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AUTECOLOGY OF BENTHIC DIATOM *STRIATELLA UNIPUNCTATA* (LYNGBYE) C. A. AGARDH, 1832 – INDICATOR OF ORGANIC WATER POLLUTION (BLACK SEA AND SEA OF JAPAN)

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Analysis of long-term data (1987–2019) was carried out on the morphology and autecology of the benthic colonial large-cell species *Striatella unipunctata* (Lyngbye) C. A. Agardh, 1832 in the microphytobenthos of the Black Sea and Sea of Japan, including water areas of specially protected natural areas of Russia. The species is widely found on natural and artificial substrates in the Black Sea year-round, and in the Sea of Japan, at a water temperature down to −1.5 °C. *St. unipunctata* quantitative data were determined by direct cell counting in the Goryaev camera under light microscopes (LMs) Biolam L-212, Axioskop 40, and Olympus BX41. Species morphology, phytogeography, and ecology are described. The cell size range of populations is presented: for the Black Sea, valves 25–148 μm long, 8–22 μm wide, frustules 36.3–50.4 μm wide, 18–24 fibulae in 10 μm, and 7–8 girdle bands in 10 μm; for the Sea of Japan, valves 85–125 μm long, 12–21 μm wide, 7–8 girdle bands in 10 μm, 20–25 fibulae in 10 μm, frustules 32.0–34.3 μm long, 10–11 μm wide, and 25 fibulae in 10 μm. For the first time, *St. unipunctata* valves and frustules were studied *in vivo* under LMs, and frustule ultrastructure, under a scanning electron microscope (SEM). For the first time, quantitative indicators of the species populations from the Black Sea and Sea of Japan were compared. The morphology of the frustule ultrastructure of *St. unipunctata* was studied under a Hitachi SEM, model SU3500 (Japan), in Leica EM ACE200 gold-palladium-coated samples. In the Kazachya Bay of the Black Sea near the Oceanarium, the absolute maximum abundance was recorded – $41.6 \cdot 10^3$ cells·cm^{-2} with a biomass of 1.73 mg·cm^{-2} in January (t = +6.9 °C) in the epizoon of the cultured mussel *Mytilus galloprovincialis* Lamarck, 1819 at a depth of 0.5 m at excessive organic pollution of water. The minimum values were of $0.26 \cdot 10^3$ cells·cm^{-2} and 0.011 mg·cm^{-2}, respectively, in July (t = +23.5 °C) at a depth of 2.5 m. In the Paris Bay (Russky Island) of the Sea of Japan in the water area of the Marine Mammal Research Base of the Primorsky Oceanarium (Vladivostok), the abundance in the asbestos plates periphyton was of $207 \cdot 10^3$ cells·cm^{-2} in the summer. For the first time, unique micrographs of the species *in vivo* were obtained under a LM, and of purified frustules – under a SEM.

Keywords: benthic diatom *Striatella unipunctata*, morphology, ecology, Black Sea, Sea of Japan

Large-cell diatoms, which have a high biomass, form large accumulations less often than small-cell species, which, under certain environmental conditions, more often reach a high abundance. The first ones include the benthic species *Striatella unipunctata* forming ribbon-like colonies, which are easily recognizable in a light microscope *in vivo* by the chloroplast rosettes resembling a flower. This work is the second communication, after the article on *Cylindrotheca closterium* populations from the Black Sea and Sea of Japan (Ryabushko et al., 2019b), devoted to the generalization of data on some pennate diatom species playing a significant role in coastal ecosystems. Both works are based on the study of morphological, ecological, and phytogeographical characteristics of the species composing microphytobenthos communities and are important in the analysis of the seasonal dynamics of the structure of their natural populations.

In publications on microphytobenthos, generalized data on the species composition, abundance, and biomass of algal communities are usually used. There are practically no data on separate species and their population indicators. Species peculiarities are often studied in cultures. Thus, in laboratory conditions, *St. unipunctata* was found to be dioecious, and reproductive process and auxospore formation were discovered; the latter is typical for diatoms alone (Davidovich & Chepurnov, 1993). So, the combination of the study of the species both from nature and when cultivated in the laboratory expands our understanding of its morphological and ecological peculiarities.

The aim of this study is to summarize long-term data on the morphology, autecology, and phytogeography of the diatom *Striatella unipunctata* (Lyngbye) C. A. Agardh, 1832 inhabiting the microphytobenthos of the Black Sea and Sea of Japan.

MATERIAL AND METHODS

Microphytobenthos was sampled in different ecotopes of the Black Sea and Sea of Japan in 1987–2019 at depths of 0.5–12 m (Fig. 1). The material from great depth was sampled by divers. *St. unipunctata* abundance and cell size were determined in a Goryaev's camera with a volume of 0.9 mm^3 in triplicates in a light microscope (hereinafter LM) Biolam L-212 at magnifications of 10×40×2.5 and 10×90×2.5, as well as in light microscopes C. Zeiss Axioskop 40 (with AxioVision Rel. 4.6 program) and Olympus BX41 UPLanF1 at magnification of 10×40.

The morphology of the ultrastructure of *St. unipunctata* frustules was studied in a Hitachi scanning electron microscope (hereinafter SEM), model SU. Diatom frustules were cleaned from organic matter by the "cold" method: processing with concentrated sulfuric acid followed by washing in distilled water (Ryabushko, 2013 ; Ryabushko & Begun, 2015). Micrographs were taken *in vivo* in the SEM.

Diatom abundance (N, cells·cm^{-2}) and biomass (B, mg·cm^{-2}) were determined by the formulas of V. I. Ryabushko (Ryabushko, 2013):

$$N = n \cdot V / S \cdot V_{\mathrm{h}} \,,$$

where n is the number of cells in the Goryaev's camera;

V is the sample volume, mL;

S is the surface area of the substrate, cm^2;

V_{h} is the volume of the Goryaev's camera equal to 0.9 mm^3;

$$B = h \cdot V \cdot b / S \cdot V_{\mathrm{h}} \,,$$

where h is algal specific gravity equal to $1.2 \cdot 10^{-9}$ mg·μm^{-3} for benthic diatoms (Oksiyuk & Yurchenko, 1971);

b is the sum of cell biovolumes in the Goryaev's camera.

The surface area of the stones (y, cm^2) was calculated by the formula of R. Calow (1972):

$$y = 2.22 + 0.26(d \cdot n)\,,$$

where d is the maximum length of the stone, cm;

n is the largest perimeter of the stone, cm.

The surface area of mussel shells (S, cm^2) was determined by the formula (Mikhailova et al., 1987):

$$S = 0.956 \cdot L^{2.085}\,,$$

where L is the distance from the shell anterior end to the posterior end, cm.

