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CLADOPHORA (CHLOROPHYTA) AS AN ECOLOGICAL ENGINEER IN HYPERSALINE LAKE CHERSONESSKOYE: DISTRIBUTION OF DIATOM ALGAE IN THE STRUCTURED SPACE OF PLANT MATS

A. V. Prazukin, R. I. Lee, D. S. Balycheva, Yu. K. Firsov, and V. V. Kholodov

A. O. Kovalevsky Institute of Biology of the Southern Seas of RAS, Sevastopol, Russian Federation

E-mail: *prazukin@mail.ru*

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The genus *Cladophora* is one of the largest genera of green algae, representatives of which are found in all water bodies throughout the world. *Cladophora* creates habitats for different groups of organisms, including epiphytic unicellular algae. The aim of the article is to examine the vertical distribution of diatoms in the structured space of *Cladophora* mats and in benthic sediments of a hypersaline lake in Crimea. In the vertical structure of the *Cladophora* mat, the floating and benthic mats were distinguished, each having a characteristic structure. The total of 20 diatom species of 12 genera were observed throughout this study. The total abundance of diatoms and their biomass on *Cladophora* (*per* unit of dry biomass) and in benthic sediments (*per* unit of dry mass) varied over a wide range. On *Cladophora*, the abundance varied from 1.85×10^6 to 69.52×10^6 cells·g^{-1}, and the biomass, from 7.77 to 157.43 mg·g^{-1}. In the bottom sediment, the abundance varied from 6.05×10^6 to 16.87×10^6 cells·g^{-1}, and the biomass, from 7.76 to 36.39 mg·g^{-1}. The share of the diatom biomass in the wet mass of the entire *Cladophora* mat averaged 1.06%.

Keywords: diatoms, epibionts, filamentous green algae, floating mats, hypersaline lake

The genus *Cladophora* Kützing, 1843 is one of the largest genera of green algae, representatives of which are found in all water bodies worldwide: freshwater, marine, and hypersaline ones [Dodds, Gudder, 1992; Higgins et al., 2008; Prazukin et al., 2020; Zulkifly et al., 2013]. Due to morphological features of *Cladophora* thallus and the ability of these algae to form extensive benthic and floating mats [Bootsma et al., 2004; Higgins et al., 2008; Gubelit, Berezina, 2010; Messyasz et al., 2015; Prazukin et al., 2008, 2018, 2019], *Cladophora* can be characterized as an ecological engineer [Zulkifly et al., 2012, 2013]. This organism creates, changes, and maintains the habitat [Jones et al., 1994]. *Cladophora* creates habitats for various groups of organisms, *inter alia* epiphytic unicellular algae. On its surface, communities of unicellular algae are formed, with a great variety of taxonomic groups [Hardwick et al., 1992; Malkin et al., 2009; Mpawenayo, Mathooko, 2005; Zulkifly et al., 2012, 2013]; those create high density and biomass of cells [Bergey et al., 1995; Malkin et al., 2009; Marks, Power, 2001; Stevenson, Stoermer, 1982; Young et al., 2010].

In Crimea, there are many saline lakes [Anufriieva, 2018; Shadrin et al., 2017] where floating and benthic *Cladophora* mats are formed constantly or with a certain periodicity, covering large parts of lake water areas [Ivanova et al., 1994; Prazukin et al., 2008, 2018, 2019].

Unicellular algae of Crimean saline lakes and, in particular, epiphytic unicellular algae on *Cladophora* remain poorly studied [Nevrova, Petrov, 2008; Senicheva et al., 2008]. There is the question: how are microepiphytes distributed along the vertical component of *Cladophora* mats? To answer, we chose a small hypersaline lake, Lake Chersonesskoye, where a biogeochemical cycle of substances with *Cladophora* participation occurs annually. We hypothesized that *Cladophora* mats are ecological engineers in Lake Chersonesskoye during the spring–autumn period. To test this hypothesis, we considered the vertical distribution of diatom algae in the structured space of *Cladophora* mats formed in different parts of the lake shoreline.

MATERIAL AND METHODS

Study area. For 20 years (2000–2020), investigations were carried out on Lake Chersonesskoye (44°35′09″N, 33°23′39″E), located at Cape Khersones, Crimean Peninsula [Gubanov, Bobko, 2012; Mukhanov et al., 2004; Pavlovskaya et al., 2009; Prazukin, 2015; Prazukin et al., 2008, 2018, 2019, 2021a, b; Senicheva et al., 2008; Shadrin et al., 2008, 2017]. The above-mentioned works portrayed a detailed description of the water body and its inhabitants, which allows us to restrict ourselves to a brief representation. It is a small lake with a surface area of 0.05 km^2, a catchment area of 0.92 km^2, an average depth of 0.38 m, and a maximum depth of 1.5 m. The lake is separated from the sea by a narrow boulder–pebble isthmus; it is fed mainly due to the filtration of seawater and its inflow during severe storms (Fig. 1A–C). In some years, the maximum values of water temperature (+43 °C) were registered in July and August in the lake upper layer; the minimum temperatures were down to –0.5 and –0.7 °C (December 2004). The maximum salinity value for the observation period was 340 $g \cdot L^{-1}$ (August 2009), and the minimum was 27 $g \cdot L^{-1}$ (May 2018). Throughout the entire study period, 61 algal species were found in the lake phytoplankton [Senicheva et al., 2008]. Macrophytes were represented by 6 species, 5 of them belonging to green filamentous algae of the phylum Chlorophyta (*Cladophora vadorum* (Areschoug) Kützing, 1849; *C. siwachensis* C. J. Meyer, 1922; *C. echinus* (Biasoletto) Kützing, 1849; *Ulothrix implexa* (Kützing) Kützing, 1849; and *Rhizoclonium tortuosum* (Dillwyn) Kützing, 1845) and 1 belonging to the seagrass phylum Angiospermae (*Ruppia cirrhosa* (Petagna) Grande, 1918) [Prazukin et al., 2008]. Macrophytic vegetation of the lake is characterized by seasonal dynamics of biomass [Prazukin et al., 2008]. In winter months, macrophytic vegetation can be preserved in small, narrow, and intermittent strands of filamentous algae along the entire lake shoreline and in small thickets of *R. cirrhosa* in the southwestern part of the lake. However, three times during the observation period (2000–2020), a complete absence of *Cladophora* in the lake was recorded in winter. In mid-March, *Cladophora* mats begin their formation along the shoreline; by mid-August, those can occupy up to 60–90% of the lake area. In autumn months, floating mats are destroyed; they lose their ability to stay afloat and sink to the lake bottom; and active destruction processes occur.

Our previous studies showed that *Cladophora* mats have a well-defined vertical structure, which changes during the vegetative cycle [Prazukin et al., 2008, 2018]. In late summer and autumn, a great variety of mat conditions is observed in different parts of the lake. Moreover, in a small lake area, one can find mats with clear signs of destruction and mats that retain their juvenile and mature structure.

In May and June 2017, practically every day, daytime air temperature in the lake area exceeded +20 °C; early to mid-July, the values varied from +26 to +35 °C. There was no precipitation during these months. *Cladophora* mats were formed only in the shore area of the lake. Apparently, due to high temperatures, those began to deteriorate in late July, and a wide range of their states was observed.

We selected two sites: at the southeastern (*D*) and northeastern (*E*) shores of the lake (Fig. 1). At each site, two visually different biotopes were identified (*D1*, *D2* and *E3*, *E4*) (Fig. 2). There were no obvious signs of mat destruction at *D1*, and the same could be said about the mat at *E3*, while the mats at *D2* and *E4* were aging.

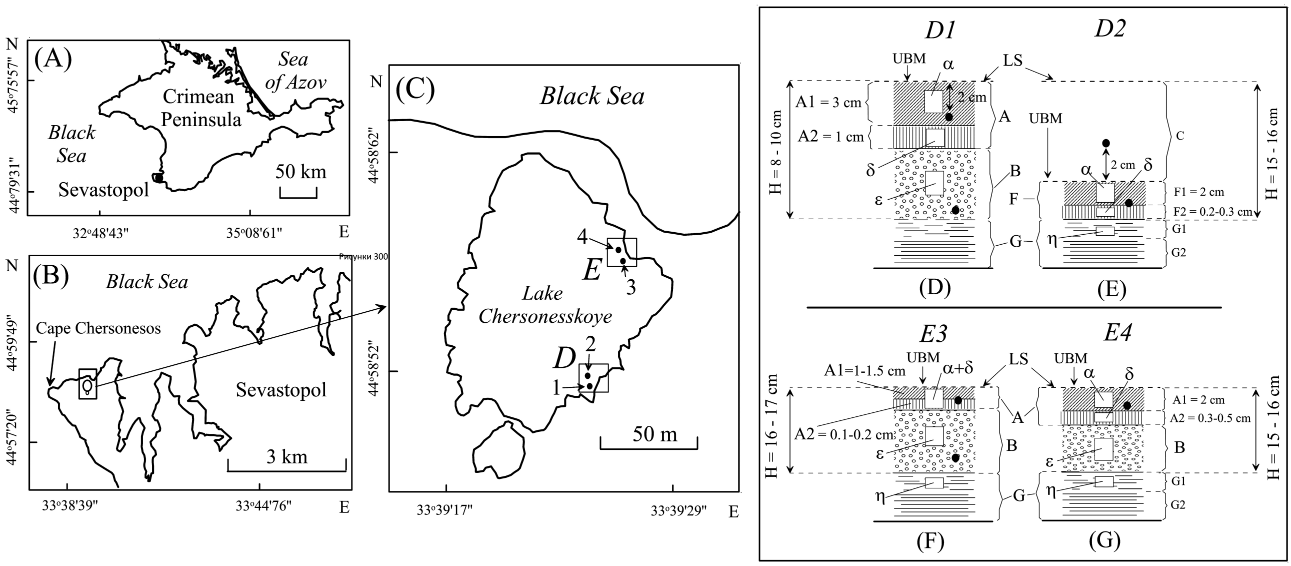

Fig. 1. Lake Chersonesskoye on Crimean Peninsula in various scales (A–C) with the layout of sampling stations (C) and algal mat layers (D–G); sampling stations near the southeastern (*D1*, *D2*) and northeastern (*E3*, *E4*) shores of the lake. On D–G: the upper (A1) and lower (A2) layers of the floating mat (A); the algal layer under the floating mat (B); the upper (F1) and lower (F2) layers of the benthic mat (F); the "liquid" (G1) and "solid" (G2) layers of the bottom sediments (G); H, depth; UBM, the upper boundary of the *Cladophora* mat; LS, the upper boundary of the lake; C, the water layer between the bottom mat and the upper boundary of the lake; α, δ, ε, η, sampling points within the boundaries of the mat and in the bottom sediments. Spots of water temperature measurements within the boundaries of the mat and beyond it are marked with black dots

