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Seasonal Dynamics of Microphytobenthos Distribution in Three Ecotopes on a Mussel Farm (Black Sea)

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Abstract: As the production of cultured bivalve mollusks is increasing worldwide, there is a growing need to study the biodiversity and ecology of microalgae in the mariculture zones. This study presents multiannual data (obtained in 2015–2016 and 2018–2020) on the species composition, abundance, biomass, and community structure of microphytobenthos from three mussel farm ecotopes (mussel shells, the epiphyton of twenty macroalgal species, and sediments under collectors). In total, 150 microalgal taxa were found, including 135 diatom species with a predominance of benthic (76%), marine (65%), and cosmopolite (30%) ones. In all habitats, 10 potentially harmful species and 44 indicators of organic pollution were noted. The maximum values on the mussel shells (abundance $N = 119 \times 10^3$ cells/cm^2 and biomass $B = 0.0489$ mg/cm^2) were recorded in winter with the dominance of *Tabularia fasciculata*; in summer, the epiphyton was on the brown alga *Nereia filiformis* ($N = 1001 \times 10^3$ cells/cm^2 and $B = 2.06$ mg/cm^2) with the dominance of toxic *Pseudo-nitzschia seriata*, on the red alga *Phyllophora crispa* ($N = 1118 \times 10^3$ cells/cm^2 and $B = 3.24$ mg/cm^2) with the dominance of *T. fasciculata*, and in sediments ($N = 104 \times 10^3$ cells/cm^3 and $B = 0.046$ mg/cm^3) with the dominance of *T. fasciculata* and *Bacillaria paxillifer*. Statistically significant effects of the ecotope and sampling season on the diatom composition were noted. The strongest effect of temperature is observed for the mussel shell diatoms, for which the trend of abundance and biomass increase in winter and their decrease in summer is most noticeable. But in sediments, the effect of the season is reflected only in the permanent changes of the microalgae species composition. For the epiphyton, it was shown that it is temperature, rather than substrate macrophyte species, that affects its numerical structure.

Keywords: microalgae diversity; diatoms; mussel farm; ecotopes; multivariate analysis; Black Sea

1. Introduction

Shellfish farming is currently becoming an increasingly popular form of aquaculture. According to the Food and Agriculture Organization of the UN, its production volume amounted to more than 20 million tons in 2020 [1]. The study of microalgae in farm areas is attracting the attention of ecologists because shellfish farming has a significant impact on the environment [2–6]. On mollusk farms, metabolites of cultivated mollusks and decomposition products of macrophytes accumulate in water and bottom sediments and can affect the species richness and quantitative characteristics of phytoplankton and microphytobenthos [7–11]. As a result, the concentration of organic matter increases, which can lead to an increase in the abundance of microalgae, including potentially toxic dinoflagellates [12–14] and diatoms [7,15–17], thus posing a threat to animals and humans who consume seafood [14,18–20]. The worldwide expansion of shellfish farming has led to an increasing number of observations of bivalves contaminated with saxitoxins and domoic and okadaic acids that cause human poisoning [21].

Another important reason for studying microalgae in farm areas is that they are the main food for benthic invertebrates, including bivalves, echinoderms, etc. [7,22–24]. For example, during the diatom bloom, the content of fatty acids in the soft tissues of cultivated oysters increased due to the increase in the contribution of planktonic and benthic food species [11]. Analysis of the gut contents of the oyster *Crassostrea gigas* and the clam *Ruditapes philippinarum* from a marine farm in Japan showed that benthic diatoms were the most abundant species in the diets of these mollusks [25]. It should be noted that some crustaceans, such as harpacticoid copepods, also feed on the diatoms of microphytobenthos [26].

Works on phytoplankton from shellfish farms are much more numerous [6,8,10,20,27–30] than on microphytobenthos. At the same time, it should be emphasized that microphytobenthos also plays an important role in mariculture [9,22,28,31,32]. For example, in the culture area in the Mediterranean Sea, it was shown that microphytobenthos in bottom sediments under mussel farms were the main primary producers during time periods when near-bottom phytoplankton were suppressed by the metabolic products of cultivated mussels, in contrast to a control station outside the farm where phytoplankton were more productive [9]. On the mussel farm in Carteau (Gulf of Fos, France), it was found that microphytobenthos production on the farm was higher (up to $500 \, mg/m^2$) in the cold season, while outside the farm its value did not exceed $175 \, mg/m^2$ [33].