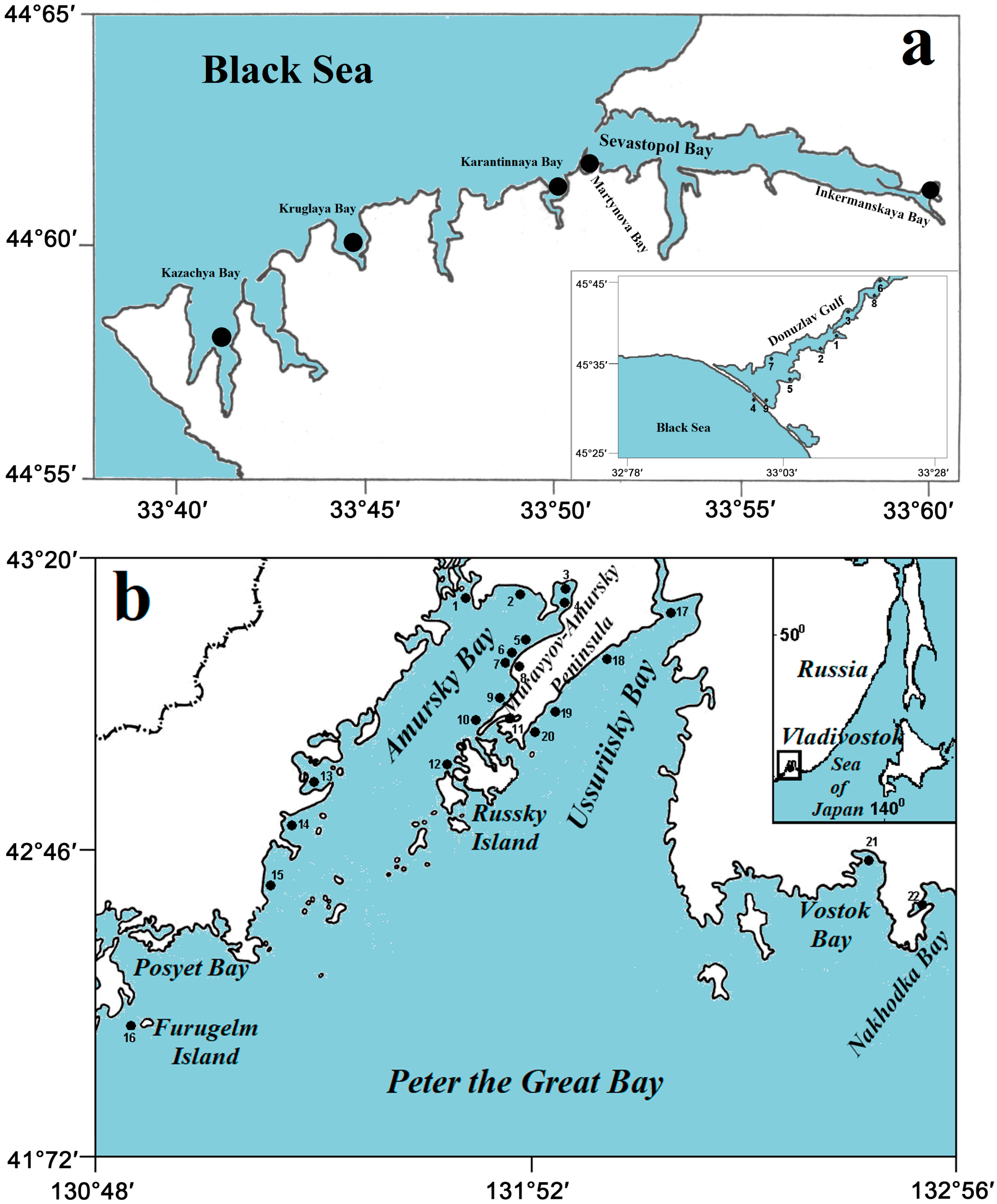

Fig. 1. Stations (●) of microphytobenthos sampling in the bays of the Crimean Peninsula, the Black Sea (a), and in Peter the Great Bay, the Sea of Japan (b)

The surface area of the macrophyte was calculated by the formula for the allometric dependence of the specific surface area of the macrophyte-basiphyte on the diameter of its thallus (Minicheva, 1989):

$$S/W = 3334/d^{0.916} \, ,$$

where S/W is the specific surface area of the macrophyte, $cm^2 \cdot g^{-1}$;

S is the surface area of the macrophyte, cm^2;

W is the wet weight of the macrophyte, g;

d is the diameter of macrophyte thallus, cm.

RESULTS

Morphology, ecology, and phytogeography of the large-celled attached colonial araphid diatom *Striatella unipunctata* (Lyngbye) C. A. Agardh, 1832 were investigated.

Taxonomy. According to the classification (Round et al., 1990), the species belongs to the class Fragilariophyceae, the order Striatellales Round, 1990, the family Striatellaceae Kützing, 1844, and the genus *Striatella* C. A. Agardh, 1832. The species has a broad synonymics, and its taxonomic formation dates back to the XIX century (basionym: *Fragilaria unipunctata* Lyngbye, 1819; synonyms: *Diatoma unipunctata* (Lyngbye) C. A. Agardh, 1824; *Achnanthes unipunctata* (Lyngbye) Carmichael ex Greville, 1827; *Achnanthes unipunctata* Greville, 1828; *Candollella unipunctata* (Lyngbye) Gaillon, 1833; *Tessella pedicellata* Dujardin, 1841; and *Tabellaria unipunctata* (Lyngbye) Schütt, 1896) (Guiry & Guiry, 2020).

Morphology. The description is given according to (Proshkina-Lavrenko, 1955 ; Hendey, 1964) with our additions. *St. unipunctata* cells are quadrangular-tabular (Figs 2 and 3) with cut corners; those are connected in zigzag or linear chains hanging on a long and thick mucilage stalk, with the help of which the species is attached to the substrate (Fig. 2b, c, e). Frustule is rather coarse, with numerous girdle bands, about 8 in 10 μm, with delicate cross fibulae along the edges. The septa are short, flat, about 4 in 10 μm; their free edge is thickened. Valves are linear-lanceolate with widely rounded ends (Fig. 5a); 38–115 μm in length; 8–18 μm wide. The fibulae are very delicate, in sidelong mutually intersecting rows, 18–22 in 10 μm (Fig. 5b). The axial field is linear, with an axial rib (Fig. 5c, d); at each its end, there is one large mucilage pore with rimoportulas [tubes penetrating through the valve and opening inside with the slit; those are indicated by arrows (Fig. 4)]. This allows maintaining the connection of the cell with the environment and attaching to the substrate with the help of a mucilage stalk (rimoportula). Chloroplasts are numerous, radially arranged in the form of a "flower" rosette (Fig. 2).

Micrographs (LM) of *St. unipunctata* cells and colonies found in the Black Sea and Sea of Japan *in vivo* are shown below (Figs 2 and 3). The cells are presented with a mucilage stalk for attaching to the substrate (Fig. 2b, d), which was previously noted by us in the glass plates periphyton in Karantinnaya Bay for another benthic diatom species: *Achnanthes armillaris* (O. F. Müller) Guiry, 2019 (= *Achnanthes longipes* C. Agardh) (Fig. 2e). SEM photographs of the frustule ultrastructure and valves of the Black Sea population are given as well (Figs 4 and 5).