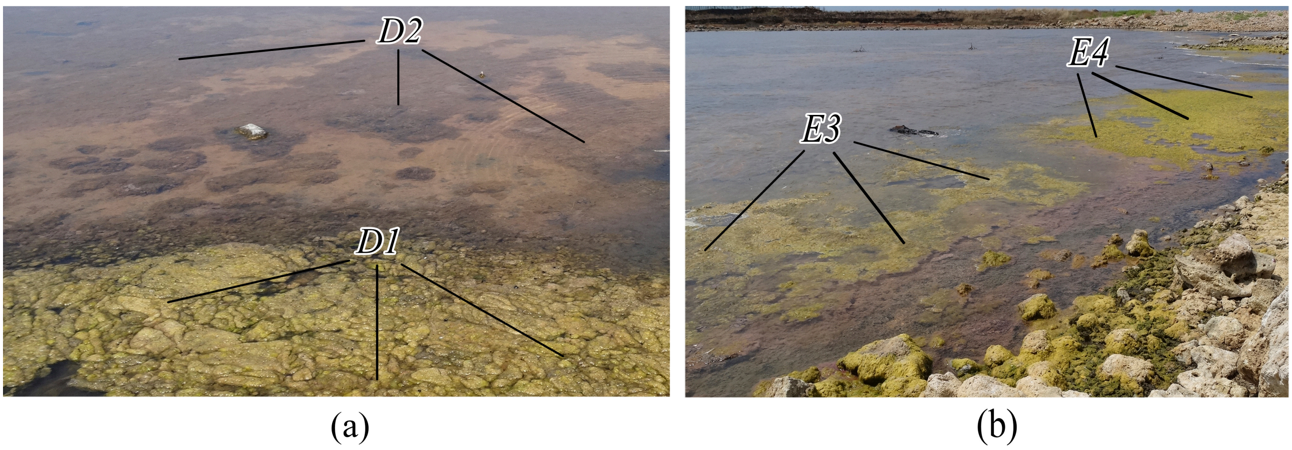

Fig. 2. Stations (*D1*, *D2*, *E3*, *E4*) and sampling points at the southeastern (a) and northeastern (b) shores of the lake. The sampling points are marked by lines

Sampling and sample processing. On 26 July, 2017, 30 samples of the *Cladophora* mat and 9 samples of benthic sediments were taken from the southeastern (sta. *D1* and *D2*) and northeastern (sta. *E3* and *E4*) shores of the lake (Figs 1C, 2) to analyze the species structure and biomass of diatoms. From each horizontal mat layer (α, δ, ε, see Fig 1D–G), 0.5–1 g (wet mass) of *Cladophora* were sampled with tweezers. Each algae sample was placed in a 10-mL glass container.

Benthic sediments were sampled in triplicate from the upper 1-cm layer using a cylindrical plastic sampler with a working section area of 7.1 cm^2. Soil was placed in a glass container and mixed with 3 mL of 40% formalin solution.

At all the stations, algae were sampled in triplicate to assess the vertical structure of *Cladophora* mats. A cylindrical sampler with a cross-sectional area S_0 = 0.0452 m^2 was used: this allowed algae sampling in layers throughout the entire water column, as described earlier [Kühl, Jørgensen, 1992]. When sampling, algae of each horizontal layer of the *Cladophora* mat were placed in separate plastic bags.

At sta. *D1*, *E3*, and *E4*, water temperature and salinity were measured directly in the floating mat (in the middle of the layer) and in the algal layer underneath (near the bottom) using a mercury thermometer with an accuracy of 0.1 °C and a Kelilong WZ212 refractometer; at sta. *D2*, measurements were carried out at a 2-cm distance above the benthic mat and in it. At sta. *D1* and *D2*, water temperature within the mat and beyond it was measured at short time intervals for 6.5 h, from 10:00 a.m. to 04:40 p.m.

Sample processing in the laboratory. Samples of the *Cladophora* mat taken to assess its vertical structure were washed in freshwater, dried on filter paper, and weighed on a WT-250 electronic balance (Techniprot, Poland) (sample wet mass, W_{wet}). To determine dry mass (W_{dry}), the samples were dried at a temperature of +105 °C to constant weight and weighed on the same balance.

Fragments of *Cladophora* thalli sampled from different horizons of the mat to determine microphytofouling were quickly delivered to the laboratory. There, the state of their fouling was assessed under a microscope, and diameters of *Cladophora* thalli were measured. Then, samples were fixed by adding 1.5 mL of 40% formalin solution and maintained for 1–3 weeks. After that, *Cladophora* thalli were placed in a Petri dish, and epiphytic algae were carefully removed with tweezers and a scalpel or a plastic spatula. Then, *Cladophora* was washed and squeezed into the dish. The process was monitored under a microscope; the washing of microalgae was continued until they were completely absent on a randomly taken fragment of macrophyte thalli (Fig. 3).

To determine the species composition of diatom algae, their shells were cleaned from organic matter by the "cold" method, and permanent preparations were made according to the technique described in [Diatoms of the USSR, 1992]. Species were identified in accordance with literature sources, including species guides [Diatomovyi analiz. Kniga 2, 1949; Diatomovyi analiz. Kniga 3, 1950; Guslyakov et al., 1992; Lange-Bertalot, 2001; Proshkina-Lavrenko, 1963; Witkowski et al., 2000] and numerous publications. Nomenclature names of microalgal taxa are given according to the Internet database https://www.algaebase.org/ [2020]. Microphotography and identification of diatoms were carried out under an Olympus BX53F light microscope using a ×100 immersion objective (Olympus immersion oil, n = 1.518), with a Jenoptik ProgRes Gryphax Arktur camera and Gryphax Arktur software. Moreover, to analyze fine structures of diatom shells, those were photographed under a Hitachi SU3500 scanning electron microscope (magnification factor 5–300,000; resolution up to 3 nm; and depth of field 0.5 mm).

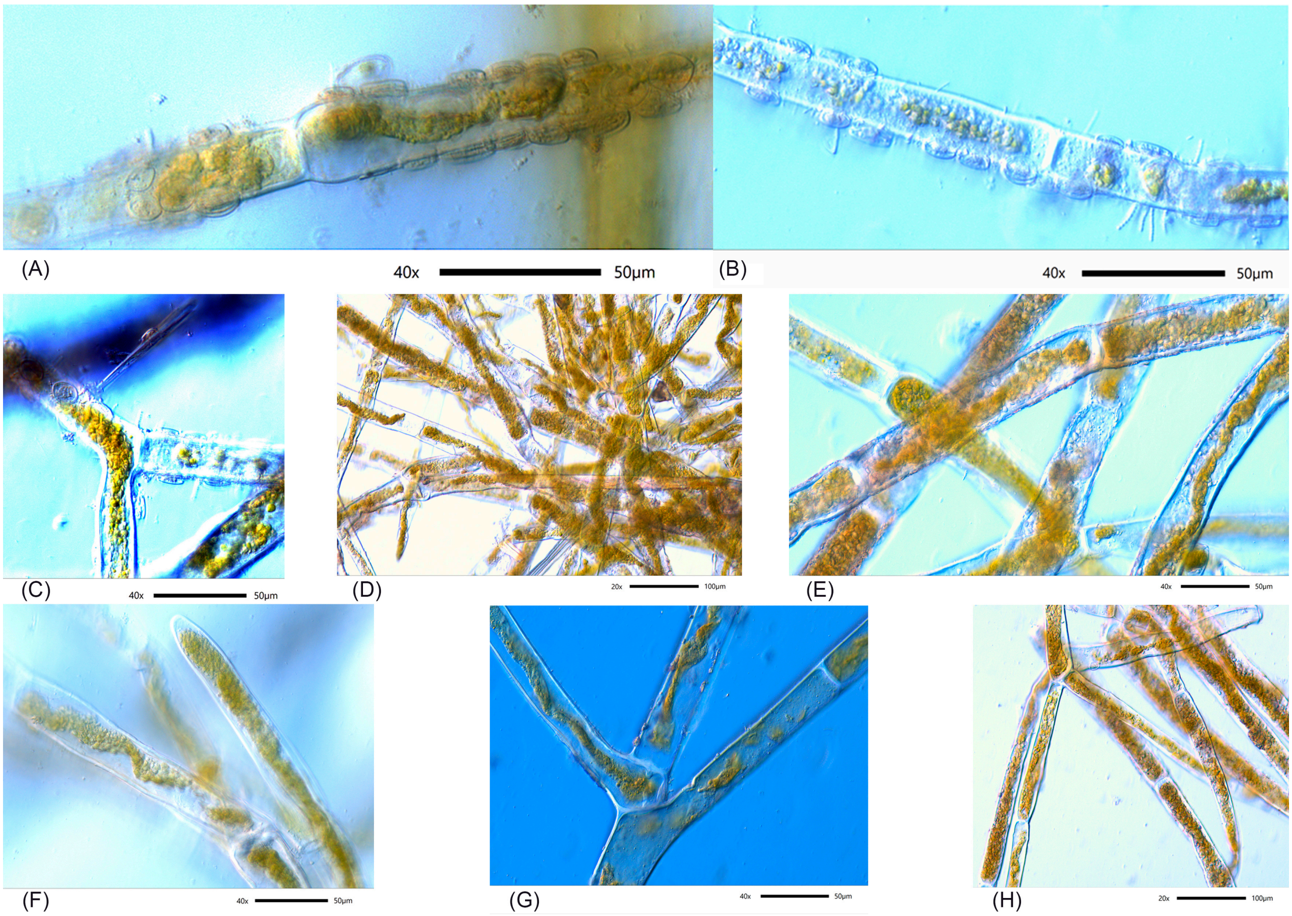

Fig. 3. Fragments of *Cladophora* thalli as seen under a light microscope (Olympus BX53F): A–C, before cleaning, overgrown with diatoms; D–H, after cleaning (processing)

The sample volume (V_{sus}), obtained as a result of the above manipulations, was measured with an accuracy of 0.1 mL; from it, a quota (V_{qu} = 0.02 mL) was taken to determine the quantitative characteristics of diatom algae. Removed *Cladophora* thalli of each sample were washed in freshwater, dried on filter paper, and weighed on a microanalytical balance with an accuracy of 10^{-4} g. Then, these samples were dried at +105 °C to constant weight (W_{Cl}) and weighed on the same balance.