It is reasonable to believe that the increasing number of marine farms will affect the ecology of benthic primary producers to a progressively greater extent. Therefore, the analysis of the quantitative characteristics of microalgal communities on shellfish farms is important for the detection of harmful algae and for water quality monitoring using indicator species of microalgae. Diatoms are the most widespread and best-studied benthic microalgae [7,34–36], and the accumulated knowledge of their ecology allows them to be successfully used for a water quality assessment [7,34,37,38].

Studies of the phytoplankton, microphytobenthos, and physicochemical parameters of the environment in the area of a mussel farm at the entrance to Karantinnaya Bay in the coastal waters of southwestern Crimea have been previously conducted both outside and inside the farm [7,31,39,40]. The present work is focused on the study of marine microphytobenthos biodiversity on a mussel farm in relation to different ecotopes (niches of microalgae occurrences) and seasons. Thus, the goal of this work was to assess differences in the composition and quantitative distribution of microphytobenthos in relation to the season, ecotope, and macrophyte species.

2. Materials and Methods

The farm for the cultivation of the indigenous mussel *Mytilus galloprovincialis* Lamarck, 1819 is located in the coastal waters of Crimea at the entrance to Karantinnaya Bay (Sevastopol, Black Sea), as shown in Figure 1.

2.1. Sample Processing in the Laboratory

Natural substrates on the farm suitable for microphytobenthos colonization included mussel shells, macrophytes, and sediments. Therefore, mussels and macrophytes were sampled to study microalgae inhabiting their surfaces (referred to as epiphyton in the case of macrophyte substrates), and sediments were sampled to study microalgae living in sand and silt on the seafloor of the farm. Microalgae were sampled from the surface of mussel shells and macroalgal thalli by scrubbing with a plastic brush and rinsing with filtered seawater into containers for identification and quantification. Microalgae from the sediments were isolated by repeated rinsing with filtered seawater and sedimentation. The collected samples were fixed with 4% formalin for further treatment. All samples were examined under a light microscope (LM), Axioskop 40 C. Zeiss (Jena, Germany), at the appropriate magnifications of 10×20, 10×40, and 10×100. For the more accurate identification of diatoms, scanning electron microscopy (SEM, Hitachi SU3500, Tokyo, Japan) was applied. The sample preparation for the examination was carried out according

to [41] in modification [42]. Cells of diatoms were counted under the microscope in a hemocytometer (Goryaev's chamber, LLC Minimed, Russian Federation, Bryansk, Russian) in three replicates for each sample. To quantify diatoms, only cells with intact chloroplasts were counted. The abundance (N, cells/cm^2 or cell/cm^3 for sediments) and biomass (B, mg/cm^2 or mg/cm^3 for sediments) of diatoms were calculated using the following relationships [7]:

$$N = \frac{n \cdot V}{S \cdot Vk},$$ (1)

where n is the number of cells in Goryaev's chamber (0.9 mm^3), V is the sample volume (mL), S is the surface area of mussel shells or macroalgal thallus examined (cm^2), and Vk is the volume of Goryaev's chamber (0.9 mm^3), and

$$B = \frac{h \cdot V \cdot b}{S \cdot Vk},$$ (2)