The size range of *Striatella* cells from two seas varies as follows. For the Black Sea, valves are 25–148 μm in length, 8–22 μm wide; frustules are 36.3–50.4 μm wide, 18–24 fibulae in 10 μm (Proshkina-Lavrenko, 1955, 1963); 40–80 μm in length, 10–20 μm wide, 20–24 fibulae in 10 μm (Cleve-Euler, 1953); 60–130 μm in length, 20–36 μm wide (Hendey, 1964); 70–81 μm in length, 18–19 μm wide, 20–22 fibulae in 10 μm (Al-Yamani & Saburova, 2011). For the Sea of Japan, valves are 85–125 µm in length, 12–21 µm wide, 7–8 bands in 10 µm, 20–25 fibulae in 10 µm; frustules are 32–34.3 µm in length, 10–11 µm wide, 25 fibulae in 10 µm (Ryabushko & Begun, 2016). Many details of the thin ultrastructure of *St. unipunctata* frustule are not visible even at high magnification in the LM (Fig. 3a–f); however, these details are very clearly visible in the SEM. The frustules from the Black Sea are 63–66.2 in length (Figs 4 and 5).

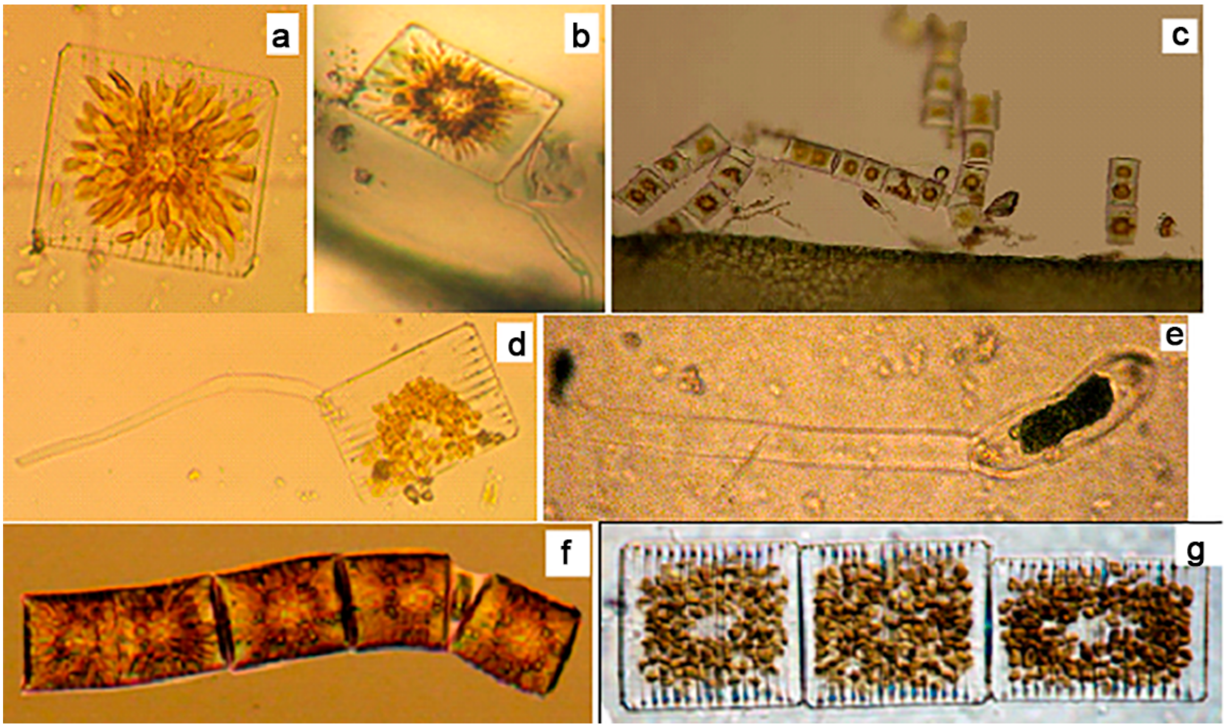

Fig. 2. Frustules of *Striatella unipunctata* with chloroplasts (a–g), cells on a mucilage stalk (b, d), diatom colonies in fouling of macrophyte (c), *Achnanthes armillaris* cell on a mucilage stalk (e), and colonies (f, g). Light microscope. The photos (b, c, e, f) by (Ryabushko, 2013)

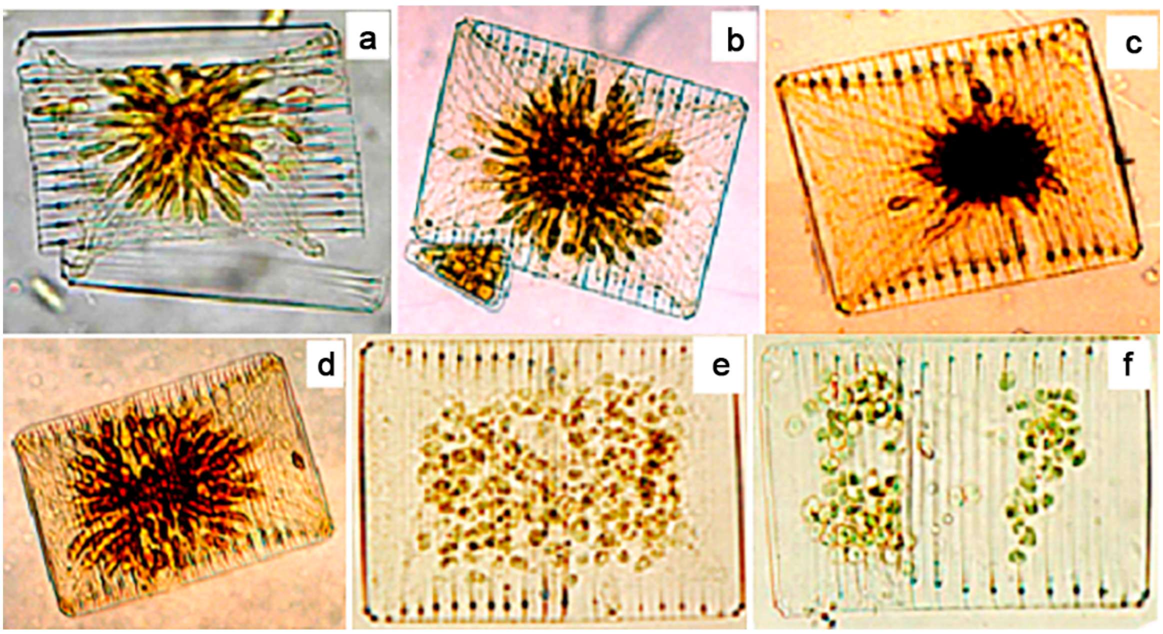

Fig. 3. *Striatella unipunctata* cells *in vivo* (a–d) and in dying state (e, f) with chloroplasts, the Sea of Japan. Light microscope (Ryabushko & Begun, 2016)