In case when *Cladophora* thalli were subject to significant destruction, a sample was vigorously shaken. The contents were homogenized and diluted with water to required suspension density (sample volume, V_{sus}); from it, a quota (V_{qu} = 0.02 mL) was taken with a dispenser to determine the quantitative characteristics of diatoms.

To analyze the species structure of diatom algae in benthic sediments, a soil sample was diluted with water to obtain an arbitrary volume (V_{sus} was measured with an accuracy of 0.1 mL) and thoroughly mixed; from this suspension, a 0.02-mL quota (V_{qu}) was taken with a dispenser for subsequent measurements of diatom characteristics under a microscope. The remaining soil suspension was centrifuged for 3 min at 500 rpm. The precipitate was placed on a metal foil, dried at a temperature of +105 °C to constant weight (W_{sed}), and weighed on a microanalytical balance. The above operation was also carried out when working with suspension obtained from destroyed *Cladophora* thalli.

Diatom cells were counted under a LOMO Mikmed-2 light microscope (magnification from ×40 to ×1,500) on special lined counting glasses; on their surface, a few drops of suspension from a thoroughly mixed test sample were applied with a 0.02-mL dispensing pipette. To calculate the cell mass of diatoms, we used the true volume method (formulas for the geometric similarity of cells) proposed by I. Kiselev [1956]. The calculation of biomass and abundance was carried out according to standard techniques [Vodorosli, 1989].

Calculation of indicators and statistical processing of data. Based on the data obtained, certain indicators were calculated.

A. The volumetric concentration of *Cladophora* biomass at different sampling points was calculated using the equation:

$$C_W = W_{dry}/V_{mat} \,, \tag{1}$$

where C_W is the amount of dry mass of algae *per* unit volume of the mat, kg·m^{-3} (dry weight);

W_{dry} is dry weight of the *Cladophora* mat sample, kg;

V_{mat} is the mat volume, m^3.

The value of V_{mat} was calculated by the formula:

$$V_{mat} = S_0 \cdot h \,, \tag{2}$$

where V_{mat} is the volume of a floating or bottom mat, m^3;

S_0 is the cross-sectional area of a cylindrical sampler equal to 0.0452 m^2;

h is the thickness of a floating or bottom mat, m.

B. Dry and wet mass of the *Cladophora* mat algae *per* unit of the lake area at the sampling point were calculated applying the following formulas:

$$m_{dry} = W_{dry}/S_0 \,, \tag{3}$$

$$m_{wet} = W_{wet}/S_0 \,, \tag{4}$$

where m_{dry} is dry mass of the *Cladophora* mat algae *per* unit of the lake area at the sampling point, g·m^{-2} (dry mass);

m_{wet} is wet mass of the *Cladophora* mat algae *per* unit of the lake area at the sampling point, g·m^{-2} (wet mass);

W_{dry} is dry weight of the mat sample, g;

W_{wet} is wet weight of the mat sample, g;

S_0 is the surface area of the lake from which the sample was taken, m^2.

C. The abundance of the *i* species of diatom algae *per* unit of dry *Cladophora* mass or dry mass of benthic sediment was calculated by the formulas as follows:

$$N_i = (N_{i(qu)}/V_{qu}) \cdot (V_{sus}/W_{Cl}) \,, \tag{5}$$

$$N_i = (N_{i(qu)}/V_{qu}) \cdot (V_{sus}/W_{sed}) \,, \tag{6}$$

where N_i is the abundance of the *i* species of diatoms *per* unit of dry mass of benthic sediment, cells·g^{-1} (dry mass);

$N_{i(qu)}$ is the abundance of the *i* species of diatom algae in the volume of a sample quota (V_{qu} = 0.02 mL), cells;

V_{sus} is the sample volume, mL;

W_{Cl} is dry mass of *Cladophora* in the sample, g;

W_{sed} is dry mass of benthic sediment in the sample, g.

D. The amount of biomass of the *i* species of diatoms *per* unit of dry *Cladophora* mass or dry mass of benthic sediment was calculated according to the formula:

$$W_i = N_i \cdot B_{mid} \, , \tag{7}$$

where W_i is the amount of biomass of the *i* diatom species *per* unit of dry *Cladophora* mass, mg·g^{-1} (dry mass);

B_{mid} is mean cell mass of each diatom species, mg.

The individual cell mass for the *i* species (B_{mid}) was calculated as follows:

$$B_{mid} = v_i \cdot \rho \, , \tag{8}$$

where v_i is the mean cell volume of the *i* diatom species, µm^{-3} (it was calculated using the formulas for the geometric similarity of cells);

ρ is the specific weight of a diatom cell (ρ = 1.2 × 10^{-9} mg·µm^{-3} [Oxiyuk, Yurchenko, 1971]).

E. The total abundance of diatom cells in the *Cladophora* mat *per* unit of the lake area at the sampling point was calculated using the formula (the number of algal species in samples varied from 3 to 13):

$$N_D/S_0 = \sum_{n=3}^{13} (m_{dry} \cdot N_i)_n \, , \tag{9}$$

where N_D/S_0 is the total abundance of diatom cells in the *Cladophora* mat *per* unit of the lake area at the sampling point, cells·m^{-2};

m_{dry} is dry mass of the *Cladophora* mat algae *per* unit of the lake area at the sampling point, g·m^{-2} (dry mass);

N_i is the abundance of the *i* diatom species *per* unit of *Cladophora* dry mass, cells·g^{-1} (dry mass);

n is the number of algal species in samples.

F. The total biomass of diatom algae in the *Cladophora* mat *per* unit of the lake area at the sampling point was calculated applying the formula:

$$W_D/S_0 = \sum_{n=3}^{13} (m_{dry} \cdot W_i)_n \, , \tag{10}$$

where W_D/S_0 is the total biomass of diatom cells in the *Cladophora* mat *per* unit of the lake area at the sampling point, g·m^{-2};

W_i is the amount of the *i* diatom species *per* unit of dry *Cladophora* mass, mg·g^{-1} (dry mass);

n is the number of algal species in samples.

G. The calculation of mean values, their standard deviations (*SD*), correlation coefficients (*R*), and variability (*CV*), as well as the parameters of the regression equations, was carried out in MS Excel 2007. To compare the species composition of the communities of unicellular algae, the indices of similarity of Jaccard and Czekanowski–Sørensen–Dice were used [Semkin, 2009]:

$$K_J = c/(a + b - c) \, , \tag{11}$$

$$K_{CSD} = 2c/(a + b) \, , \tag{12}$$

where K_J and K_{CSD} are the indices of similarity of Jaccard and Czekanowski–Sørensen–Dice, respectively;

c is the number of species common for both sites or time periods;

a is the number of species found in the first case;

b is the number of species found in the second case.

The threshold values for making a conclusion about the similarity of the species composition are 0.42 (Jaccard) and 0.59 (Czekanowski–Sørensen–Dice) [Semkin, 2009].

RESULTS

Temperature and salinity inside and outside the mat. In the upper mat layer at sta. *D1*, salinity was 71 g·L^{-1}; at sta. *E3* and *E4*, the values were 67 and 67.3 g·L^{-1}, respectively.

Air temperature at 2:40 p.m. at a height of 1 m from the mat was +32.8 °C. Water temperature in the floating mat and in the algal layer underneath (sta. *D1*), as well as in the benthic mat and above it (sta. *D2*), changed regularly throughout the day (from 10 a.m. to 04:40 p.m.) (Fig. 4A, B). As a function of the time of day (t), at this time interval, it is described by the equations as follows.

Variation of water temperature (T) in the floating mat (sta. *D1*):

$$T = 28.984 + 0042t - 0.000086t^2$$

$$\text{(the standard error of approximation, } s = 0.51;\ R^2 = 0.95) \text{ .}$$

Variation of water temperature (T) in the algal layer under the mat (sta. *D1*):

$$T = 27.107 + 0.038t - 0.000066t^2 (s = 0.29;\ R^2 = 0.99) \text{ .}$$

Variation of water temperature (T) in the water layer above the benthic mat (sta. *D2*):

$$T = 28.157 + 0.042t - 0.000079t^2 (s = 0.38;\ R^2 = 0.98) \text{ .}$$

Variation of water temperature (T) in the benthic mat (sta. *D2*):

$$T = 28.202 + 0.042t - 0.000076t^2 (s = 0.48;\ R^2 = 0.97) \text{ .}$$

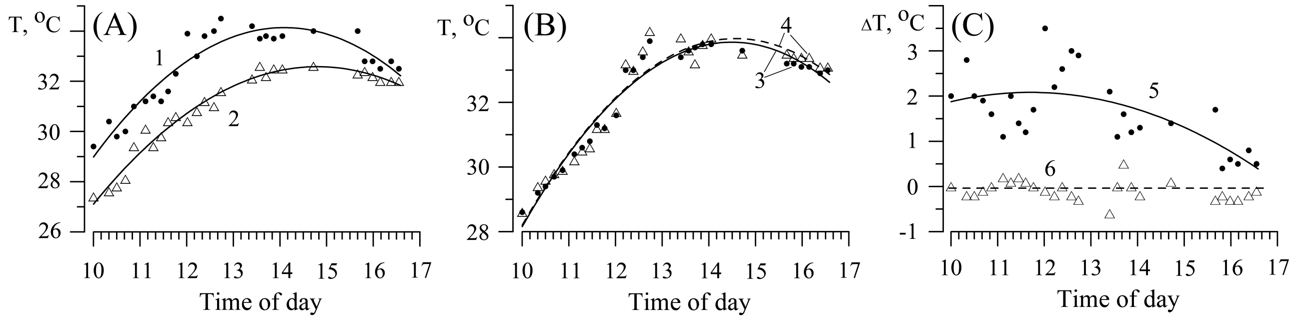

Fig. 4. A, water temperature variations in the floating mat (1) and in the algal layer underneath (2) at station *D1*; B, water temperature variations in the bottom mat (4) and above it (3) at station *D2*; C, difference (ΔT) between water temperature in the floating mat and in the algal layer underneath (5) and water temperature within the bottom mat and above it (6)

The values of water temperature in the floating mat (sta. *D1*) throughout the considered time period were higher than in the algal layer underneath. The temperature difference in the first half of the day averaged 2 °C; in the second half, it decreased to 0.5–1 °C (Fig. 4A, C). Water temperature values in the benthic mat and in 2 cm above it (sta. *D2*) almost did not differ (Fig. 4B, C); the temperature difference was 0.1–0.3 °C. For one hour, from 03:40 p.m. to 04:40 p.m., water temperature in the benthic mat was higher than above it.

