Depth profiles of spectral and hydrological characteristics of water and their relation to abundances of green sulfur bacteria in the stratified lakes of the White Sea

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ABSTRACT

We analyze the results received from two expeditions performed in August-September 2013, August-September 2014 and February 2015 in the Kandalaksha Bay of the White Sea. Depth profiles of hydrological characteristics and optical properties of water were recorded for five marine lakes being on different stages of isolation from the White Sea. Those relic lakes demonstrate a tendency to meromixis and are characterized by apparent stratification of the water bodies from the brackish top layer to the bottom salt water. Maximal concentrations of anoxygenic phototrophs (green sulfur bacteria) were found at depths close to the redox interface in all the studied lakes. To discriminate differently pigmented groups of microorganisms the fluorescence emission spectra of bacteriochlorophylls from the living cells were used. We puzzle out the data on light spectrum propagation through the water body in each lake using optical properties of water (attenuation spectra) in the UV, visible and NIR ranges, as well as direct measurements of the total irradiances at various depths. The changes in optical characteristics of water in the stratified reservoirs due to cromophoric dissolved organic matter (CDOM) and microbial pigments affect the light intensity and its spectral distribution at each water layer thus influencing the living conditions for differently pigmented phototrophic microorganisms and determining the composition of microbial community.

Keywords: bacteriochlorophyll fluorescence, absorbance, light attenuation, hydrological characteristics, anoxygenic phototrophic microorganisms, green sulfur bacteria, stratified water reservoirs.

1. INTRODUCTION

Over the past decade the scientific interest is growing to the impacts of climate change and human activities on the Arctic ecosystems.[1-5] Exploration of Arctic resources promotes regional economic activities, expansion of the transport network and construction of the tidal power plants. Due to these factors some water areas will be artificially separated from the sea, undergoing changes in their ecological status including stagnant phenomenon and hydrosulfuric accumulation. Arctic zones face the need to preserve the unique nature and biological diversity of the polar and sub-polar marine ecosystems, where the anoxygenic phototrophic microorganisms, green sulfur bacteria, may be of a particular interest.[6-10] In such emergent situation the reliable environmental monitoring is inevitable with desirable involvement of spectral methods giving possibility to study organisms in their natural habitat. [11-14]

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Chlorophyll fluorescence analysis has become one of the most powerful and widely used techniques available to study plants, algae and cyanobacteria *in vivo* and *in situ*.[11-17] Fluorescence of bacteriochlorophyll, the photosynthetic pigment of phototrophic bacteria is rarely used in diagnostics of microorganisms. [18-20] However in some environmental tasks the measurement of bacteriochlorophyll fluorescence may be of a particular interest.

2. STRATIFIED MARINE LAKES AND PHOTOSYNTHETIC INHABITANTS OF THE ANOXIC ZONE

2.1. Stratified water reservoirs

Because of the isostatic postglacial uplift of the White Sea coast many marine bays undergo separation from the sea and gradually transform into the freshwater lakes.[5, 21] One of the features of the water basins at the intermediate stages of the separation from the sea is strong stratification of the water column. Stratified water reservoirs consist of several layers which do not mix completely or mix irregularly when density gradients limit vertical transport of dissolved substances.[22] Between oxygenated epilimnion (top water layer) and anoxic hypolimnion (deeper water column often with high concentration of hydrogen sulfide) there is a thick intermediate layer, chemocline, with maximum value of vertical abiotic gradients.[16,19] If the depth of the chemocline allows penetration of the sufficient amounts of sunlight, it becomes an ideal habitat for anoxygenic phototrophs, for instance green sulfur bacteria, because of presence of hydrogen sulfide.[6-10] Quantitative data of anoxigenic phototrophic bacteria contribution in the production of carbon in the water column of Kislo-Sladkoe lake, one of the marine lakes at the shore of the White Sea, were obtained with the use of radioisotope studies. [9] Maximal abundances of anoxygenic phototrophic bacteria (green and purple sulfur bacteria) in the Kislo-Sladkoe lake were found at the redox zone.[6]

2.2. Green sulfur bacteria

Anoxygenic photosynthesis requires reduced sulfur compounds (and therefore strictly anaerobic conditions) and light. This combination of conditions is very unusual; one of the habitats that meet such conditions is oxic-anoxic interface in the shallow coastal stratified lakes.

The green sulfur bacteria are a family of obligatory anaerobic photoautotrophic bacteria. They utilize hydrogen sulfide in the photosynthesis process. They are commonly found in meromictic lakes and ponds, sediments, and some sinkholes.[6-9, 23-26] In the lakes intensive growth of green sulfur bacteria is most often observed in summer and autumn months, when aquatic organic matter is actively decomposed resulting in appearance of hydrogen sulfide.

Green sulfur bacteria contain bacteriochlorophyll *a* in the reaction center and bacteriochlorophylls *c*, *d*, or *e* in the antenna inside their photosynthetic apparatus. The color of bacterial cells can be emerald-green due to bacteriochlorophylls *c*, *d* and carotenoid chlorobactene in their chlorosomes, or brown, due to bacteriochlorophyll *e* and carotenoid isorenieratene. Brown-colored green sulfur bacteria contain elevated amount of carotenoids which help to absorb the light in the short wavelength spectral range; that is why brown species are dominant at depth[11].

2.3. Photosynthetic pigments and spectral properties

Spectral properties of the cultures of green sulfur bacteria are determined by their bacteriochlorophyll pigments. The main photosynthetic pigments of green sulfur bacteria are bacteriochlorophylls with the following absorption maxima: bacteriochlorophyll c in the region 745-755 nm, bacteriochlorophyll *d* (725-745 nm) and bacteriochlorophyll *e* (710-725 nm). The green sulfur bacteria are also characterized by a small number of bacteriochlorophyll *a* (805-812 nm), which is part of the reaction centers.

Chlorobactene, a carotenoid light harvesting pigment of green-colored species, absorbs light in the blue and green spectral regions (400-500 nm). Isorenieratene, a carotenoid pigment with the chemical formula $C_{40}H_{48}$, is presented in the cells of brown-colored bacteria and is characterized by absorbance at 480-550 nm. Isorenieratene and its derivatives are useful to marine chemists studying the carbon cycle as biomarkers that indicate photic zone anoxia.[12-13] Hence, two groups of bacteria, green-colored or brown-colored, have differing maxima in absorption and fluorescence spectra.

The peaks in extracts of pigments in organic solvents are shifted compared to that in the living cells. The absorption spectrum of bacteriochlorophyll *a* in acetone extract has main peaks at wavelengths of 358, 579 and 771 nm, bacteriochlorophyll *c* at 433 and 663 nm, bacteriochlorophyll *d* at 425 and 654 nm, bacteriochlorophyll *e* at 459 and 648 nm. Living cells of green sulfur bacteria have two main fluorescence maxima in the 740-770 nm and 810-815 nm. Depending on the type, color and pigment consistence peaks can be shifted. Brown forms of bacteria, containing in the pigment composition bacteriochlorophyll *e*, have maxima at wavelengths of 740 and 815 nm. For green forms – bacteriochlorophylls *c* and *d* emitted light of 770 and 815 nm.