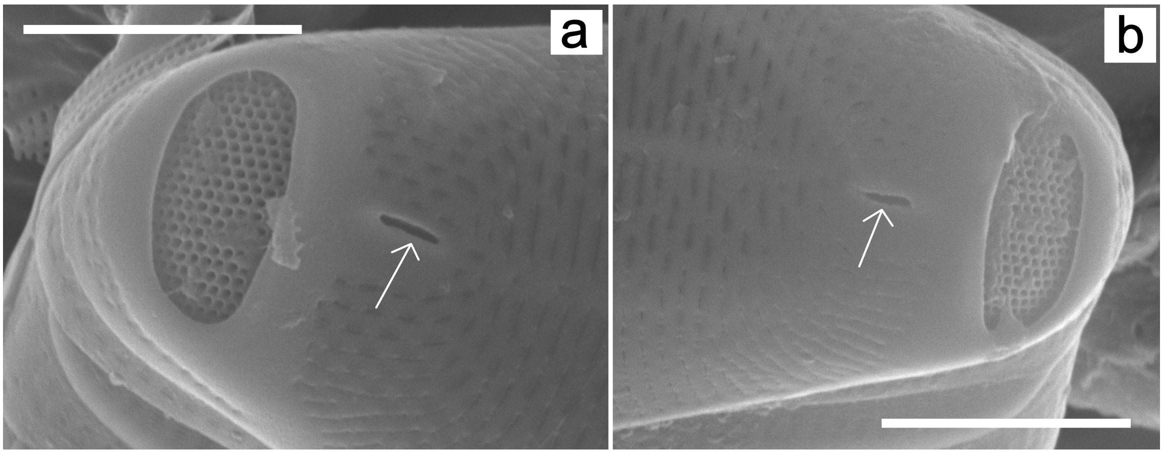

Fig. 4. Fragments of *Striatella unipunctata* external valve view (a, b) with rimoportulas indicated by arrows. SEM. Scale bar: 4 μm

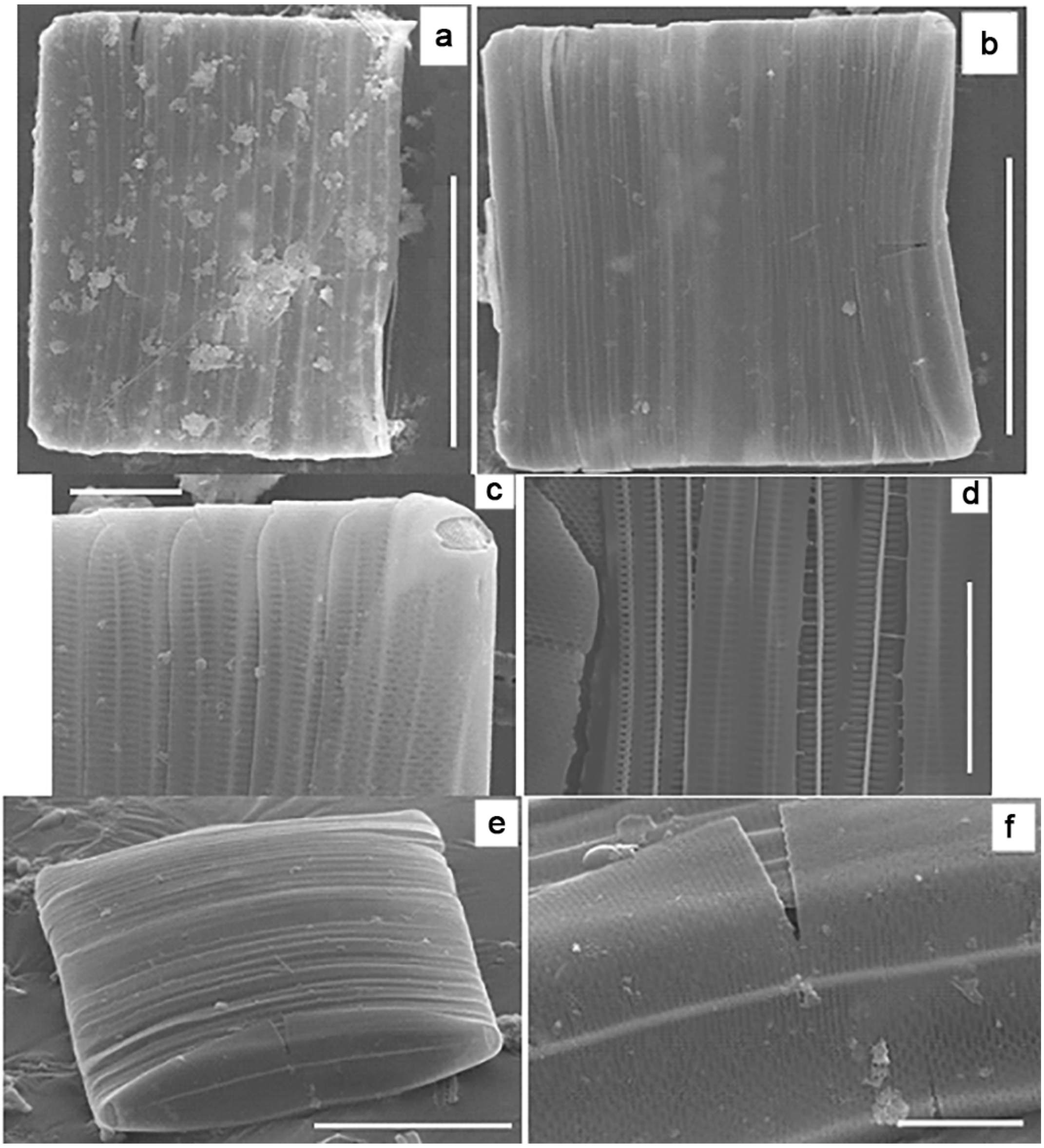

Fig. 5. *Striatella unipunctata* external frustules view with numerous girdle bands with a structure (a–f) and longitudinal axial of rib in the central area (e, f). SEM. Scale bars: 40 μm (a, b), 30 μm (e), 5 μm (c, d, f)

Phytogeography. The species is cosmopolite. It is known in the European seas of both the Northern and Southern hemispheres. The species is found in the Baltic, Barents, and North seas; in the Sea of Japan; in the Caribbean, Mediterranean, Marmara, Aegean, and Black seas; in the Sea of Azov; in Sivash, Bosporus, Great Britain, Ireland, Mexico, Sweden, Finland, the Netherlands, Denmark, Germany, Latvia, France, Kuwait, India, Australia, and New Zealand; and on the Atlantic coast of North America and the Bahamas (Proshkina-Lavrenko, 1955, 1963 ; Ryabushko, 2013 ; Ryabushko & Begun, 2016 ; Al-Yamani & Saburova, 2011 ; Guiry & Guiry, 2020 ; Hendey, 1964).