Water temperature measured in the floating mat and in the algal layer underneath at sta. *E3* at 05 p.m. was +31.2 and +31.5 °C, respectively.

Structure of the *Cladophora* mat. At sta. *D1*, *E3*, and *E4*, in the vertical structure of the *Cladophora* mat, a floating mat (A) and the algal layer underneath (B) are distinguished (Fig. 1D, F, G). In all these cases, the floating mat was a dense accumulation of *Cladophora* near the water surface (3.6–15.2 kg·m^{-3} of dry mass, Table 1), where two horizontal layers were clearly distinguished: the upper (A1), relatively thick (1–3 cm), dirty green or yellow, and the lower (A2), thin (0.1–1 cm), green or dark green (Fig. 5). The algal layer under the floating mat, freely floating in water of *Cladophora* thalli, was characterized by a low bulk density (0.2–1.4 kg·m^{-3} of dry mass, see Table 1), and the algae forming it differed in color at various stations. Thus, at sta. *D1*, those were dark green; at sta. *E3*, dirty green; and at sta. *E4*, pink. In the latter case, the algae were in a state of decomposition; on their surface, purple bacteria *Chromatium* Perty, 1852 and *Ectothiorhodospira* Pelsh, 1936 developed, giving them the appropriate color. Within the entire algal mat, the floating mat accounted for 86.9% of *Cladophora* biomass at sta. *D1* and 62.2 and 66% at sta. *E3* and *E4*, respectively; the share of the upper layer in the floating mat ranged from 75 to 86.7% of its mass (Table 1, Fig. 6a–c).

At sta. *D2*, the benthic mat of algae, a mat lying on the bottom, was structurally similar to the floating mat; on the bottom surface, it occurred in separate "spots" of different sizes (Figs 1E, 2A). The upper mat layer was no more than 2 cm thick and was dirty orange, which indicated the presence of purple bacteria in high abundance. The bottom layer was thin, 0.2–0.3 cm, and dark green.

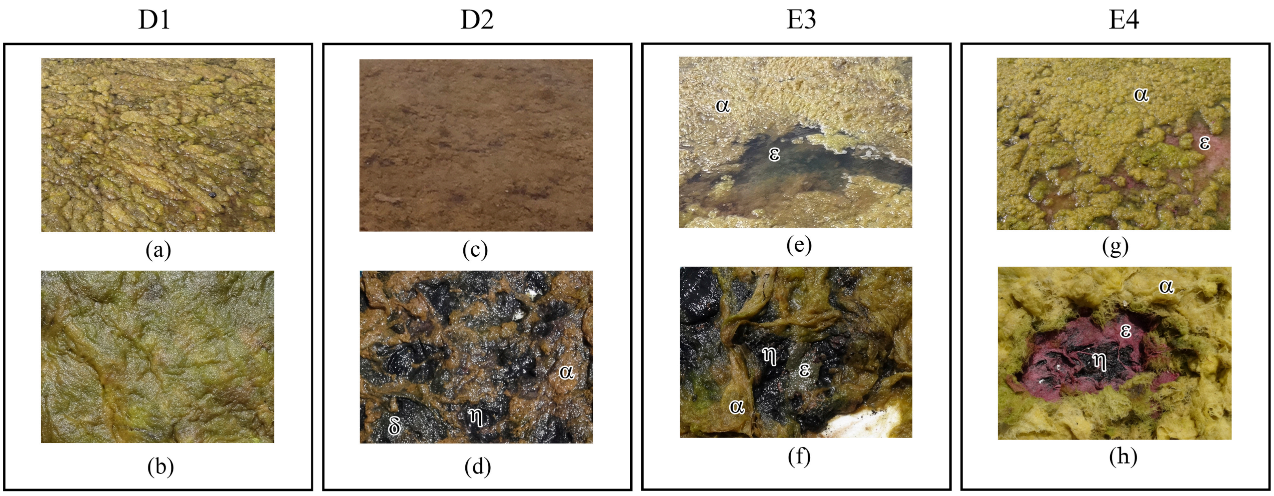

Fig. 5. View of *Cladophora* mats and their separate elements at sampling stations (*D1*, *D2*, *E3*, *E4*). Top (a) and bottom view (b) of the floating mat at station *D1*. Top view (c, d) of the bottom mat at station *D2*. On d: the bottom mat upper layer is partially removed (α), uncovering underlying layers (δ, η). Top view of the floating mat at stations *E3*, *E4* (e, g). On f, h: the floating mat upper layer is partially removed (α), uncovering underlying layers (ε, η)

Table 1. Quantitative characteristics of the *Cladophora* mat and epiphytic diatoms, Lake Chersonesskoye, 26.07.2017

Sta.	Vertical layer	*Cladophora*						Diatoms			
								per unit of *Cladophora* dry biomass		*per* unit of the lake area	
		m_{dry}, $g \cdot m^{-2}$ (dry mass)	*SD*	*CV*	C_w, $kg \cdot m^{-3}$ (dry weight)	*SD*	*CV*	N_D/W_{Cl}, $\times 10^6$ $cells \cdot g^{-1}$	W_D/W_{Cl}, $mg \cdot g^{-1}$ (wet mass)	N_D/S_0, $\times 10^8$ $cells \cdot m^{-2}$	W_D/S_0, $g \cdot m^{-2}$ (wet mass)
D1	The floating mat (A)	441.740	40.719	0.092	11.044	1.018	0.092	24.892	55.284	109.959	24.421
	Algae under the floating mat (B)	66.369	5.967	0.090	1.368	0.317	0.232	30.907	73.263	20.513	4.862
	A + B	508.109	42.673	0.084	–	–	–	–	–	130.472	29.284
E3	The floating mat (A)	54.646	12.978	0.237	3.643	0.865	0.237	20.559	45.802	11.234	2.503
	Algae under the floating mat (B)	33.181	9.113	0.275	0.222	0.052	0.233	10.124	21.746	3.359	0.722
	A + B	87.827	22.040	0.251	–	–	–	–	–	14.594	3.224
E4	The floating mat (A)	342.035	33.135	0.097	15.202	1.473	0.097	2.881	13.291	10.073	4.647
	Algae under the floating mat (B)	176.564	16.031	0.091	1.315	0.084	0.064	3.108	10.319	5.488	1.822
	A + B	518.600	49.149	0.095	–	–	–	–	–	15.560	6.469

Note: m_{dry}, dry *Cladophora* biomass *per* unit of the lake surface; *SD*, standard deviation; *CV*, coefficient of variation; C_w, concentration of dry mass of *Cladophora* in the mat volume; N_D/W_{Cl}, the abundance of diatom cells *per* unit of dry *Cladophora* biomass; W_D/W_{Cl}, wet mass of diatom cells *per* unit of dry *Cladophora* biomass; N_D/S_0, the abundance of diatom cells *per* unit of the lake surface area; W_D/S_0, wet biomass of diatom cells *per* unit of the lake surface area.

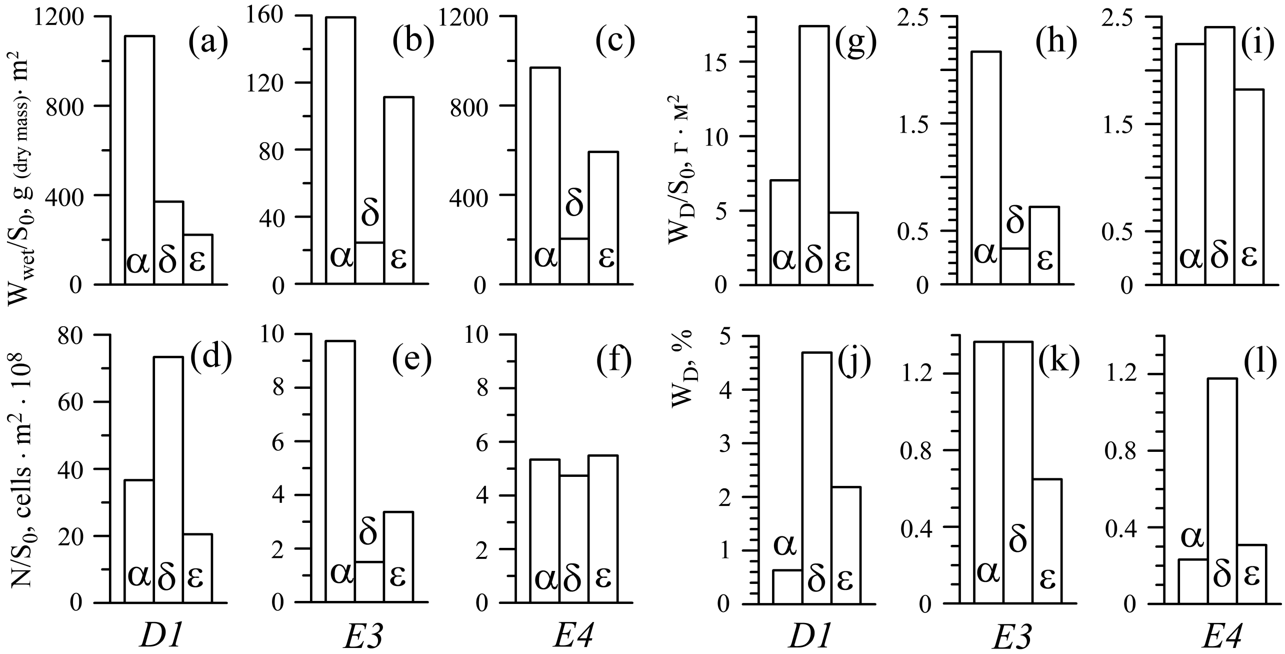

Fig. 6. *Cladophora* biomass *per* unit of the lake bottom surface at various horizons of the mat (a–c). The total abundance (d–f) and biomass (g–i) of diatoms *per* unit of the lake bottom surface at various horizons of the mat. The share of diatom mass in the total mass of the *Cladophora* mat (j–l). *D1*, *E3*, *E4*, sampling stations; α, δ, ε, sampling points