where b is the sum of diatom cell biovolumes in Goryaev's chamber, and h is the mass density equal to 1.2×10^{-9} mg/μm^3 for benthic diatoms. The volume of each cell was calculated from its size and shape using the geometric similarity method. The species richness (R) is the number of species that were observed in the hemocytometer when counting the diatom cells.
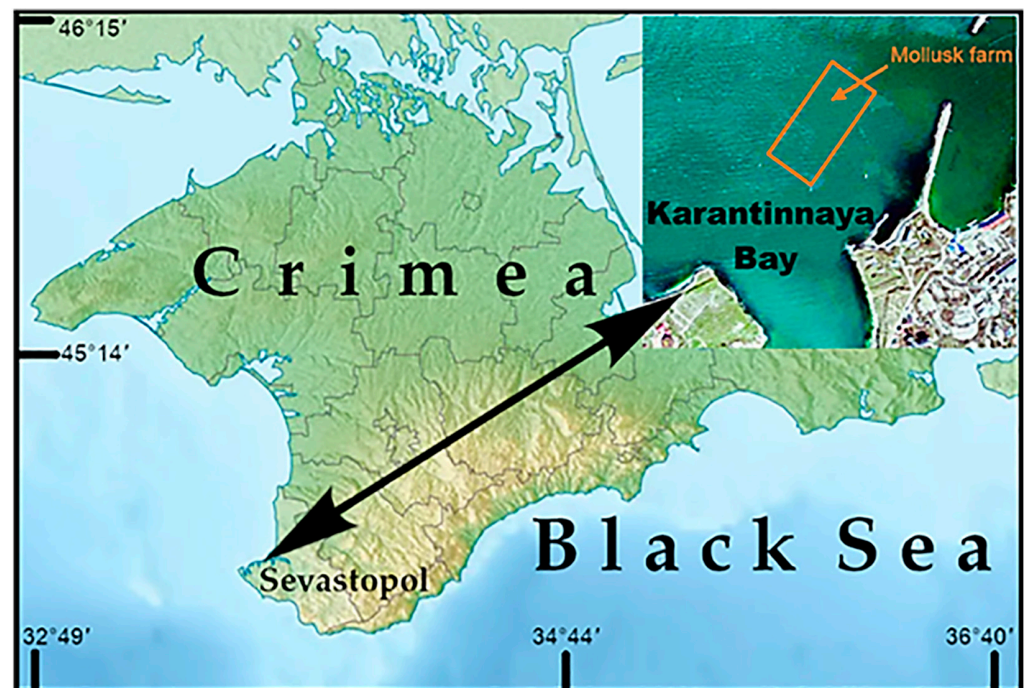

Figure 1. Map of the sampling site (mussel farm) at the entrance to Karantinnaya Bay (Black Sea).

The surface area of mussel shells (S) for the abundance and biomass was determined according to the following equation [43]:

$$S = 0.956 \, L^{2.085},$$ (3)

where L is the distance from the umbo to the posterior edge of the shell (along the dorsoventral axis). The shell length ranged from 29 to 87 mm. The specific surface area of the macroalgae with a cylindric thallus was calculated according to the allometric correlation with the thallus diameter [44]:

$$S/W = 3334/d^{0.916},$$ (4)

where S/W is the specific surface area of a macrophyte (cm^2/g), S is the surface area of the macroalgae, W is the wet weight (g), and d is the average thallus diameter (cm). The macrophyte thallus diameter was measured using a light microscope (with at least 10 measurements for each sample). For macroalgae with a planar thallus, S/W was calculated according to the allometric correlation with the thallus thickness [44]:

$$S/W = 2000/h^{0.988}, \tag{5}$$

where h is the mean value of the thickness of a transverse slice of the thallus (cm).

The classification system for diatoms was used in [45,46]. The relation of species to water salinity, geographical characteristics of microalgae, and saprobity indices of species (the ability of organisms to tolerate varying degrees of organic pollution of water) was determined as described in [7,23,38,40,47–49].

Analysis of the diatom community structure was carried out on the basis of information theory [50] using the Shannon diversity index (H) calculated using the binary logarithm [51], Pielou evenness index (e) [52], and the Bray–Curtis dissimilarity coefficient calculated for values of microalgal species abundance [53]. To compare the species composition from different ecotopes, the Sörensen–Dice (K_{SD}) [54,55] similarity index was calculated. In total, 84 microalgae samples from mussel shells, 36 samples of epiphyton microalgae, and 24 samples of sediment microalgae were processed.