Ecology. *St. unipunctata* is marine, benthic, eurythermal, euryhaline, and sublittoral species. It is recorded at salinity above 10 ‰ in bays and near the shores of the open sea, rarely in the northwestern Black Sea; in the Crimean coastal area, it is found all year round (Kucherova, 1957 ; Ryabushko, 1994, 2013). In the benthos of Vostok Gulf in the northwestern Sea of Japan, it was registered in the epilithon of stones in winter and summer at a depth of 0.5 m, as well as in the anthropogenic substrate periphyton (Begun, 2012 ; Ryabushko, 1984). In the coastal waters of Rhodes, the Aegean Sea, the species was first found in the epiphyton of the green alga *Bryopsis plumosa* (Hudson) C. Agardh, 1823 (Ryabushko et al., 2019a). It is recorded in plankton, epilithon of stones, and epiphyton of macrophytes of Great Britain (Hendey, 1964), Sweden, and Kuwait (Al-Yamani & Saburova, 2011 ; Kuylenstierna, 1989).

In the microphytobenthos of the coastal waters of the Crimean Black Sea, the study of *St. unipunctata* started in 1987 and was episodic (Ryabushko, 2013). In August 1988, during an emergency discharge of domestic wastewater in the Kalamitsky Bay near the city beach adjacent to Saki Lake, while studying diatoms in the epiphyton of red, brown, and green macrophytic algae at depths of 1.5–12 m at a water temperature of +23 °C, water bloom was registered for the first time, which was caused by the abundant colonies of *St. unipunctata* (Ryabushko, 1997). Other species of pennate diatoms were found as well: from the genera *Amphora* Ehrenberg ex Kützing, 1844, *Cylindrotheca* L. Rabenhorst, 1859, *Licmophora* C. A. Agardh, 1827, *Navicula* Bory, 1822, *Nitzschia* A. H. Hassall, 1845, and *Pleurosigma* W. Smith, 1852. The composition of microalgae at all depths was not very diverse, and those were not abundant. Colonies of *St. unipunctata* were the most abundant out of the colonies of all species, but the greatest abundance was recorded at depths of 2–10 m in the epiphyton of the green alga *Cladophora albida* (Nees) Kützing, 1843 and the brown alga *Feldmannia lebelii* (Areschoug) Hamel, 1939. At a depth of 10 m, *Striatella* frustule was of 44.8–128.8 µm in length and 36.3–50.4 µm wide.

In the relatively clean open coastal waters of the Crimean Black Sea, *St. unipunctata* was less common. In February and November 1990 in Tebenkov Bay (Sevastopol) at a depth of 0.5 m and t = +6 °C, the species was recorded on thalli of *Ericaria crinita* (Duby) Molinari & Guiry, 2020 (= *Cystoseira crinita* Duby, 1830). In April 1998 in Kazachya Bay at 4.5 m and t = +15 °C, the species was registered on thalli of the red alga *Ceramium rubrum* (Hudson) C. Agardh, 1811 (Ryabushko, 2013).

When studying the epiphyton of 15 species of red, brown, and green macrophytic algae in May and August 1990 in the open coastal area of the sea near Omega Cape and in the area of the sanatorium beach at the Kruglaya Bay mouth, not subject to strong anthropogenic impact, no mass development of this alga was noted (Ryabushko, 1996). *St. unipunctata* was found in small abundance only in five out of them. For the first time, quantitative estimates of its abundance were obtained in the epiphyton as follows: of the red algae *Laurencia papillosa* (Forsskål) Greville, 1830 at a depth of 10 m – 200 cells·cm^{-2}, *Phyllophora crispa* (Hudson) P. S. Dixon, 1964 at 20 m – 280 cells·cm^{-2};

of the brown algae *E. crinita* at 5 m – 30 cells·cm^{-2}, *Stilophora rhizodes* (C. Agardh) J. Agardh, 1841 – 110 cells·cm^{-2}; and the green alga *Ulva rigida* C. Agardh, 1823 at a water's edge – 20 cells·cm^{-2}.

Quantitative data on the abundance and biomass of *Striatella* populations in various ecotopes of the coastal waters of the Crimean Black Sea are given below (Tables 1–3).

In the Kazachya Bay April to June 1995 at a depth of 0.5 m, *St. unipunctata* was found on thalli of various macrophytes: *Ulva rigida*, *Enteromorpha prolifera* (O. F. Müller) J. Agardh, 1883, *Chaetomorpha linum* (O. F. Müller) Kützing, 1845, *Sphacelaria cirrosa* (Roth) C. Agardh, 1824, *Ectocarpus siliculosus* (Dillwyn) Lyngbye, 1819, *E. crinita*, *C. rubrum*, and *Laurencia coronopus* J. Agardh, 1852, as well as on the leaves of the eelgrass *Zostera marina* Linnaeus, 1753. Moreover, in 1995–1996 at depths of 0.5–4.5 m in the same bay, annual and seasonal dynamics of the quantitative distribution of *St. unipunctata* populations was studied on the epiphyton of macrophytes and epizoon of shells of the live mussel *Mytilus galloprovincialis* Lamarck, 1819 (Table 1) in the spots with high content of biogenic elements (Ryabushko, 2013). The abundance and biomass of cells ranged 0.26·10^3 to 41.6·10^3 cells·cm^{-2} and 0.011 to 1.73 mg·cm^{-2}. The absolute maximum values were recorded on 29.01.1996 at a water temperature of +6.9 °C with average values of 5.08·10^3 cells·cm^{-2} and 0.21 mg·cm^{-2}. *Striatella* minimum abundance (0.63·10^3 cells·cm^{-2}) and biomass (0.093 mg·cm^{-2}) were registered in the mussel epizoon on 28.11.1995 at a depth of 0.5 m at +12 °C (Table 1).