3. OBJECTS AND METHODS

3.1. Marine lakes separating from the White Sea

The research was targeted to measure the depth distributions of green- and brown-colored green sulfur bacteria living in the several marine lakes found in different stage of isolation from the White Sea, in the Kandalaksha Bay: lagoon on the cape Zeleny ("Green Cape Lagoon"), lakes Kislo-Sladkoe ("Sour-Sweet"), N. Ershovskoe, Elovoe, Trekhtzvetnoe ("Tricolor"). These lakes represent a sequence of water bodies from connected with the White Sea, fully marine yet, to almost isolated brackish or fresh. Spectral analysis of the natural water samples was performed in the field during the expeditions in August-September 2013, August-September 2014 and February 2015. The samples from different water layers were collected by the submersible pump, placed in sealed bottles and kept in the refrigerator prior to spectral measurements.

3.2. Spectral measurements and vertical distribution of green sulfur bacteria

Spectral measurements were performed in the laboratory conditions in standard quartz cells of 1 cm optical path length. Optical density spectra of the natural water samples were measured with the Unico spectrophotometer within spectral range of 200-1100 nm. Fluorescence emission spectra were recorded by the luminescence spectrometer Solar CM2203 with the excitation at 440 nm.

Acetone-methanol extractions (7:2) of water samples with green sulfur bacteria were prepared to quantify pigments. Absorption spectra of extractions were measured at room temperature using the same photometer. Concentration of bacteriochlorophyll *d*+*e* was calculated using the following formulae[27]:

$$C(\mu\text{g BChl}(d+e)) = (1.315 \times \text{E655} - 0.643 \times \text{E667} + 0.005)\, v \times 10^6/(V \times d \times \varepsilon \times \text{BChl } d), \qquad (1)$$

where E655 and E667 are absorbencies of the pigment extraction taken at the wavelengths 655 and 667 nm, respectively (minus turbidity measured at E850); v is the volume of acetone-methanol extraction (mL); V is the volume of filtered lake water sample (mL); d is the path length of the cuvette (cm); ε is the absorption coefficient: $\varepsilon(\text{BChl } d) = 98.0$ mg/cm.

4. RESULTS AND DISCUSSION

4.1. Physical-chemical characteristics of natural water

The Figures 1-5 shows depth profiles of physicochemical characteristics in the studied lakes measured in August-September 2014. The lakes are arranged in the order according to the degree of the isolation from the sea. Lagoon on the cape Zeleny is salt, the lake Kislo-Sladkoe is salt at the bottom with the brackish epilimnion, the lakes Elovoe and Trekhtzvetnoe are characterized by freshwater epilimnion and salty hypolimnion, and the N. Ershovskoe lake is freshwater with the brackish bottom layer. In spite of the difference in the salinity values all studied lakes are characterized by strong stratification and similar vertical structure.

Salinity profiles allow dividing the lakes to three layers: upper with less salinity values, saltier lower layer, and halocline in between. According to the temperature curves four of all studied lakes consist of the surface layer with the temperature following the synoptic variations, warmer intermediate layer and bottom water mass with the minimal temperature in the water column. Thermocline and halocline usually don't coincide resulted in the more complicated vertical structure than expected. Dissolved oxygen concentration is maximal in the middle of the water column in the layer with high salinity and maximal temperature. This allows suggesting that oxygen maximum is of oxygenic photosynthesis origin. This is additionally supported by the data on pH values which significantly increase in the layer with high oxygen concentration possibly because of carbonates depletion by photosynthesis. Below the highly oxygenated layer its concentration steeply declines, so from 1/2 to 2/3 of the water column is anaerobic. The interface between aerobic and anaerobic zones is marked by steep decline of the redox potential from positive to negative values. Due to the proximity of the aerobic and anaerobic layers the chemocline between them is very narrow, thickness of just 10-30 cm. These thin layers provide good conditions for the anoxygenic phototrophs like sulfur bacteria in all studied lakes.

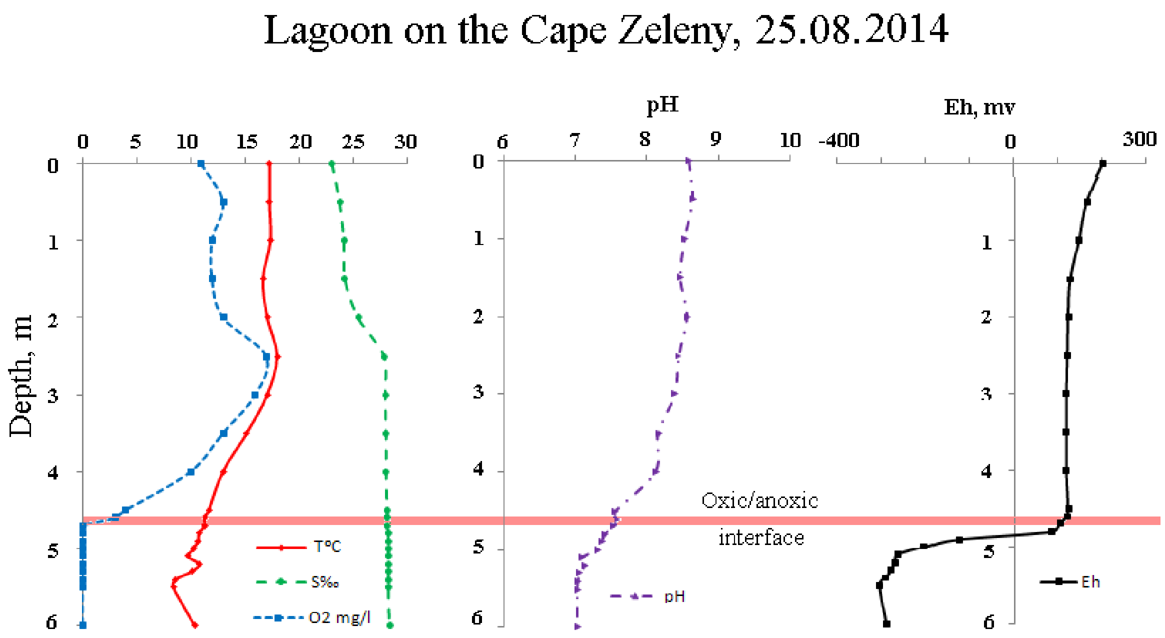
Lagoon on the Cape Zeleny, 25.08.2014

Figure 1. Depth profiles of physico-chemical charactristics in the Lagoon on the cape Zeleny.

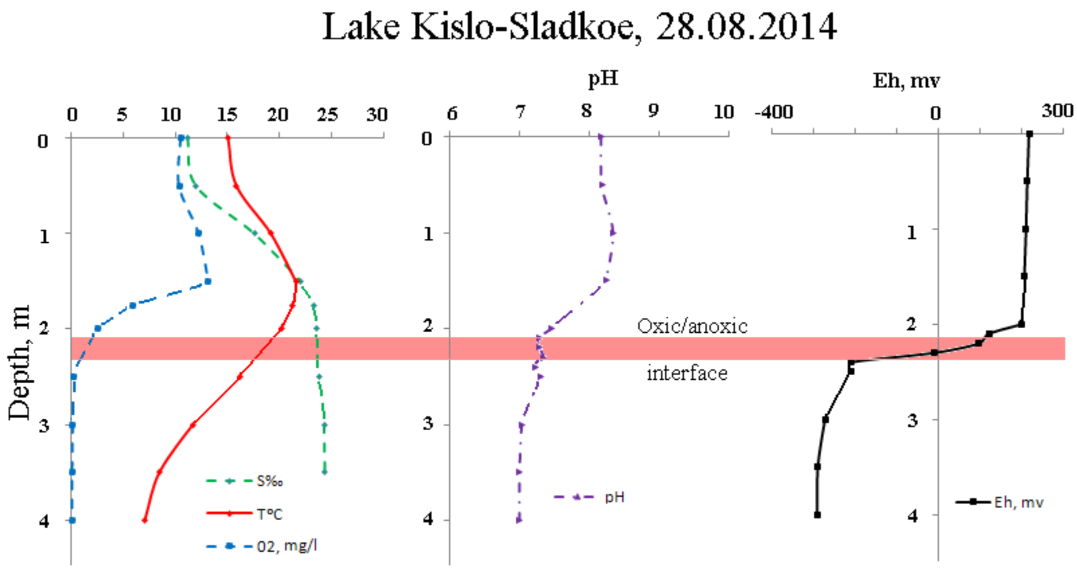
Lake Kislo-Sladkoe, 28.08.2014

Figure 2. Depth profiles of physico-chemical charactristics in the Kislo-Sladkoe lake.