The species composition of diatom algae in *Cladophora* mats and benthic sediments. At the time of the study, 23 microalgal species were found on *Cladophora* and in bottom sediments in the area of the stations surveyed: Chromista (Ochrophyta, Bacillariophyceae), 20 species (Table 2, Fig. 7); Chromista (Myzozoa, Dinophyceae), 3 species (*Gymnodinium* sp.; *Kryptoperidinium foliaceum* (F. Stein) Lindemann, 1924; and *Protoceratium reticulatum* (Claparède & Lachmann) Bütschli, 1885). Within this article, we are going to limit ourselves to considering the species composition and quantitative characteristics of diatom algae of *Cladophora* mats and benthic sediments. Out of the diatoms identified, only one species (*Cocconeis kujalnitzkensis* Gusliakov et Gerasimiuk, 1992) was recorded in all the samples studied (see Supplement s1). Frequency of occurrence of *Nitzschia inconspicua* Grunow, 1862 in the samples was 92%, and the value for *Halamphora coffeiformis* (C. A. Agardh) Levkov, 2009 and *Mastogloia braunii* Grunow, 1863 was 85%. Four species (*Achnanthes brevipes* C. A. Agardh, 1824; *Mastogloia lanceolata* Thwaites ex W. Smith, 1856; *Navicula cancellata* Donkin, 1872; and *Nitzschia pusilla* Grunow, 1862), accounting for 20% of the species number, were identified only in 2 samples out of 13. Other four species (*Amphora* sp. 1; *Neosynedra provincialis* (Grunow) D. M. Williams & Round, 1986; *Nitzschia sigma* (Kützing) W. Smith, 1853; and *Thalassiosira eccentrica* (Ehrenberg) Cleve, 1904) were registered just in 1 sample. The maximum species diversity, 14 species, was observed in the benthic mat. In the floating mat, the value varied from 3 to 8, averaging 5.7 (SD = 2.517; CV = 0.444); in the algal layer under the floating mat, it varied from 4 to 10, averaging 6.3 (SD = 3.25; CV = 0.507). In terms of species richness, the samples of benthic sediments were less variable (CV = 0.143); the number of species in these samples ranged within 6–8, averaging 7 (SD = 1.000).

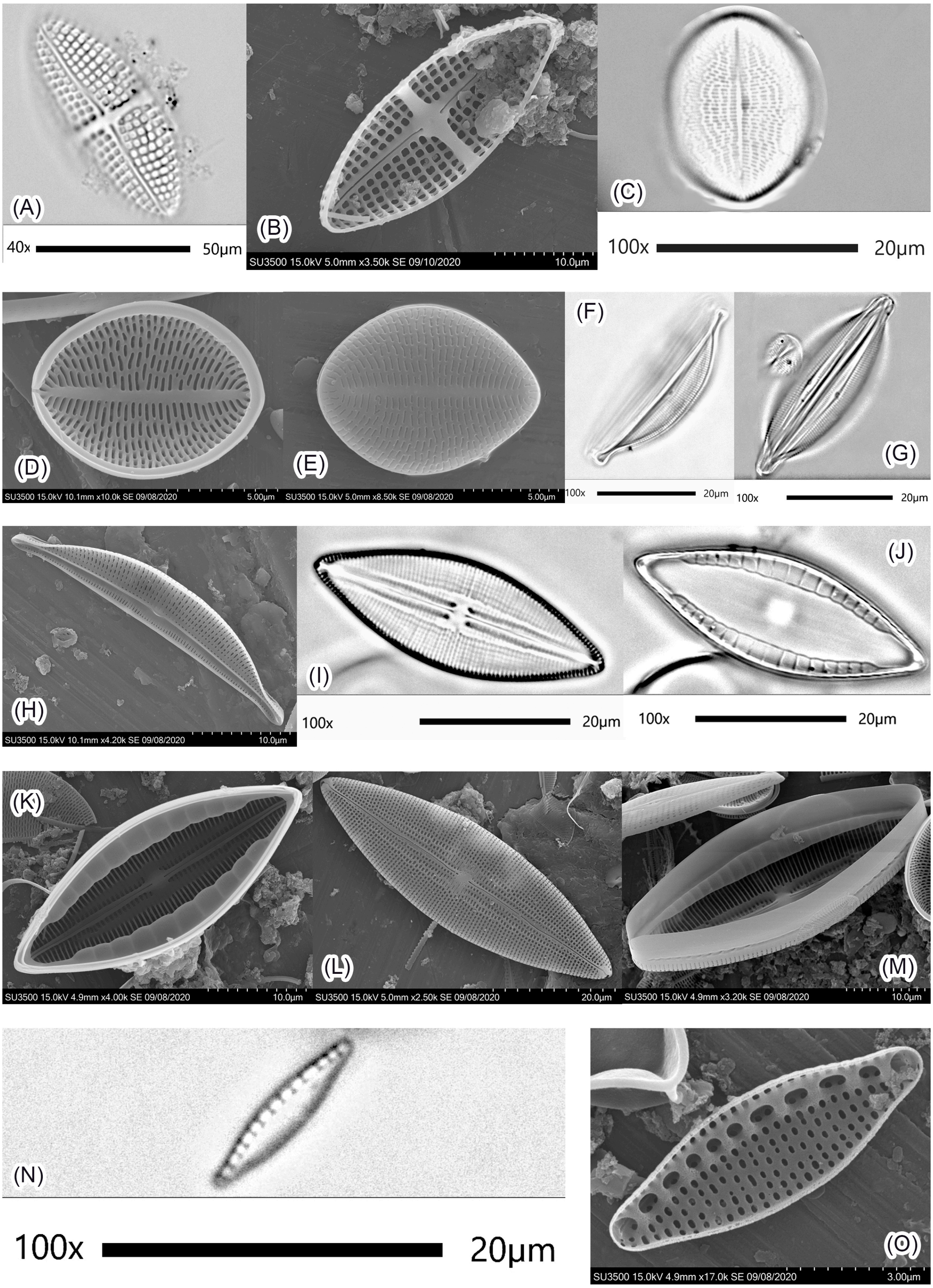

Fig. 7. Diatom species to be frequently found on *Cladophora* thalli in Lake Chersonesskoye as seen from different angles: A, B, *Achnanthes brevipes*; C–E, *Cocconeis kujalnitzkensis*; F–H, *Halamphora coffeiformis*; I–M, *Mastogloia braunii*; N–O, *Nitzschia inconspicua*. A, C, F, G, L, J, N, under a light microscope (Olympus BX53F); B, D, E, H, K–M, O, under a scanning electron microscope (Hitachi SU3500)

Table 2. Average, minimum, and maximum values of the individual cell mass for diatoms identified in the samples (Lake Chersonesskoye, 26.07.2017)

Species	Individual cell mass, $B_i \times 10^{-6}$, mg		
	average	minimum	maximum
Achnanthes brevipes C. A. Agardh, 1824	3.842	3.458	4.226
Achnanthes longipes C. A. Agardh, 1824	5.795	2.151	8.904
Amphora sp. 1	4.421	–	–
Cocconeis kujalnitzkensis Gusliakov et Gerasimiuk, 1992	2.082	1.345	2.954
Cyclotella caspia Grunow, 1878	0.467	0.111	0.926
Cylindrotheca closterium (Ehrenberg) Reimann et J. C. Lewin, 1964	0.128	0.095	0.178
Halamphora coffeiformis (C. A. Agardh) Levkov, 2009	2.239	0.342	4.746
Halamphora hyalina (Kützing) Rimet et R. Jahn in Rimet et al., 2018	3.824	3.455	4.521
Mastogloia braunii Grunow, 1863	6.802	5.469	9.260
Mastogloia lanceolata Thwaites ex W. Smith, 1856	8.619	7.988	9.250
Navicula cancellata Donkin, 1872	0.452	0.415	0.490
Navicula pennata var. *pontica* Mereschkowsky, 1902	1.061	0.381	2.355
Navicula ramosissima (C. Agardh) Cleve, 1895	0.231	0.117	0.283
Neosynedra provincialis (Grunow) D. M. Williams & Round, 1986	0.227	–	–
Nitzschia inconspicua Grunow, 1862	0.192	0.118	0.286
Nitzschia pusilla Grunow, 1862	0.116	0.100	0.132
Nitzschia sigma (Kützing) W. Smith, 1853	7.438	–	–
Nitzschia tenuirostris Mereschkowsky, 1902	0.186	0.132	0.235
Parlibellus delognei (Van Heurck) E. J. Cox, 1988	1.845	1.082	2.628
Thalassiosira eccentrica (Ehrenberg) Cleve, 1904	1.654	–	–

The values of the similarity coefficients of the species composition (K_J and K_{CSD}) between the samples are given in Table 3. K_J and K_{CSD} values, calculated when comparing the diatoms of plant mats at sta. *E3* and *E4* (the northeastern shore of the lake), were 0.67 and 0.80, respectively. This means a lack of clear dissimilarity in the species composition of the compared objects. Comparison of the species composition of diatoms at sta. *D1* and *D2* (the southeastern shore of the lake) showed their similarity as well; however, the values of the coefficients were close to the threshold ones (0.44 and 0.62, respectively), exceeding them only slightly. A pairwise comparison of diatoms in plant mats of the stations on the southeastern and northeastern shores revealed a noticeable dissimilarity between them (see Table 3). A more detailed comparison of diatoms, separately for the floating mat and for the algal layer underneath at different stations, also revealed a clear similarity between stations on the same shore and a dissimilarity between stations on the northeastern and southeastern shores (Table 3). Comparison of the species composition of the benthic mat, its upper and lower layers (sta. *D2*), with that of similar layers of the floating mat at sta. *D1* and *E4* did not reveal any similarity for diatom communities. A pairwise comparison of benthic sediment samples from different stations showed as follows: in benthic sediments at each station, the composition of diatoms peculiar to them alone is formed. Another type of comparison, comparison of the samples by the vertical component of the mat at all the stations studied, revealed that the upper and lower layers of the floating mat, the algal layer underneath, and benthic sediments do not differ in diatom species composition. There is an exception, a slight dissimilarity at sta. *D2* between the benthic mat and benthic sediments; K_J and K_{CSD} values are in the threshold zone, accounting for 0.40 and 0.57, respectively.