Table 1. Abundance (N) and biomass (B) of *Striatella unipunctata* populations in different ecotopes of the Kazachya Bay of the Crimean coastal waters of the Black Sea

Sampling date	Ecotope	Depth, m	Temperature, °C	N, ×10^3 cells·cm^{-2}	B, mg·cm^{-2}
17.11.1987	Epiphyton of *Gracilaria verrucosa*	1.0	13.1	often	
17.12.1987	–″–	4.0	10.3	single	
21.01.1988	–″–	4–5	8.2	–″–	
26.01.1988	Epiphyton of *Zostera marina*	1–3	8.2	–″–	
24.02.1988	–″–	–″–	6.0	–″–	
02.03.1988	–″–	–″–	8.0	1.25	0.052
16.03.1988	Epiphyton of *Gr. verrucosa*	–″–	8.0	0.90	0.037
13.04.1988	–″–	5–7	13.0	single	
04.07.1988	–″–	–″–	17.0	–″–	
18.04.1995	Epizoon of mussel	0.5	9.6	–″–	
26.04.1995	–″–	–″–	10.5	9.14	0.38
–″–	Epilithon of stones	–″–	16.0	single	
12.05.1995	Epizoon of mussel	–″–	17.5	1.78	0.074
–″–	Epiphyton of *Ulva rigida*	–″–	–″–	single	
–″–	Epiphyton of *Ceramium rubrum*	–″–	–″–	single	
–″–	Epilithon of stones	–″–	–″–	single	
–″–	Epizoon of mussel	–″–	–″–	1.65	0.070
05.06.1995	–″–	–″–	21.0	3.26	0.14

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Sampling date	Ecotope	Depth, m	Temperature, °C	N, $\times10^3$ cells·cm^{-2}	B, mg·cm^{-2}
–″–	–″–	–″–	–″–	1.51	0.063
–″–	Epiphyton of *C. rubrum*	–″–	–″–	single	
–″–	Epiphyton of *Chaetomorpha linum*	–″–	–″–	–″–	
–″–	Epiphyton of *Ericaria crinita*	–″–	–″–	–″–	
–″–	Epiphyton of *Ectocarpus confervoides*	–″–	–″–	–″–	
–″–	Epiphyton of *Enteromorpha prolifera*	–″–	–″–	–″–	
–″–	Epiphyton of *U. rigida*	–″–	–″–	–″–	
29.06.1995	Epizoon of mussel	–″–	22.8	0.91	0.038
–″–	Epiphyton of *Ch. linum*	–″–	–″–	single	
–″–	Epiphyton of *E. prolifera*	–″–	–″–	1.50	0.062
27.07.1995	Epizoon of mussel	2.5	23.5	0.96	0.040
–″–	–″–	–″–	–″–	0.33	0.014
–″–	–″–	–″–	–″–	0.26	0.011
01.08.1995	–″–	2.0	24.0	single	
29.08.1995	–″–	0.5	23.5	1.22	0.050
–″–	–″–	–″–	–″–	1.10	0.046
–″–	–″–	–″–	–″–	single	
–″–	Epiphyton of *Ericaria crinita*	–″–	–″–	–″–	
27.09.1995	Epizoon of mussel	–″–	19.0	1.19	0.049
–″–	–″–	2.5	–″–	0.76	0.032
25.10.1995	–″–	0.5	15.0	7.74	0.052
–″–	–″–	2.5	–″–	1.0	0.042
–″–	Epiphyton of *Sphacelaria cirrosa*	0.5; 4.5	–″–	single	
28.11.1995	Epizoon of mussel	0.5	12.0	2.23	0.093
–″–	–″–	–″–	–″–	0.63	0.026
26.12.1995	–″–	–″–	9.2	1.60	0.066
29.01.1996	–″–	–″–	6.9	41.6	1.730
–″–	–″–	–″–	–″–	0.96	0.040
–″–	–″–	2.5	–″–	2.43	0.100
05.03.1996	–″–	0.5	6.8	1.73	0.072
–″–	–″–	–″–	–″–	2.06	0.086
–″–	–″–	2.5	–″–	4.32	0.180
–″–	–″–	–″–	–″–	3.40	0.141
25.03.1996	–″–	0.5	7.7	6.25	0.259
–″–	–″–	–″–	–″–	1.14	0.047
–″–	–″–	2.5	–″–	1.87	0.050
–″–	–″–	–″–	–″–	3.50	0.150
–″–	–″–	–″–	–″–	2.87	0.120
–″–	–″–	4.5	–″–	2.07	0.086

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Sampling date	Ecotope	Depth, m	Temperature, °C	N, ×10³ cells·cm⁻²	B, mg·cm⁻²
–″–	–″–	–″–	–″–	1.39	0.057
–″–	–″–	–″–	–″–	2.73	0.113
25.04.1996	–″–	2.5	10.5	6.64	0.276
–″–	–″–	–″–	–″–	4.51	1.187
–″–	–″–	–″–	–″–	6.64	0.28
27.05.1996	–″–	–″–	18.7	4.64	0.192
–″–	–″–	–″–	–″–	2.73	0.113
–″–	–″–	–″–	–″–	1.22	0.051
–″–	–″–	2.5	–″–	2.89	0.120
–″–	–″–	–″–	–″–	1.56	0.064
–″–	–″–	4.5	–″–	1.98	0.082
–″–	–″–	–″–	–″–	1.67	0.069
26.09.2003	–″–	–″–	20.0	single	
23.01.2004	–″–	–″–	7.1	colonies	

The research was continued in 2018–2019 when studying the epilithon of stones and the epiphyton of macrophytes in Donuzlav Gulf (Western Crimea), as well as in Inkerman and Karantinnaya bays within Sevastopol (Tables 2 and 3). In the epilithon of Donuzlav Gulf during the annual cycle at depths of 0.1–1.0 m and at a water temperature range from +9.0 °C (December) to +26.4 °C (July), *Striatella* maximum abundance was recorded in July in the spots of pollution by domestic wastewater, where high values of BOD_5, water oxidizability, nitrates, and phosphates were observed (Ryabushko et al., 2019c). In Inkerman Bay, similar abundance and biomass values were recorded in April and July.

Table 2. Dependence of abundance (N) and biomass (B) of *Striatella unipunctata* in the epilithon of Donuzlav Gulf and Inkerman Bay on environmental factors (Crimea, the Black Sea)

Sampling date	Depth, m	Temperature, °C	Salinity, ‰	N, ×10³ cells·cm⁻²	B, mg·cm⁻²
Donuzlav Gulf					
13.04.2018	0.5	11.0	17.81	2.54	0.01
21.06.2018	1.0	24.4	18.54	1.65	0.011
12.07.2018	0.5	26.4	18.62	5.47	0.065
05.10.2018	0.2	19.8	16.58	2.33	0.02
08.04.2019	–″–	10.6	17.97	2.74	0.02
21.06.2019	0.5	25.3	13.86	1.71	0.046
11.07.2019	–″–	24.6	15.67	0.43	0.001
09.10.2019	1.0	15.9	17.71	2.27	0.016
Inkerman Bay					
24.12.2018	0.3	9.0	16.76	1.34	0.005
25.04.2019	0.1	10.0	16.50	3.58	0.025
25.05.2019	–″–	20.0	13.31	2.05	0.017
08.07.2019	–″–	26.0	12.86	3.88	0.008

For comparison with the epilithon data, the results are presented of studying *Striatella* morphology and quantitative characteristics in epiphyton of 15 species of red, brown, and green macrophytes and eelgrass *Zostera marina* from Donuzlav Gulf and Karantinnaya Bay for 2018–2019 at depths of 0.1–12 m (Table 3).