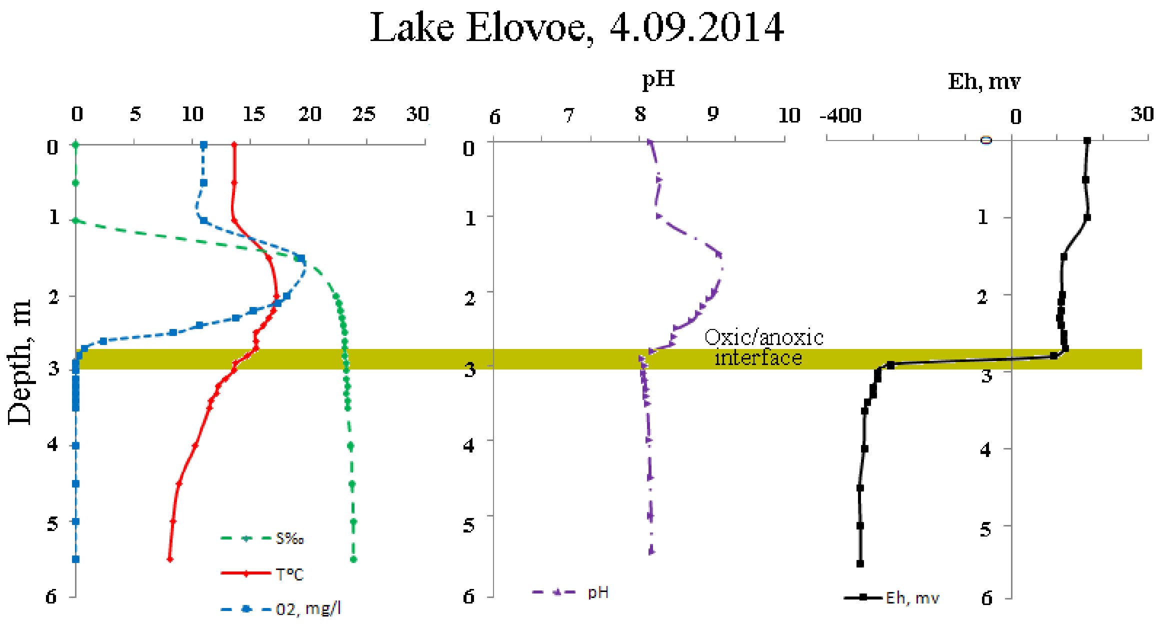

Figure 3. Depth profiles of physico-chemical charactristics in the lake Elovoe.

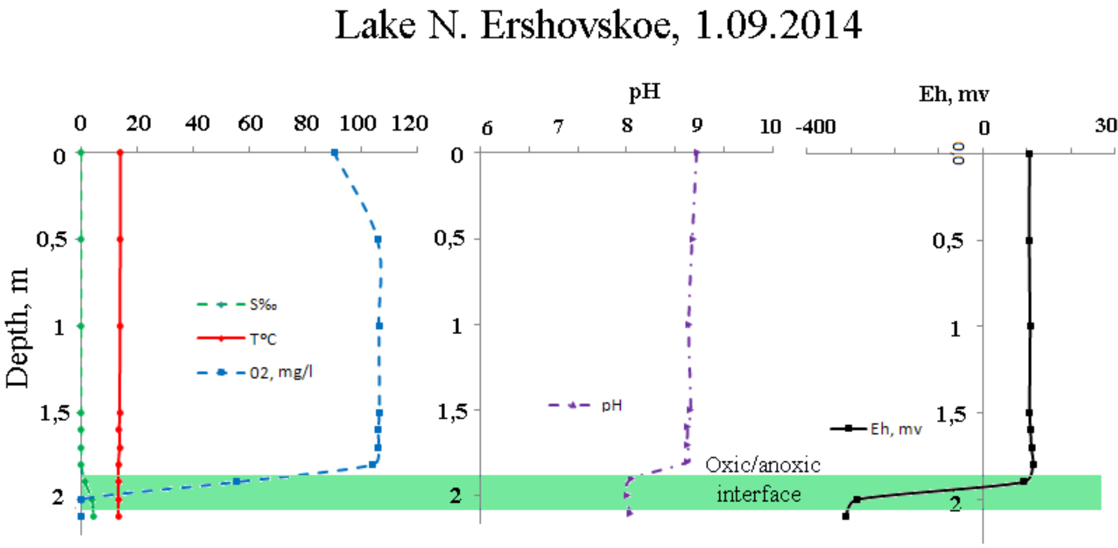

Figure 4. Depth profiles of physico-chemical charactristics in the lake N. Ershovskoe.

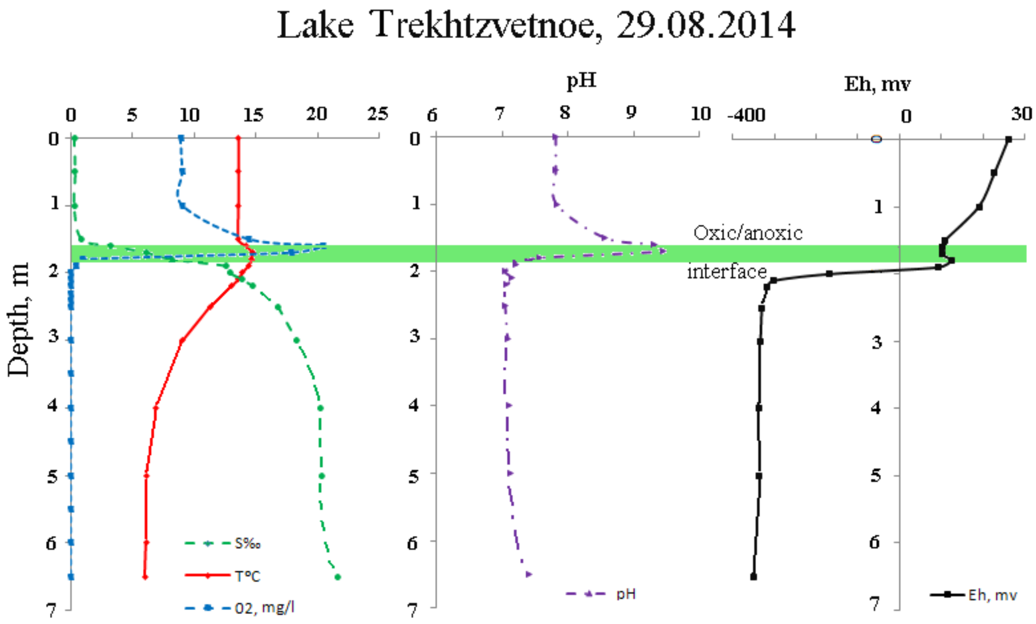

Figure 5. Depth profiles of physico-chemical charactristics in the lake Trekhtzvetnoe.