Table 3. The similarity coefficients of the diatom species composition in the considered objects under pairwise comparison (Lake Chersonesskoye, 26.07.2017)

Pairwise comparison objects	K_J	K_{CSD}
Comparison of the upper and lower layers of the mat at different stations		
1α – 1δ	0.44	0.62
2α – 2δ	0.71	0.83
4α – 4δ	0.67	0.80
Comparison of the upper layer of the floating mat and the algal layer underneath at different stations		
1α – 1ε	0.55	0.71
4α – 4ε	1.00	1.00
Comparison of the floating mat and the algal layer underneath at different stations		
1(α + δ) – 1ε	0.73	0.84
3(α + δ) – 3ε	0.75	0.86
4(α + δ) – 4ε	0.83	0.91
Comparison of the floating mat and the soil layer underneath at different stations		
2(α + δ) – 2η	0.40	0.57
3(α + δ) – 3η	0.50	0.67
4(α + δ) – 4η	0.56	0.71
Comparison of the algal layer under the floating mat and the soil layer underneath at different stations		
3ε – 3η	0.67	0.80
4ε – 4η	0.63	0.77
Comparison of the upper layer of the floating mat at sta. *D1* and *E4*		
1α – 4α	0.33	0.50
Comparison of the upper layer of the bottom mat at sta. *D2* with the upper layer of the floating mat at sta. *D1* and *D4*		
2α – 1α	0.38	0.56
2α – 4α	0.33	0.50
2α – (1 + 4)α	0.33	0.50
Comparison of the lower layer of the floating mat at sta. *D1* and *E4*		
1δ – 4δ	0.38	0.55
Comparison of the lower layer of the bottom mat at sta. *D2* with the lower layer of the floating mat at sta. *D1* and *D4*		
2δ – 1δ	0.36	0.53
2δ – 4δ	0.29	0.44
2δ – (1 + 4)δ	0.40	0.57
Comparison of the bottom mat under the floating mat at different stations with each other		
1ε – 3ε	0.40	0.57
1ε – 4ε	0.36	0.53
3ε – 4ε	0.80	0.89
Comparison of floating mats at different stations with each other		
1(α + δ) – 3(α + δ)	0.20	0.33
1(α + δ) – 4(α + δ)	0.25	0.40
3(α + δ) – 4(α + δ)	0.80	0.89
Comparison of the bottom mat at sta. *D2* with the floating mat at different stations		
2(α + δ) – 1(α + δ)	0.35	0.52
2(α + δ) – 3(α + δ)	0.21	0.35
2(α + δ) – 4(α + δ)	0.33	0.50
2(α + δ) – (1 + 3 + 4)(α + δ)	0.50	0.67

Continue on the next page…

Pairwise comparison objects	K_J	K_{CSD}
Comparison of soils under the mat at different stations with each other		
2η – 3η	0.18	0.31
2η – 4η	0.36	0.53
3η – 4η	0.40	0.57
Comparison of entire plant mats at different stations with each other		
D1 – D2	0.44	0.62
D1 – E3	0.33	0.50
D1 – E4	0.29	0.44
D2 – E3	0.29	0.44
D2 – E4	0.33	0.50
E3 – E4	0.67	0.80

Average, minimum, and maximum values of the individual cell mass for diatoms identified in the samples. These values are given in Table 2. The total row of cell biomass values fits into two orders of magnitude, with the minimum registered cell biomass in *Cylindrotheca closterium* (Ehrenberg) Reimann et J. C. Lewin, 1964 (0.095×10^{-6} mg) and the maximum recorded in *M. braunii* (9.26×10^{-6} mg). Each algal species occurred within its characteristic range of B_i values, and it was relatively narrow for most species (Fig. 8A). Four algae stood out (*Achnanthes longipes* C. A. Agardh, 1824; *Cyclotella caspia* Grunow, 1878; *H. coffeiformis*; and *N. pennata* var. *pontica* Mereschkowsky, 1902): their individual cell mass varied within a relatively wide range. Moreover, there were four species (*Amphora* sp. 1; *N. sigma*; *N. provincialis*; and *T. eccentrica*) represented by single specimens in the samples. The range of variation of the individual cell mass (ΔB_i) expands with an increase in the average cell size (B_{mid}), characteristic of each algal species (Fig. 8B), and this relationship is described by the equation:

$$\log \Delta B_i = -0.578 + 0.944 \log B_{mid} \; (s = 0.361; R^2 = 0.87) \; .$$

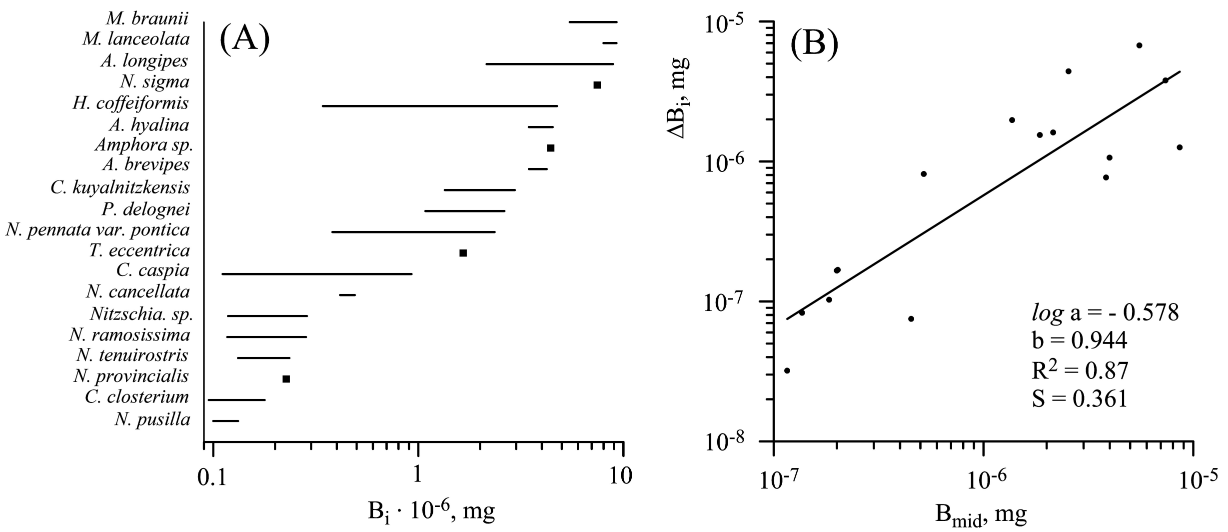

Fig. 8. A, the individual cell mass (B_i) variation ranges in different diatom species identified in the samples (Lake Chersonesskoye, 26.07.2017); B, dependence of the individual cell mass (ΔB_i) variation range on the average cell size (B_{mid}) characteristic of each algal species

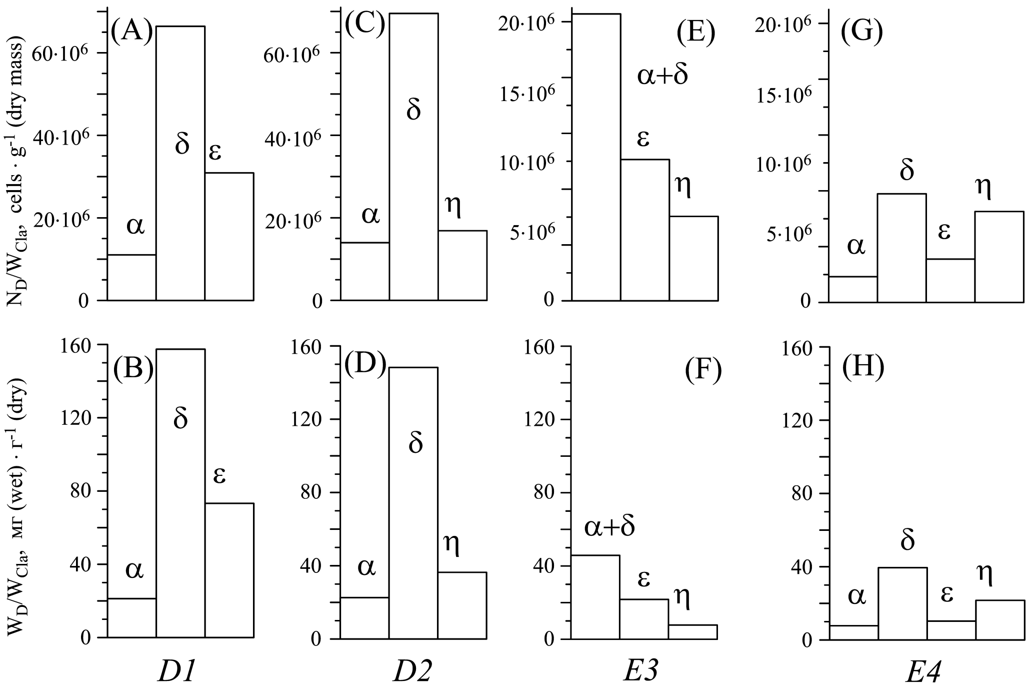

Fig. 9. Total abundance (A, C, E, G) and biomass (B, D, F, H) of diatom algae *per* unit of dry *Cladophora* mass and bottom sediments at stations *D1*, *D2*, *E3*, *E4*; α, δ, ε, η, sampling points