Table 3. Dependence of abundance (N) and biomass (B) of *Striatella unipunctata* in the epiphyton of Donuzlav Gulf and Karantinnaya Bay on environmental factors (Crimea, the Black Sea)

Sampling date	Macrophyte-basiphyte	Depth, m	Temperature, °C	Salinity, ‰	N, $\times10^3$ cells·cm^{-2}	B, mg·cm^{-2}
Donuzlav Gulf						
13.04.2018	*Ericaria crinita*	0.5	11.0	17.81	4.06	0.01
19.06.2018	–″–	0.3	23.4	18.66	1.53	0.05
20.06.2018	–″–	0.5	25.0	18.52	2.62	0.005
–″–	*Zostera marina*	–″–	–″–	–″–	single	–
12.07.2018	–″–	4.0	26.0	18.62	single	–
05.10.2018	–″–	0.2	19.8	16.58	1.63	0.06
–″–	*E. crinita*	–″–	–″–	–″–	2.87	0.003
27.05.2018	*Gongolaria barbata*	–″–	20.7	15.56	0.34	0.004
Karantinnaya Bay						
18.05.2018	*Chaetomorpha chlorotica*	0.1	18.0	17.70	2.32	0.01
08.06.2018	*Cladophora liniformis*	–″–	22.6	18.0	0.46	0.014
11.09.2018	*G. barbata*	0.1	22.6	18.0	0.99	0.003
28.02.2019	–″–	0.2	3.4	17.10	0.91	0.001
04.03.2019	*Cl. liniformis*	4.5	10.0	17.24	0.1	0.002
–″–	*Ulva linza*	–″–	–″–	–″–	1.1	0.03
–″–	*Polysiphonia denudata*	–″–	–″–	–″–	0.06	0.001
05.04.2019	*Cl. liniformis*	1.5	10.6	17.70	14.2	0.10
–″–	*Ceramium arborescens*	–″–	–″–	–″–	14.0	0.08
Mussel and oyster farm in Karantinnaya Bay						
20.07 2018	*Nereia filiformis*	12.0	25.0	18.03	3.1	0.014
08.02.2019	*Laurensia coronopus*	4.0	3.4	16.88	4.2	0.10
04.03.2019	*Callithamnion corymbozum*	6.0	10.0	18.0	0.90	0.01
–″–	*Bryopsis plumosa*	–″–	–″–	–″–	17.7	0.10
–″–	*Pyaiella littoralis*	–″–	–″–	–″–	0.6	0.008
04.04.2019	*Ulva clathrata*	3.0	9.8	17.70	1.0	0.006
–″–	*C. arborescens*	–″–	–″–	–″–	1.6	0.03
–″–	*Ulva compressa*	–″–	–″–	–″–	13.3	0.20
–″–	*P. littoralis*	–″–	–″–	–″–	4.0	0.10
14.05.2019	*Feldmannia paradoxa*	2.0	15.2	18.07	7.2	0.27

Striatella reached the highest abundance values of $13.3 \cdot 10^3$ and $14 \cdot 10^3$ cells·cm^{-2} in April in Karantinnaya Bay in the epiphyton of *Ulva compressa*, *Cladophora liniformis*, and *Ceramium arborescens*, with maximum value of $17.7 \cdot 10^3$ cells·cm^{-2} in March on thalli of the green alga *Bryopsis plumosa*.

The data were obtained from the latest sampling of communities of diatoms and cyanobacteria in the epilithon of stones near the beach of Karantinnaya Bay on 12.11.2019 (t = +15 °C; water salinity of 18.5 ‰; depth of 0.3 m) and on a mussel and oyster farm in the same bay on 19.12.2019 (t = +11.2 °C; 17.2 ‰; depth of 0.1 m). The samples showed abundant winter development of *Striatella* colonies along with cyanobacteria. In the quantitative distribution of the species, mosaic structure was observed; the abundance varied 629 to 3383.4 cells·cm^{-2}; the biomass, 0.013 to 0.077 mg·cm^{-2}. At the same time, the species abundance in December was 5.4 times higher than in November.

For comparison with the data for the Black Sea, similar results are presented of *St. unipunctata* study in the microphytobenthos of the northwestern Sea of Japan. The species was registered in different ecotopes: on 10.11.1983 in the epilithon of stones in the Vityaz and Astafyev bays of the Posyet Bay at a depth of 0.2 m (Nikolaev, 1970, 1976); in summer in Vostok Gulf and in winter in Vityaz Bay at a depth of 0.5 m (Ryabushko, 1984, 2014 ; Ryabushko & Begun, 2016); in periphyton, epiphyton of macrophytes, and epizoon of molluscs in Amursky, Ussuriisky, Vostok, and Slavyanka gulfs, in the Golden Horn, Rynda, and Baklan bays, as well as in the epiphyton of the red alga *Mastocarpus stellatus* (Stackhouse) Guiry, 1984 in March 2014 in Troitsa Bay of Posyet Bay at depths of 3–6 m at a water temperature of −1.5 °C. In the periphyton of navigation buoys in the Troitsa Bay (the seaport area contaminated with petroleum products) on 22.11.2011 at depths of 0–8 m, the abundance was of $2.33 \cdot 10^3$ and $31.8 \cdot 10^3$ cells·g^{-1}, respectively (Ryabushko & Begun, 2016).

Moreover, the results were obtained of the species abundance for a 15-day exposure in the periphyton of Rynda Bay on 02.08.2000 on substrates made of plexiglass ($0.6 \cdot 10^3$ cells·cm^{-2}), wood ($20 \cdot 10^3$ cells·cm^{-2}), high-alloy steel ($0.15 \cdot 10^3$ cells·cm^{-2}), and asbestos cement ($0.3 \cdot 10^3$ cells·cm^{-2}), as well as in the epizoon of bay barnacle *Amphibalanus improvisus* (Darwin, 1854), mussel *Mytilus trossulus* Gould, 1850, ascidians *Aplidium tenuicaudum* (Beniaminson, 1974), and *Styela clava* Herdman, 1881 ($0.84 \cdot 10^3$ cells·cm^{-2}) and in the epiphyton of green and brown algae ($1.45 \cdot 10^3$ and $1.01 \cdot 10^3$ cells·g^{-1} of the wet weight of the macrophyte) (Begun, 2012 ; Ryabushko & Begun, 2015, 2016). In the periphyton of asbestos cement plates exposed on 02.07.2013–06.08.2013 in the Paris Bay (Russky Island) in the water area of the Marine Mammal Research Base of the Primorsky Oceanarium of the National Scientific Center of Marine Biology FEB RAS at depths of 0.5–5 m, high values of *Striatella* abundance were obtained: $177.3 \cdot 10^3$ to $207 \cdot 10^3$ cells·cm^{-2}.