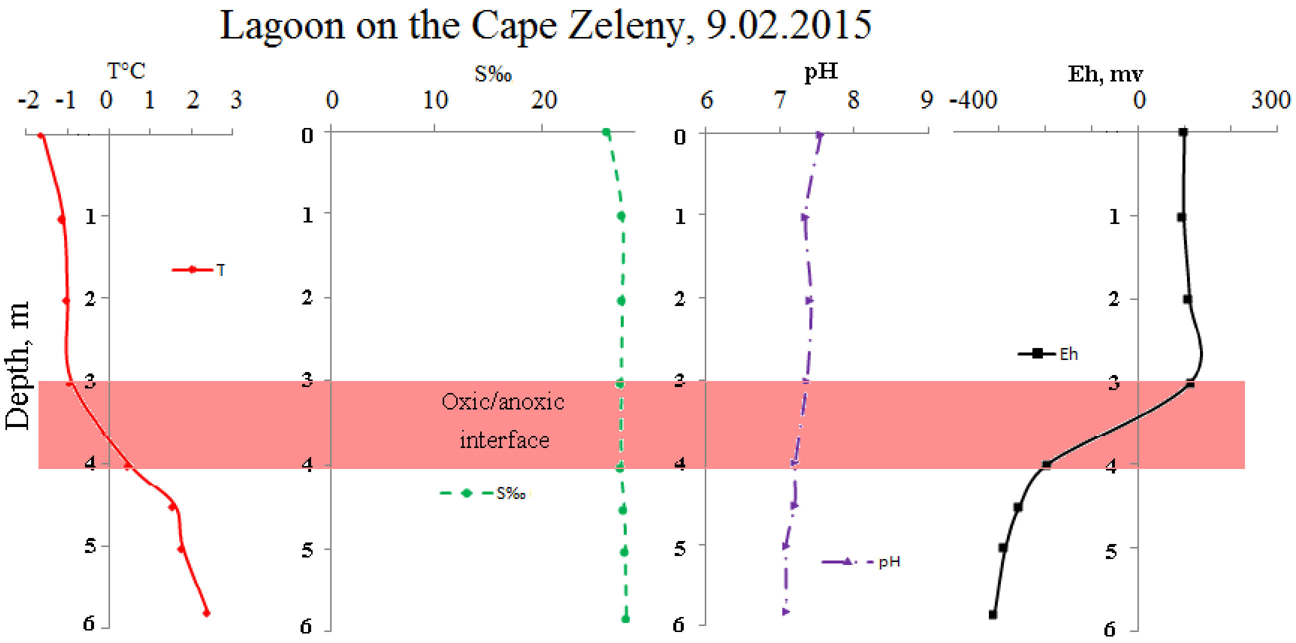

Figure 6. Depth profiles of physico-chemical charactristics in the Lagoon on the cape Zeleny.

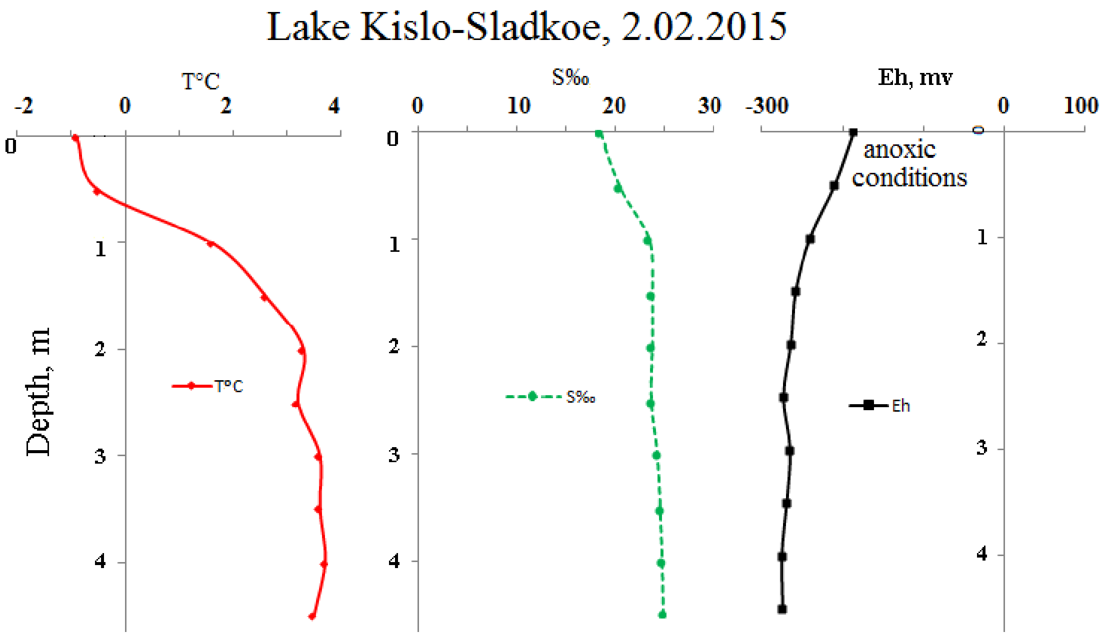

Figure 7. Depth profiles of physico-chemical charactristics in the Kislo-Sladkoe lake.

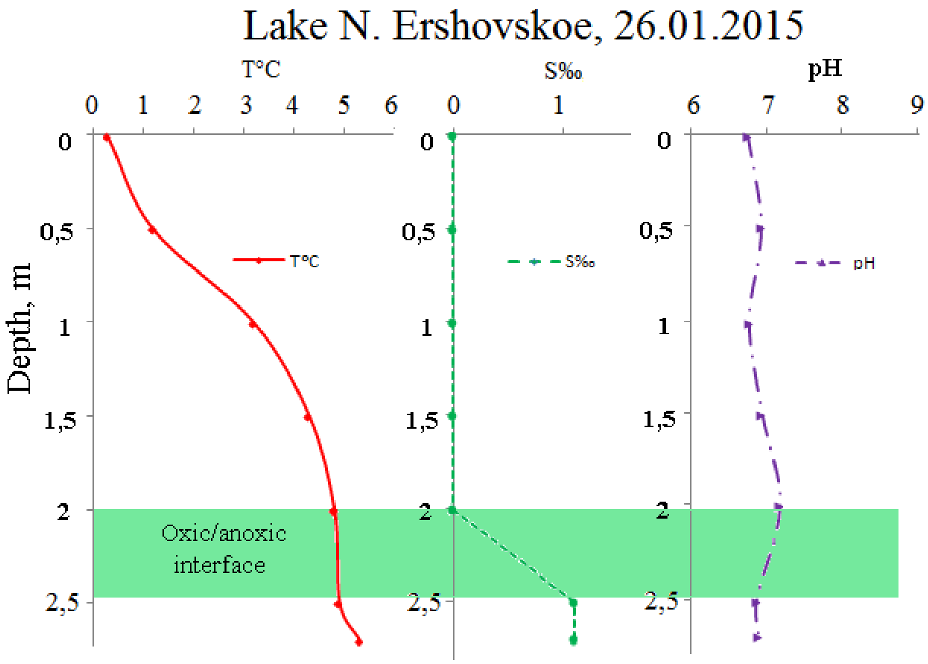

Figure 8. Depth profiles of physico-chemical charactristics in the lake N. Ershovskoe.

