating from the White Sea: composition, abundance, and vertical distribution, in *Morskaya biologiya, geologiya, okeanologiya—mezhdistsiplinarnye issledovaniya na morskikh statsionarakh* (Marine Biology, Geology, Oceanology—Interdisciplinary Studies

- at Marine Stations), Proc. Sci. Conf., Moscow: KMK, 2013, pp. 104–108.
21. Balzano, S., Marie, D., Gourvil, P., and Vaultot, D., Composition of the summer photosynthetic pico and nanoplankton communities in the Beaufort Sea assessed by T-RFLP and sequences of the 18S rRNA gene from flow cytometry sorted samples, *The ISME J.*, 2012, vol. 6, pp. 1480–1498.
 22. Proshkina-Lavrenko, A.I., Diatoms as indicators of water salinity, in *Diatomovyi sbornik* (The Diatom Collection), Leningrad: Izd-vo Leningrad. Univ., 1953, pp. 186–205.
 23. Sommer, U., Vertical niche separation between two closely related planktonic flagellate species (*Rhodomonas lens* and *Rhodomonas minuta* v. *planctonica*), *J. Plankton Res.*, 1982, vol. 4, pp. 137–142.
 24. Gasol, J.M., García-Cantizano, J., Massana, R., Guerrero, R., Pedrós-Alió, C., Physiological ecology of a metalimnetic *Cryptomonas* population: relationships to light, sulfide and nutrients, *J. Plankton Res.*, 1993, vol. 15, pp. 255–275.
 25. Stoeck, T. and Behnke, A., The anoxic Framvaren Fjord as a model system to study protistan diversity and evolution, in *Anoxia. Evidence for Eukaryote Survival and Paleontological Strategies*, Altenbach, A., Bernhard, J., and Seckbach, J., Eds., Springer, 2012, vol. 21, pp. 421–448.
 26. Camacho, A., On the occurrence and ecological features of deep chlorophyll maxima (DCM) in Spanish stratified lakes, *Limnetica*, 2006, vol. 25, nos. 1–2, pp. 453–478.
 27. Tranvik, L.J., Porter, K.G., and Sieburth, J.Mc.-N., Occurrence of bacterivory in *Cryptomonas*, a common freshwater phytoplankter, *Oecologia*, 1989, vol. 78, pp. 473–476.
 28. Marshall, W. and Laybourn-Parry, J., The balance between photosynthesis and grazing in Antarctic mixotrophic cryptophytes, *Freshwater Biol.*, 2002, vol. 47, pp. 2060–2070.
 29. Pedrós-Alió, C., Massana, R., Latasa, M., García-Cantizano, J., and Gasol, J.M., Predation by ciliates on a metalimnetic *Cryptomonas* population—feeding rates, impact and effects of vertical migration, *J. Plankton Res.*, 1995, vol. 17, pp. 2131–2154.
 30. Sigsgaard, S.J., Petersen, J.K., and Iversen, J.J.L., Relationship between specific dynamic action and food quality in the solitary ascidian *Ciona intestinalis*, *Mar. Biol.*, 2003, vol. 143, no. 6, pp. 1143–1149.

Translated by E. Babchenko