DISCUSSION

In the literature sources, *St. unipunctata* is noted in the phytoplankton of the seas (Konovalova, 1984 ; Morozova-Vodyanitskaya, 1948 ; Orlova, 1984 ; Pautova, 1984 ; Pitsyk, 1963 ; Proshkina-Lavrenko, 1955 ; Ryabushko et al., 2004), Eastern Sivash, and Molochnyi Lyman (Ivanov, 1960). This is explained as follows: after being detached from the substrate due to a storm or another sea disturbance or due to death, cells can float into the water column. Therefore, in shallow seawater, when sampling with a bathometer, the species is often registered in the phytoplankton. Z. Kucherova (1957) classified *Striatella* as a year-round benthos species of the Black Sea. Our research confirmed these data.

She registered single cells on the shell surface of the mussel *Mytilus galloprovincialis* in the Sevastopol Bay at a depth of 1 m and in the Ayu-Dag area at 45 m, as well as at a depth of 4 m on the shell of a grass crab inhabiting thickets of macrophytes (Kucherova, 1960).

The first data on *St. unipunctata* abundance in the epiphyton of *Gongolaria barbata* (= *Cystoseira barbata*) in the Kazachya Bay can be found in (Makkaveeva, 1960). In August 1955 at +22.5 °C, the abundance was of $11.9{\cdot}10^3$ cells$\cdot$cm^{-2}; in September at +19.5 °C, the value was of $1.8{\cdot}10^3$ cells$\cdot$cm^{-2}; in October at +17.0 °C, the abundance was of $55.4{\cdot}10^3$ cells$\cdot$cm^{-2}. That information was supplemented by our data on the settlement of various ecotopes in different seasons of the year at depths of 0.1–12 m. *Striatella* size range depends on the life cycle of alga, type of substrate, season of the year, water temperature, and abundance of biogenic elements in habitats. In spring, the species plays a significant role on anthropogenic substrates: glass plates exposed in the sea (Ryabushko, 2013). Also, the species reached high abundance in Karantinnaya Bay in April in the epiphyton of *Ulva compressa*, *Cladophora liniformis*, and *Ceramium arborescens*; the maximum value of $17.7{\cdot}10^3$ cells$\cdot$cm^{-2} was recorded in March on thalli of the green alga *Bryopsis plumosa*. The minimum values of abundance and biomass in the Black Sea were noted both in winter and summer. In summer on the epiphyton of macrophytes and epizoon of mussel, these indicators decreased, species populations were in a depressed state, and the cells were found singularly.

In the microphytobenthos of the Black Sea and the Sea of Japan, the species is widely registered on natural and artificial substrates (Ryabushko et al., 2018). In the Sea of Japan in the periphyton of various anthropogenic substrates, the highest abundance was recorded on wood (Begun, 2012); that was noted by other authors as well (Bangqin et al., 1989). According to our data, *Striatella* predominantly inhabits the surface of different macrophytes, and its colonies are found in masse in the spots where domestic wastewater is discharged and biogenic pollution increases. Therefore, *St. unipunctata* is classified as an indicator species for the saprobity of organic pollution of the Black Sea water (Ryabushko, 2013, 1997).

Conclusion. A retrospective analysis of long-term own and published data was carried out on various aspects of studying the benthic marine araphid attached pennate diatom *St. unipunctata* inhabiting different ecotopes of the Black Sea and the Sea of Japan. By phytogeographical affiliation, the species is cosmopolite. In the Sea of Japan, the species was recorded at a water temperature down to −1.5 °C. In two seas, the size ranges of cells overlap. In general, regardless of the depth, season, and ecotope inhabited, the species abundance is higher in water with excessive organic pollution, including the spots where molluscs are grown and mammals are kept in oceanariums. *Striatella* predominantly inhabits the surface of benthic vegetation, stones, and mollusc shells; this allows the species to form abundant colonies, which can detach from the substrate and penetrate in the phytoplankton because of the sea waves.

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АУТЭКОЛОГИЯ БЕНТОСНОЙ ДИАТОМОВОЙ ВОДОРОСЛИ *STRIATELLA UNIPUNCTATA* (LYNGBYE) C. A. AGARDH, 1832 — ИНДИКАТОРА ОРГАНИЧЕСКОГО ЗАГРЯЗНЕНИЯ ВОД (ЧЁРНОЕ И ЯПОНСКОЕ МОРЯ)

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Впервые проведён анализ многолетних данных (1987–2019) изучения морфологии и аутэкологии бентосной колониальной диатомовой водоросли *Striatella unipunctata* (Lyngbye) C. A. Agardh, 1832, обитающей в микрофитобентосе Чёрного и Японского морей, включая акватории заповедных и особо охраняемых природных территорий России. Вид широко встречается на природных и искусственных субстратах в Чёрном море круглогодично, в Японском море зарегистрирован при температуре воды до −1,5 °C. Количественные данные *St. unipunctata* определяли прямым подсчётом клеток в камере Горяева, используя световые микроскопы (СМ) типа Биолам Л-212, Axioskop 40 и Olympus BX41. Морфология ультраструктуры панциря *St. unipunctata* изучена в сканирующем электронном микроскопе (СЭМ) Hitachi SU3500 в образцах с золотопалладиевым напылением Leica EM ACE200. Представлен размерный диапазон клеток популяций: для Чёрного моря — створки 25–148 мкм длины, 8–22 мкм ширины, панцири 36,3–50,4 мкм шир., 18–24 штрихов в 10 мкм, 7–8 вставочных ободков в 10 мкм; для Японского моря — створки 85–125 мкм дл., 12–21 мкм шир., 7–8 вставочных ободков в 10 мкм, 20–25 штр. в 10 мкм, панцири 32,0–34,3 мкм дл., 10–11 мкм шир., 25 штр. в 10 мкм. Впервые изучены створки и панцири *St. unipunctata* в прижизненном состоянии в СМ и ультраструктура панцирей в СЭМ. Приведено описание морфологии, фитогеографии и экологии вида. Впервые проведено сравнение количественных показателей черноморской и япономорской популяций вида. В Казачьей бухте Чёрного моря вблизи океанариума зарегистрирована абсолютная максимальная численность клеток — $41{,}6\cdot10^3$ кл.$\cdot$см$^{-2}$ при биомассе 1,73 мг$\cdot$см$^{-2}$ в эпизооне культивируемой мидии *Mytilus galloprovincialis* Lamarck, 1819 в январе (t = +6,9 °C) на глубине 0,5 м при избыточном органическом загрязнении вод.

Минимальные значения показателей составляли 0,26·10^3 кл.·см$^{-2}$ и 0,011 мг·см$^{-2}$ соответственно в июле (t = +23,5 °C) на глубине 2,5 м. В бухте Парис (остров Русский) Японского моря в акватории Базы исследования морских млекопитающих Приморского океанариума (г. Владивосток) максимальная численность в перифитоне достигала 207·10^3 кл.·см$^{-2}$. Впервые представлены снимки видов в прижизненном состоянии в СМ и очищенные панцири в СЭМ.

Ключевые слова: диатомовая водоросль *Striatella unipunctata*, морфология, экология, Чёрное море, Японское море