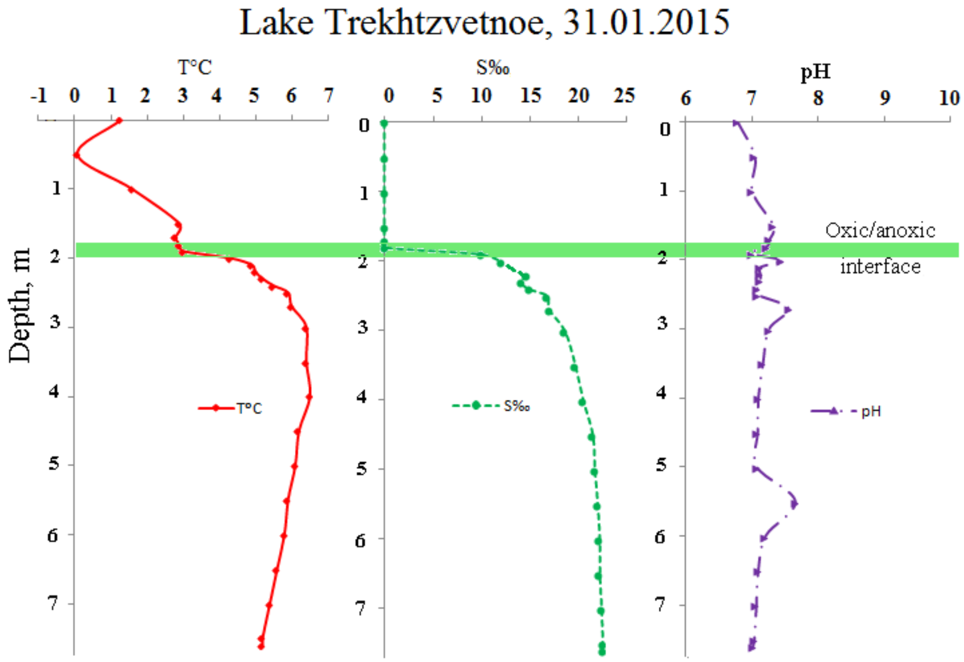

Figure 9. Depth profiles of physico-chemical charactristics in the lake Trekhtzvetnoe.

Seasonal variation of abiotic parameters are just that the temperature declines and ice formes on the surface of water. Winter stratification in most of the studied lakes (fig. 6-9) resembles summer one. In the lagoon on the Cape Zeleny oxic-anoxic interface rised uo in 0.5...1 meter and became not so steep; in the lake N. Ershovskoe redox boundary in winter it was at the same level as in summer, just became thicker. In the lake Trekhtzvetnoe the position and thickness of the chemocline was same in winter and in autumn. The lake Kislo-Sladkoe was the only where in winter anoxic condition spread over whole water column up to the ice.

4.2. Absorbance spectra of natural water samples with microorganisms

Each water layer was characterized by the optical properties that practically were found unchanged during the annual cycle of surveillance.

For all samples of water containing green sulfur bacteria the characteristic peaks at wavelengths 450-460 and 720 nm were observed which corresponded to the absorption of light by bacteriochlorophylls *c*, *d* and *e*. All the studied lakes were characterized by a sharp increase in optical density at the depth of the most vivid coloration of water, followed by gradual reduction of these peaks. High absorption in the spectral range of 400-450 nm corresponded to the absorption by carotenoids.

The height of these peaks depends on the pigments concentration in the bacterial cells in the water sample (water layer) and can be used for quantification of bacterial cells in different marine lakes and water layers. For instance, using the long-wave peak of bacteriochlorophyll located at 725 nm (see Figure 10) it was found that in February 2015 the concentration of green sulfur bacteria was maximal in the lake Trekhtzvetnoe compared to other studied lake. In the lake N. Ershovskoe it was 20 times smaller, in the lake Kislo-Sladkoe 50 times smaller and in the lagoon at the Cape Zeleny 40 times smaller that in the lake Trekhtzvetnoe.

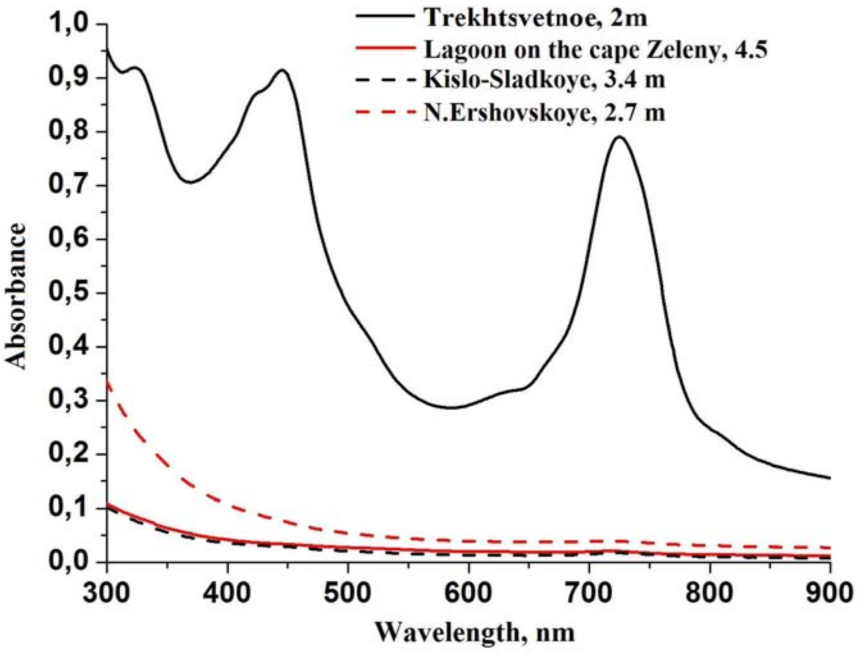

Figure 10. Absorbance spectra of water layers of 1 cm thickness from various depth in different marine lakes (February 2015).

4.3. Fluorescence spectra of water samples

Fluorescence emission spectra of water samples from stratified lakes containing green sulfur bacteria were recorded at λ_{ex} = 440 nm. Fluorescence spectra within range of emission of bacteriochlorophylls contained two emission bands, first with maxima at 740-770 nm corresponding to the emission of bacteriochlorophylls *c*, *d* or *e*, and the second one, with maximum at a wavelength of 815 nm, attributed to the emission of bacteriochlorophyll *a*.