The total abundance and biomass of diatoms *per* unit of dry mass of *Cladophora* and benthic sediments. At the sampling points, the total abundance of diatoms and their biomass on *Cladophora* (*per* unit of dry biomass) and in benthic sediments (*per* unit of dry mass) varied over a wide range (see Supplements s1, s2, Fig. 9). On *Cladophora*, the abundance varied from 1.85×10^6 to 69.52×10^6 cells·g^{-1}; the biomass, from 7.77 to 157.43 mg·g^{-1}. In benthic sediments, the abundance varied from 6.05×10^6 to 16.87×10^6 cells·g^{-1}; the biomass, from 7.76 to 36.39 mg·g^{-1}. At all the stations, high values of the cell abundance and biomass *per* unit of *Cladophora* mass were recorded in the lower layer of the floating mat: 47.911×10^6 cells·g^{-1} (*SD* = 34.783; *CV* = 0.726) and 115.06 mg·g^{-1} (*SD* = 65.599; *CV* = 0.570), respectively. Low values were registered in its upper layer: 8.957×10^6 cells·g^{-1} (*SD* = 6.329; *CV* = 0.707) and 17.21 mg·g^{-1} (*SD* = 8.197; *CV* = 0.476), respectively. In the algal layer under the floating mat, mean values of the abundance and biomass were 14.713×10^6 cells·g^{-1} (*SD* = 14.457; *CV* = 0.983) and 35.11 mg·g^{-1} (*SD* = 33.532; *CV* = 0.955), respectively. The values of the characteristics studied at sta. *D1* and *D2* (the southeastern shore of the lake) were approximately the same and noticeably higher than those observed at sta. *E3* and *E4* (the northeastern shore of the lake), with the lowest values at sta. *E4*. In terms of the cell abundance *per* unit of dry mass of benthic sediment, sta. *E3* and *E4* did not differ much from one another, but the values were 3 times lower than those determined at sta. *D2*. At the same time, in terms of cell mass *per* unit of dry mass of benthic sediment, sta. *E3* and *E4* differed from one another by 3 times, while sta. *D2* exceeded them by 5 and 3 times, respectively.

At sta. *D1*, *D2*, and *E3*, one species, *C. kujalnitzkensis*, prevailed in the abundance in both the upper and lower mat layers. At sta. *D1* and *E3*, it averaged 96.1% (*SD* = 1.9; *CV* = 0.02); at sta. *D2*, 54.1%. At sta. *E4*, two species, *M. braunii* and *C. kujalnitzkensis*, contributed much to the total abundance of the floating mat diatoms. There, in the upper mat layer, *M. braunii* accounted for 67.5% of the total abundance, and *C. kujalnitzkensis*, for 20.2%. In the lower mat layer, their contribution was approximately the same: 44.8 and 54.1%, respectively.

At all the stations studied, *C. kujalnitzkensis* prevailed in the abundance in the algal layer under the floating mat, where its share averaged 72.2% (*SD* = 15.33; *CV* = 0.212). At sta. *D2* and *E4*, this species prevailed in the abundance in benthic sediments as well (70.3 and 66.8%, respectively); at sta. *E3*, the prevailing species was *N. inconspicua* (76.3%).

The distribution of various diatom species taking into account their contribution to the total mass at different stations is largely repeated in the samples with their distribution by the abundance. The main contributor to the total biomass of diatoms (from 63 to 99%) in the upper and lower mat layers at sta. *D1*, *D2*, and *E3* was *C. kujalnitzkensis*. This species also prevailed (79.2% of the diatom mass) in the algal layer under the mat at sta. *D1* and *E3*. At sta. *E4*, *M. braunii* prevailed in the floating mat and in the algal layer underneath (84.7 and 55.2% of the diatom mass, respectively). At the same station, in the algal layer under the floating mat, the contribution of *C. kujalnitzkensis* to the total diatom biomass was 38.5%. In the upper and lower layers of the floating mat, its contribution was even less, 6.47 and 18%, respectively.

In benthic sediments at sta. *D2*, *C. kujalnitzkensis* accounted for 66.4% of the total diatom biomass, while at sta. *E4* and *E3*, its value dropped to 38 and 4.97%, respectively. At sta. *E4*, 58.3% of the diatom biomass in benthic sediments was formed by *M. braunii*. At sta. *E3*, the main contributors to its formation were two algal species, *H. coffeiformis* and *M. braunii* (40.9 and 43.1%, respectively).

The total abundance and biomass of diatoms of the *Cladophora* mat *per* unit of the lake bottom surface. The total abundance of diatoms of the *Cladophora* mat *per* unit of the lake bottom surface varied from 14.59×10^8 cells·m^{-2} at sta. *E3* to 130.47×10^8 cells·m^{-2} at sta. *D1* and averaged 53.54×10^8 cells·m^{-2} (*SD* = 66.63×10^8; *CV* = 1.24). Their total biomass ranged from 3.22 to 29.28 g·m^{-2} (wet weight), with average value of 12.99 g·m^{-2} (*SD* = 14.20; *CV* = 1.09) (see Table 1, Fig. 6d–i). The share of the diatom biomass in the wet mass of the entire *Cladophora* mat averaged 1.06% (*SD* = 0.68; *CV* = 0.64), while in separate mat layers, it differed noticeably. For example, in the lower layer of the floating mat (δ) at sta. *D1*, it reached 4.69% with average values of 2.41% (*SD* = 1.98; *CV* = 0.82) calculated for three stations (Fig. 6j–l). In the upper layer of the floating mat (α), this indicator varied widely as well, but average value was low, 0.74% (*SD* = 0.57; *CV* = 0.77). The same was observed in the *Cladophora* layer under the floating mat (ε), 1.05% (*SD* = 0.99; *CV* = 0.95).

The absolute values of the abundance and biomass of diatoms calculated *per* unit of the lake bottom surface in relation to various mat layers at sta. *D1* were many times higher than those observed at sta. *E3* and *E4* (Fig. 6d–i). The nature of the distribution of diatoms over the layers of the *Cladophora* mat is peculiar to each station. In terms of diatom mass and abundance, the lower layer of the floating mat stands out at sta. *D1*, and the upper layer, at sta. *E3*. At sta. *E4*, the distribution of diatoms over the *Cladophora* mat layers was relatively uniform.

DISCUSSION

This investigation is one of the areas of our activity in studying Crimean hypersaline lakes and, in particular, Lake Chersonesskoye near the city of Sevastopol. The research is driven by the hypothesis that *Cladophora* mats in Lake Chersonesskoye are the main habitat-forming elements in spring–autumn and that they spatially structure communities of epiphytic unicellular algae.

In literature, different numbers of diatom species found as epiphytes on *Cladophora* are published. Specifically, in [Malkin et al., 2009], the number is 17; that is how many species were identified on 26 May on *Cladophora* (*Cladophora glomerata* (L.) Kützing, 1843), which begins its vegetative growth in the Great Lakes. Interestingly, 57 species belonging to 26 genera were identified by [Mpawenayo, Mathooko, 2005] on *Cladophora* sampled in various areas of the Niero River in Kenya. Moreover, on *Cladophora* sampled from the Colorado River, there were 78 diatom species representing 20 genera [Hardwick et al., 1992]. On *Cladophora albida* (Nees) Kützing, 1843 in two Black Sea areas, 24 diatom species were recorded [Ryabushko et al., 2013].

As shown in the present study, in Lake Chersonesskoye in July 2017, on *Cladophora* organized in mats, 20 diatom species belonging to 12 genera were identified; in benthic sediments, 13 diatom species representing 10 genera were registered. In the same lake, during the observation period from August 2002 to March 2006, 61 species of unicellular algae belonging to 7 divisions, 10 classes, 22 orders, and 41 genera were found and described in a water column outside the *Cladophora* mat [Senicheva et al., 2008]. The first place in the species number was occupied by dinophytes (19 species); the second place, diatoms (15 species). Out of diatoms, benthic forms prevailed (*Nitzschia tenuirostris* Mereschkowsky, 1902; *Nitzschia* sp.; *Cocconeis scutellum* Ehrenberg, 1838; and *Pleurosigma elongatum* W. Smith, 1852); there were practically no planktonic species, except for individual finds of *C. caspia* and *T. eccentrica*. In Crimean saline lakes, 68 species and 69 intraspecific taxa of bottom diatoms were recorded [Nevrova, Shadrin, 2008]; off the Crimean coast, 465 species, *inter alia* 769 intraspecific taxa, were registered [Nevrova, Petrov, 2008]. To date, more than 1,000 species of all benthic microalgae have been found in the Black Sea, including about 650 species of diatoms [Ryabushko, 2013].

Our study also reveals that epiphytic communities of diatoms in various areas of *Cladophora* mats differ in species composition, total abundance, and biomass, as well as in the significance of certain algal species in the community structure. Most taxa show overlapping distributions in the vertical component of a vegetation mat, while some are found in its specific horizons alone. For example, *Amphora* sp. 1 and *N. provincialis* were registered only in lower layers of the floating mat; *N. sigma*, in bottom sediments alone.

Based on information in literature, we are going to discuss the possible causes of the observed distributions of epiphytic unicellular algae within the *Cladophora* mat.

The upper and lower layers of the floating mat and the algal layer underneath are biotopes with pronounced environmental conditions, both for *Cladophora* and its epiphytes. The floating mat, especially its upper layer, experiences strong daily temperature fluctuations [Prazukin et al., 2008]; moreover, a high level of solar radiation is observed there. According to our previous studies [Prazukin et al., 2018], in the upper thin layer of the floating mat, algae can undergo drying (dehydration); in other cases, a dense layer of salt can be formed on the mat surface. B. Ibelings and L. Mur [1992] found out that the absorption of carbon dioxide and nitrogen by algal cells decreases as those become dehydrated. High levels of ultraviolet radiation can cause photoinhibition, degradation of photosynthetic pigments, and cell death in the upper mat layers [Jiang, Qiu, 2005]; as a consequence, in this part of the mat, there are relatively low values of the intensity of photosynthesis compared to the values in the underlying layer [Prazukin et al., 2019]. In the daytime, oxygen content can be 200% of saturation in the upper mat layer against the backdrop of a lack of oxygen in the lower mat [Shadrin, Anufriieva, 2018]. Insects and their larvae actively develop on the mat surface, and they graze on epiphytic algae [Furey et al., 2012]. Algae of the floating mat may be limited in their access to biogenic elements from bottom sediments, as noted for pelagic phytoplankton populations [Bootsma et al., 2004].