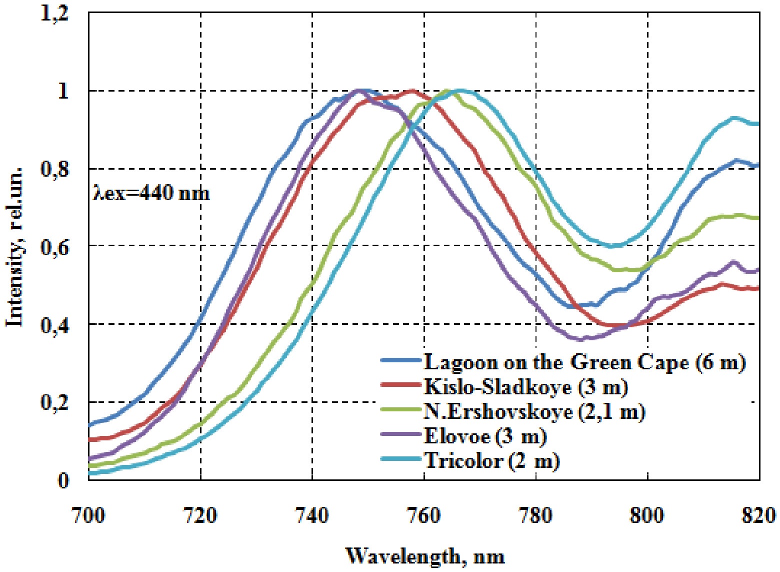

Figure 11. Fluorescence emission spectra (λ_{ex}=440 nm) of water samples with green sulfur bacteria (August-September 2014). All spectra are normalized to the intensity of the first peak.

For green-colored green sulfur bacteria maximum at the region of 740-770 nm is located at longer wavelengths in comparison with the brown-colored green sulfur bacteria.

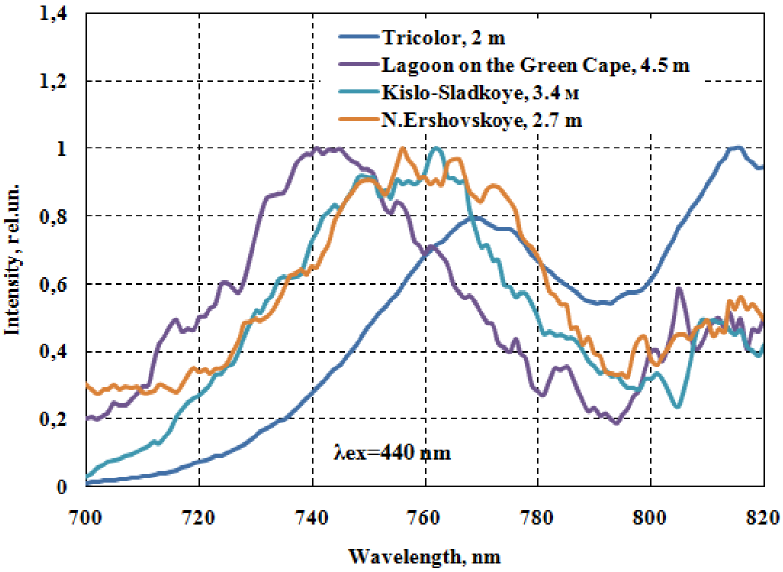

Figure 12. Fluorescence emission spectra (λ_{ex}=440 nm) of water samples with green sulfur bacteria (February 2015). All spectra are normalized to the intensity of the first peak.

4.4. Quantification of differently colored forms of green sulfur bacteria in the water layers of various depths

Spectral deconvolution of the emission band at 740-770 nm into two Gaussian components peaked at 745 and 765 nm provided information about content of green- and brown-colored forms of green sulfur bacteria found in the natural water sample. Using specially developed algorithm we have found out the ratio of different types of bacteria at various depths in all the studied water bodies and analyzed the correspondence of bacteria concentration to the physico-chemical characteristics of water (temperature, salinity, pH, light conditions, concentration of humic substances).

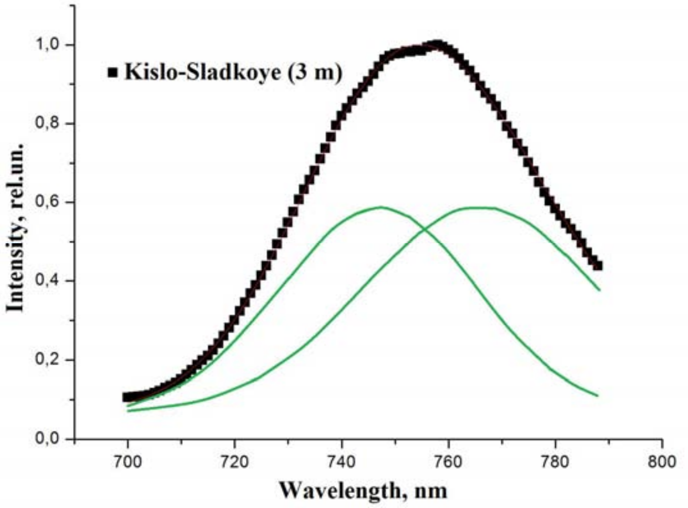

Figure 13. The illustration of the method of quantification of different types of green sulfur bacteria using deconvolution of the bacteriochlorophyll fluorescence band into two Gaussian components.

In August-September 2014 it was found that the water in the lakes Tricolor and N. Ershovskoe at depths with the highest concentration of green sulfur bacteria contained only green-colored green sulfur bacteria, (98.0 ± 2.0)%. In the lake

Kislo-Sladkoe at the depth of 3 m water contained about equal amounts of green- and brown-colored forms of green sulfur bacteria (50.0 ± 4.7)%. In the lagoon on the Cape Zeleny and the lake Elovoe brown-colored green sulfur bacteria prevailed compared to green-colored: (61.0 ± 2.8)% in the lagoon on the Green Cape and (61.7 ± 2.5)% in the lake Elovoe.

Along with increasing the depth of the layer, the ratio of green- to brown-colored green sulfur bacteria was changed: more brown-colored bacterial cells appeared in deeper layers. In the lake Elovoe the amount of brown-colored green sulfur bacteria increased from (61.7 ± 2.5) % at a depth of a maximum concentration of anoxygenic microorganisms to (76.3 ± 2.9)% at the bottom. The lake Tricolor content green-color green sulfur bacteria is reduced from (98.0 ± 2.0)% at a depth of 2.0 m to (79.2 ± 4.2)% at a depth of 2.2 m, then practically keeps constant at deeper layers.

In February 2015 in the lake Tricolor at a depth of 2 m as well was attended only by green colored green sulfur bacteria (98.0 ± 2.0)%, in the lakes N. Ershovskoe at a depth of 2.7 m and Kislo-Sladkoe at a depth of 3.4 m was discovered a large quantity of brown-colored green sulfur bacteria, (70.1 ± 2.5)% and (60.1 ± 3.0)%, respectively, bigger that in summer season. In the lagoon on the Green Cape at a depth of 4.5 m prevailed green-colored green sulfur bacteria (53.3 ± 3.3)% instead of 39% in summer. In comparison with the measurements carried out in August and September 2014 relative content of green-colored green sulfur bacteria in the lake Kislo-Sladkoe and the Lagoon on the Green Cape has increased by 10%, in the lake N.Ershovskoe decreased by 30%.

From absorption spectra of acetone-methanol extractions of water samples from the lakes the concentration of BChl (d + e) was calculated according to the formula (1). The results are given in the Table 1.

Table 1. Concentration of bacteriochlorophylls *d* and *e* in water samples with the highest content of green sulfur bacteria in the studied lakes (February 2015).