For the communities of unicellular algae in the lower layer of the floating mat and the algal layer of the benthic mat, habitat conditions are completely different from those observed in the upper layer of the floating mat. Thus, even in thin periphyton films of unicellular algae, there is a strong vertical gradient of light [Kühl, Jørgensen, 1992]. In the floating mat of *Pithophora* Wittrock, 1877, only 1% of the incident light reaches a 1-cm depth [O'Neal, Lembi, 1983], while in the *Cladophora* mat, the value is 2% [Eiseltová, Pokorný, 1994]. In dense mats of *Chaetomorpha linum* (O. F. Müller) Kützing, 1845, the light zone is limited to 8 cm [Krause-Jensen et al., 1996]. In turn, the floating mat in relation to the benthic mat is a screen that prevents the passage of light into benthic layers, causing a deterioration in photosynthesis conditions and a decrease in water temperature [Goldsborough, Robinson, 1996; Prazukin, 2015; Prazukin et al., 2008, 2019]. G. Hardwick *et al.* [1992] associate vertical zoning of epiphytic diatoms on *C. glomerata* in the Colorado River (Arizona) (a decrease in cell density) with the weakening of light as the depth increases.

The fact of the mutual metabolic effect of epiphytes and the host plant [Young et al., 2010] cannot be excluded either. This may be reflected in the vertical distribution of epiphytic unicellular algae in the space of *Cladophora* mats.

Conclusion. Each of the factors considered, in varying degrees, can determine the vertical distribution of microalgae within the *Cladophora* mat, but none of them can be called the only determining one. *Cladophora*, forming mats that occupy in some years 80–100% of the surface area of Lake Chersonesskoye, acts here as an ecological engineer. In the space of the mat, a multiplicity of biotic and abiotic gradients is formed, generating a great variety of habitat conditions, which can naturally or accidentally be manifested in time.

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Supplement s1. Species composition and abundance of diatoms on *Cladophora* threads and in biogenic sediments (Lake Chersonesskoye, 26.07.2017).

Supplement s2. Biomass of diatoms on *Cladophora* threads and in biogenic sediments (Lake Chersonesskoye, 26.07.2017).

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CLADOPHORA (CHLOROPHYTA) КАК «ИНЖЕНЕР-ЭКОЛОГ» В ГИПЕРСОЛЁНОМ ОЗЕРЕ ХЕРСОНЕССКОМ: РАСПРЕДЕЛЕНИЕ ДИАТОМОВЫХ ВОДОРОСЛЕЙ В СТРУКТУРИРОВАННОМ ПРОСТРАНСТВЕ РАСТИТЕЛЬНЫХ МАТОВ

А. В. Празукин, Р. И. Ли, Д. С. Балычева, Ю. К. Фирсов, В. В. Холодов

ФГБУН ФИЦ «Институт биологии южных морей имени А. О. Ковалевского РАН», Севастополь, Российская Федерация

E-mail: *prazukin@mail.ru*

Род *Cladophora* — один из крупнейших родов зелёных водорослей, представители которого встречаются во всех водоёмах мира. Кладофора организует среду обитания для разных групп организмов, в том числе для эпифитных одноклеточных водорослей. Цель работы — изучить вертикальное распределение диатомей в структурированном пространстве матов *Cladophora* и в донных отложениях гиперсолёного озера в Крыму. В вертикальном строении мата кладофоры различали плавучий и донный маты, каждый из которых имел характерную структуру. Всего в ходе данного исследования зарегистрированы 20 видов диатомовых водорослей из 12 родов. Общая численность диатомей и их биомасса на *Cladophora* (в расчёте на единицу сухой биомассы) и в донных отложениях (в расчёте на единицу сухой массы) варьировали в широком диапазоне. На кладофоре численность изменялась от $1{,}85 \times 10^6$ до $69{,}52 \times 10^6$ кл.·г$^{-1}$, а биомасса — от 7,77 до 157,43 мг·г$^{-1}$. В донных осадках численность варьировала от $6{,}05 \times 10^6$ до $16{,}87 \times 10^6$ кл.·г$^{-1}$, биомасса — от 7,76 до 36,39 мг·г$^{-1}$. Доля биомассы диатомовых водорослей в сырой массе всего мата *Cladophora* в среднем составила 1,06 %.

Ключевые слова: диатомовые водоросли, эпибионты, нитчатые зелёные водоросли, плавучие маты, гиперсолёное озеро

Supplement 1. Species composition and abundance of diatoms on *Cladophora* threads and in biogenic sediments (Lake Chersonesskoye, 26.07.2017)

Species	Sampling station and position in the *Cladophora* mats and bottom biogenic sediments													*FO*, %
	D1			*D2*			*E3*			*E4*				
	α	δ	ε	α	δ	η	α + δ	ε	η	α	δ	ε	η	
	Abundance *per* unit of *Cladophora* dry biomass and bottom biogenic sediments, $\times 10^4$ cells·g^{-1}													
Kingdom Chromista Phylum Ochrophyta Class Bacillariophyceae														
Achnanthes brevipes	–	–	6	–	–	–	–	–	3	–	–	–	–	15
Achnanthes longipes	–	–	–	–	–	–	–	–	–	2	–	4	7	23
Amphora sp. 1	–	5	–	–	–	–	–	–	–	–	–	–	–	8
Cocconeis kujalnitzkensis	1,039	6,506	1,970	731	3,882	1,187	1,982	910	19	37	421	195	435	100
Cyclotella caspia	–	–	–	–	248	46	–	–	–	–	–	–	7	23
Cylindrotheca closterium	6	–	70	–	–	65	–	–	–	–	–	–	–	23
Halamphora coffeiformis	10	20	70	54	175	–	–	15	74	10	3	7	3	85
Halamphora hyalina	–	–	122	86	769	122	–	–	–	–	–	–	4	38
Mastogloia braunii	–	–	96	17	180	91	53	53	45	125	349	100	189	85
Mastogloia lanceolata	–	–	–	–	116	–	–	–	–	–	–	–	1	15
Navicula cancellata	–	–	–	29	146	–	–	–	–	–	–	–	–	15
Navicula pennata var. *pontica*	–	–	–	123	96	26	–	–	–	–	–	–	–	23
Navicula ramosissima	–	36	141	51	589	150	–	–	–	–	–	–	–	38
Neosynedra provincialis	–	–	–	–	26	–	–	–	–	–	–	–	–	8
Nitzschia inconspicua	22	29	531	30	474	–	21	35	462	11	5	4	5	92
Nitzschia pusilla	–	–	–	177	–	–	–	–	–	–	1	–	–	15
Nitzschia sigma	–	–	–	–	–	–	–	–	2	–	–	–	–	8
Nitzschia tenuirostris	11	–	23	81	126	–	–	–	–	–	–	–	–	31
Parlibellus delognei	5	46	62	18	125	–	–	–	–	–	–	–	–	38
Thalassiosira eccentrica	11	–	–	–	–	–	–	–	–	–	–	–	–	8
Species number in a sample	7	6	10	11	13	7	3	4	6	5	5	5	8	–
Total abundance of diatoms in a sample, $\times 10^6$ cells·g^{-1}	11.05	66.43	30.91	13.98	69.52	16.87	20.56	10.12	6.05	1.85	7.79	3.11	6.52	–

Note: α, the upper layer of the floating mat; δ, the lower layer of the floating mat; ε, the algal layer under the floating mat; η, layer of bottom biogenic sediments; and *FO*, frequency of occurrence.

Supplement 2. Biomass of diatoms on *Cladophora* threads and in biogenic sediments (Lake Chersonesskoye, 26.07.2017)

Species	Sampling station and position in the *Cladophora* mats and bottom biogenic sediments												
	D1			*D2*			*E3*			*E4*			
	α	δ	ε	α	δ	η	α + δ	ε	η	α	δ	ε	η
	Biomass *per* unit of *Cladophora* dry biomass and bottom biogenic sediments, mg·g^{-1} (wet mass)												
Kingdom Chromista Phylum Ochrophyta Class Bacillariophyceae													
Achnanthes brevipes	–	–	0.27	–	–	–	–	–	0.11	–	–	–	–
Achnanthes longipes	–	–	–	–	–	–	–	–	–	0.05	–	0.38	0.42
Amphora sp. 1	–	0.23	–	–	–	–	–	–	–	–	–	–	–
Cocconeis kujalnitzkensis	20.88	155.94	58.20	16.47	93.52	24.15	42.50	17.18	0.39	0.50	7.09	3.97	8.22
Cyclotella caspia	–	–	–	–	0.28	0.43	–	–	–	–	–	–	0.03
Cylindrotheca closterium	0.006	–	0.12	–	–	0.07	–	–	–	–	–	–	–
Halamphora coffeiformis	0.06	0.08	0.28	0.18	0.83	–	–	0.70	3.17	0.37	0.11	0.27	0.05
Halamphora hyalina	–	–	4.34	3.21	26.56	4.70	–	–	–	–	–	–	0.18
Mastogloia braunii	–	–	7.32	1.15	10.73	6.09	3.28	3.83	3.35	6.82	32.28	5.69	12.62
Mastogloia lanceolata	–	–	–	–	10.76	–	–	–	–	–	–	–	0.11
Navicula cancellata	–	–	–	0.12	0.72	–	–	–	–	–	–	–	–
Navicula pennata var. *pontica*	–	–	–	0.47	0.43	0.60	–	–	–	–	–	–	–
Navicula ramosissima	–	0.10	0.36	0.06	1.67	0.35	–	–	–	–	–	–	–
Neosynedra provincialis	–	–	–	–	0.06	–	–	–	–	–	–	–	–
Nitzschia inconspicua	0.04	0.04	1.00	0.07	1.05	–	0.03	0.05	0.60	0.03	0.01	0.005	0.01
Nitzschia pusilla	–	–	–	0.23	–	–	–	–	–	–	0.001	–	–
Nitzschia sigma	–	–	–	–	–	–	–	–	0.15	–	–	–	–
Nitzschia tenuirostris	0.01	–	0.04	0.16	0.30	–	–	–	–	–	–	–	–
Parlibellus delognei	0.06	1.04	1.33	0.48	1.36	–	–	–	–	–	–	–	–
Thalassiosira eccentrica	0.18	–	–	–	–	–	–	–	–	–	–	–	–
Total biomass of diatoms, mg·g^{-1}	21.24	157.43	73.26	22.61	148.25	36.39	45.80	21.75	7.76	7.77	39.50	10.32	21.64

Note: α, the upper layer of the floating mat; δ, the lower layer of the floating mat; ε, the algal layer under the floating mat; and η, layer of bottom biogenic sediments.