Lake	**Depth of layer, m**	**BChl *d* concentration, mg/m^3**	**BChl *e* concentration, mg/m^3**
Lagoon on the cape Zeleny	4.5	18 ± 1	20 ± 1
Kislo-Sladkoe	3.4	19 ± 1	13 ± 1
N. Ershovskoe	2.7	51 ± 2	21 ± 1
Trekhtzvetnoe	2.0	1430 ± 30	29 ± 1

4.5. Light attenuation in the water body and abundance of green-colored forms

Figure 6 shows the light irradiation at various depths measured directly in the water body of the Lagoon on the Cape Zeleny and its approximation with the exponential decay versus depth. As one can see, the depth profile for the irradiation deviates apparently from the exponential dependence.

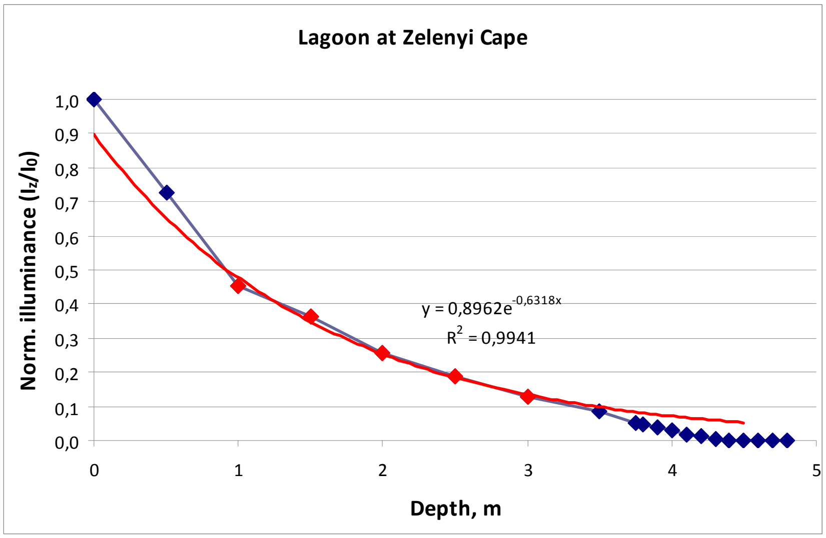

Figure 14. The irradiation at various depths measured *in situ* in the Lagoon on the Cape Zeleny.

The same tendency was found for all the studied water bodies. The deviation from exponential decrease in surface waters (first one meter of depth) we explain by the different attenuation of light through spectrum. Short wavelength blue light is more readily absorbed by humic substances dissolved in water than the green one.

We analyzed the data on light propagation through the water body in each lake using optical characteristics of water (attenuation spectra) in the UV, visible and NIR ranges.

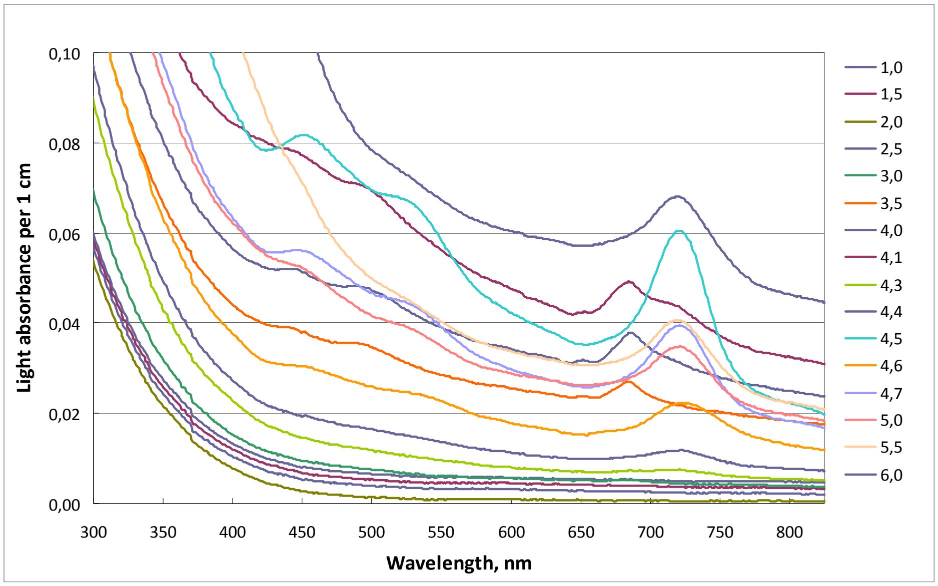

Figure 15. Absorbance spectra of water layers of 1 cm thickness from various depths in the Lagoon on the cape Zeleny.

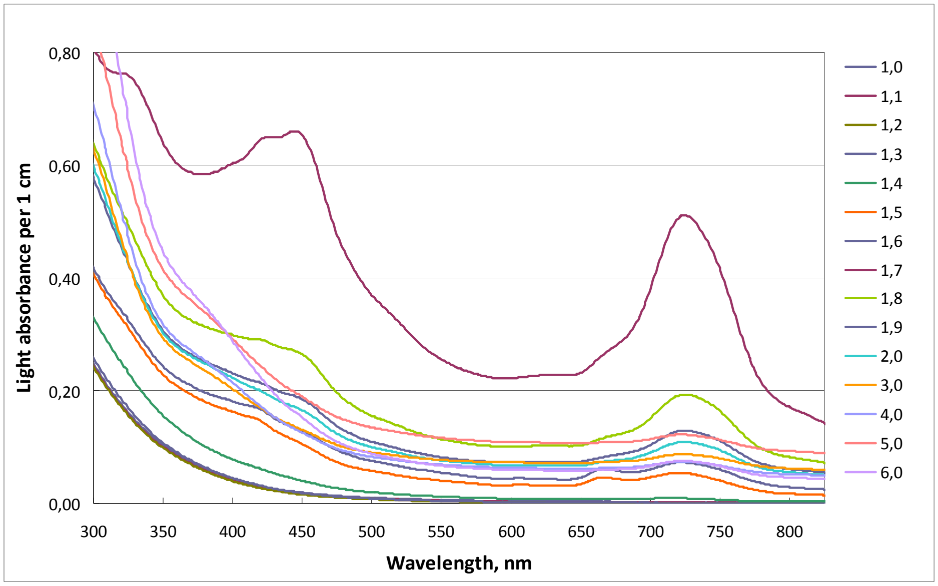

Figure 16. Absorbance spectra of water layers of 1 cm thickness from various depths in the lake Trekhtzvetnoe.

The changes in optical characteristics of water in the stratified reservoirs due to cromophoric dissolved organic matter (CDOM) and microbial pigments affect the light intensity and its spectral distribution at each depth. Typical absorption spectra of CDOM are featureless, with a monotonic decline with wavelength increasing from 200 to the NIR wavelengths. [30-32] The CDOM absorption is clearly seen in Figure 15-16 for water layers at depths 1 m in the Lagoon on the cape Zeleny and in the lake Trekhtzvetnoe. The Figures 17-18 illustrate the effect of light penetration through the water column of various depths calculated using the absorption spectra given in Figure 15-16 in the same lakes.

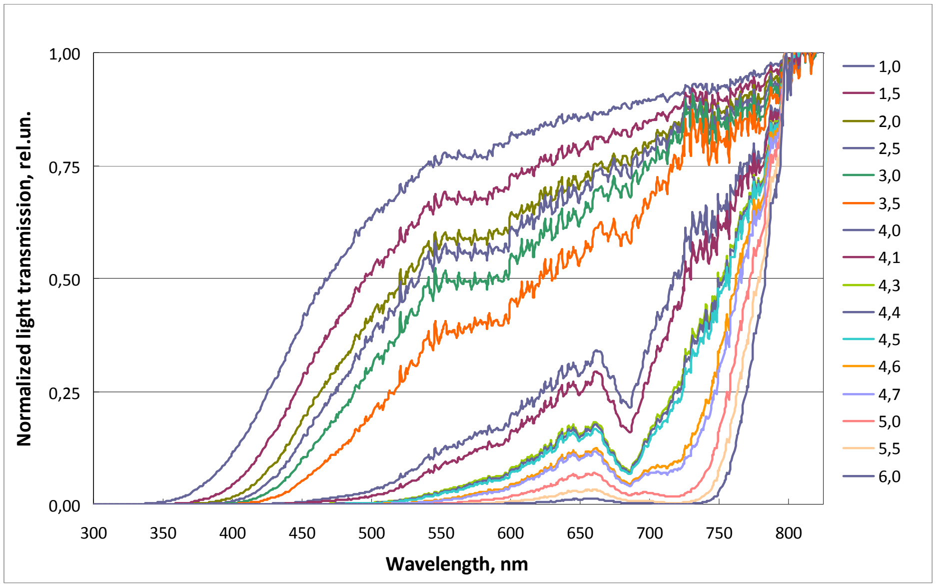

Figure 17. Calculated transmission spectrum for the layers of various depth in the Lagoon on the cape Zeleny.

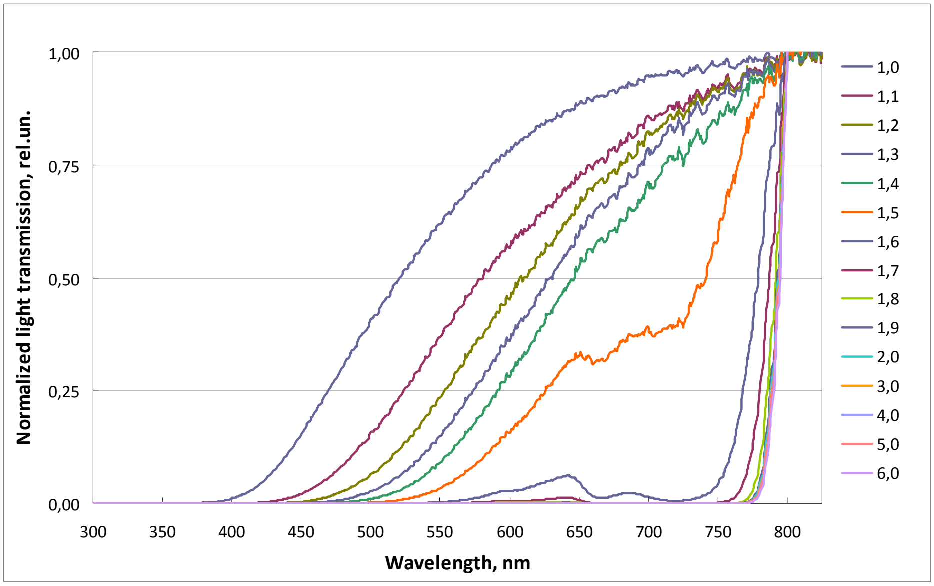

Figure 18. Calculated transmission spectrum for the layers of various depth in the lake Trekhtzvetnoe.

As we received from fluorescence spectra in the lake Trekhtzvetnoe green-colored sulfur bacteria are dominating and comprise 98% in summer season and in winter. The water salinity at the edge of the hydrogen sulfide zone was 10.5 g/l and increased to 19.6 g/l towards the bottom. The upper limit of the hydrogen sulfide zone in the lake Trekhtzvetnoe was located at a depth of 2 m and, therefore, was better lit than in the lake Elovoe and the lagoon on the cape Zeleny. The combination of these environmental factors (moderate water salinity and sunlight) gave an undoubted advantage for growth of green-colored forms of green sulfur bacteria in the lake Trekhtzvetnoe.

On the contrary, in the lagoon on the cape Zeleny and Lake Elovoe brown-colored bacteria were dominant in the community of phototrophic bacteria. The upper limit of hydrogen sulfide zone in these reservoirs was located deeper than in Trekhtzvetnoe, at a depth of 2.9 - 3 m and 4.9 - 5 m. The salinity of water in the anaerobic zone reached 21.8 - 22.4 and 26.5 g/l, respectively in the lagoon on the cape Zeleny and Lake Elovoe. Taken together, these habitat conditions met better the needs of brown-colored forms of sulfur bacteria than that of the light-preferring green-colored forms.

The interpretation of this founding is linked to carotenoid pigments found in green- and brown-colored species. Light harvesting carotenoid pigment of green-colored species, chlorobactene, absorbs light at shorter wavelengths (400-500 nm) compared to isorenieratene presented in the cells of brown-colored bacteria which absorbs light at 480-550 nm. Moreover brown-colored green sulfur bacteria contain elevated amount of carotenoids which help to absorb the light in the short wavelength spectral range; that is why brown species are dominant at depth. The attenuation of light due to occurring CDOM and microbial pigments affects the light intensity and its spectral distribution along with the depth. As a result, this influences the living conditions for differently pigmented phototrophic microorganisms and determines the composition of microbial community.

5. CONCLUSIONS

We studied the spectral-properties of green sulfur bacteria and their habitat conditions in marine lakes separated from the White Sea. During two expeditions carried out in at August-September 2014 and February 2015 we have measured vertical distributions of hydrological and chemical characteristics of water in the five water reservoirs in the Kandalaksha Bay at different stages of isolation from the Sea. Those relic lakes are characterized by apparent stratification of the water bodies from the freshwater top layer to the bottom water of marine origin.

As shown by the measurement of physical and chemical characteristics of water studied reservoirs have the apparent vertical stratification of the water column and its splitting into oxygenated epilimnion, anoxic hypolimnion, and chemocline or redox zone between them. Each layer is characterized by the optical and spectral characteristics of the water, practically unchanged during the annual cycle of surveillance.

Quantitative assessment of the microorganism concentrations was made using spectral data. Absorbance spectra of the water samples with green sulfur bacteria contain absorption bands of bacteriochlorophylls *c*, *d* and *e* (710-725 nm) and carotenoids (400-500 nm). The fluorescence spectra of the water samples with green sulfur bacteria peak wavelength λ = 770 nm and 820 correspond to the emission of bacteriochlorophylls *c*, *d* and *e*. According to the absorption spectra of acetone-methanol extract concentrations were determined bacteriochlorophylls *d* and *e* to prove algorithm of quantification of bacterial cells with different pigmentation.

According to the measures optical properties of water from various depths the maximal concentrations of green sulfur bacteria were found at depths close to the redox zones in all the studied lakes. The contents of bacteria in winter and summer periods were compared. To discriminate different groups of anoxygenic bacteria emission fluorescence spectra of living cells were used. Applying specially developed spectral algorithm we have found out the ratio of different types of bacteria at various depths in all the studied water bodies and analyzed the correspondence of bacteria concentration to their habitat conditions (water temperature, salinity, pH, light conditions).

We analyzed the data on light propagation through the water body in each lake using optical characteristics of water (attenuation spectra) in the UV and visible ranges and direct measurement of total irradiance at various depths. The changes in optical characteristics of water in the stratified reservoirs due to cromophoric dissolved organic matter (CDOM) and microbial pigments affect the light intensity and its spectral distribution at each depth. This influences the living conditions for different phototrophic microorganisms and determines the composition of microbial community.

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