2.2. Multivariate Statistics

Analysis of similarity (ANOSIM) and permutational multivariate analysis of variance (PERMANOVA) were applied to examine whether there were differences in the numerical structure or compositions of the diatom communities grouped according to certain attributes (ecotope, sampling season, substrate macrophyte species). The underlying null hypothesis was the similarity of the numerical structure or composition of the microphytobenthic communities in relation to season and ecotope, including substrate macrophyte species. For estimating the numerical structure of the communities, the abundances were log-transformed, and the Bray–Curtis similarity coefficients were calculated and further used. K_{SD} coefficients were used to find differences in the compositions of the diatom communities. Cluster analysis in the group average clustering mode was run along with the similarity profile (SIMPROF) routine to examine whether clusters of variables were coherently associated [56] at the 5% significance level.

Canonical analysis of principal coordinates (CAPs) is an ordination technique that employs principal coordinate analysis (metric multidimensional scaling) followed by either a canonical discriminant analysis (for testing effects of groups) or a canonical correlation analysis (for testing other variables) [57]. Only the effects of groups were examined using CAPs in the present study. The null hypothesis of this technique found no significant differences in multivariate location among groups. All analyses were run in PRIMER 6.1.16 and PERMANOVA + 1.0.6 [58] using 999 permutations per test, unless otherwise stated.

Redundancy analysis (RDA) performs principal component analysis on the response variables (log-transformed epiphytic diatom abundances) under the constraint that the produced canonical axes are also a linear combination of the explanatory variables (temperature, macrophyte species). The null hypothesis that follows from the statistics of this technique is that the linear relationship strength manifested in R^2 is not larger than that for uncorrelated explanatory and response variable matrices of the same size. In this work, RDA was carried out using the *f_rda* function from the Fathom Toolbox [59] in the Matlab 8.2.0 environment.

3. Results

In 2015–2016, the average salinity reached 17.9, and monthly fluctuations at the two depths (6 and 17 m) were comparable and did not exceed 0.4. The temperature during the year varied from 7.6 to 25.6 °C. In 2018–2020, the salinity in the farm area varied from 14.64 to 19.17, and the temperature ranged from 8.1 to 26.6 °C. Due to the fact that salinity

fluctuations were small, more attention was paid to the temperature in this study. The minimum and maximum values of the physicochemical parameters of seawater at the sampling site in 2015–2016 are given in Table 1 [39]. The trophic index (TRIX) values [39] ranged from 1.0 to 2.9, which allows classifying the water area as oligotrophic.

Table 1. Min-max values of seawater parameters registered at the sampling site in 2015–2016: temperature (t °C), salinity, dissolved oxygen O_2 (mL/L), pH, five-day biochemical oxygen demand BOD_5 (mg O_2/L), alkaline permanganate oxidizability Ox (mg O_2/L), nitrite NO_2, nitrate NO_3, ammonium NH_4, phosphate PO_4, silicate Si, organic phosphorus P_{org}, and organic nitrogen N_{org} (all in μM). BDL = below detection limit.

t °C	Salinity	O_2	pH	BOD_5	Ox	NO_2	NO_3	NH_4	PO_4	Si	P_{org}	N_{org}
7.6–25.6	17.65–18.24	5.01–7.69	8.14–8.47	0.11–2.62	1.45–3.69	BDL-0.33	BDL-5.83	0.34–4.26	BDL-0.76	0.59–12.6	0.054–1.15	14.7–343

The list of microphytobenthos includes 150 taxa from Bacillariophyta (135), Dinoflagellata (6), Haptophyta (4), Ochrophyta (2), and Cyanobacteria (3) in 2015–2016 and 2018–2020. Diatoms were represented by 62 genera, and the largest number of species in the genera were *Navicula* (10), *Nitzschia* (10), *Licmophora* (8), *Diploneis* (8), and *Amphora* (6). In addition, 10 potentially harmful diatom species, *Halamphora coffeiformis*, *Pseudo-nitzschia calliantha*, *P. delicatissima*, *P. pungens* and *P. seriata*, Dinoflagellata *Dinophysis fortii*, *Prorocentrum compressum*, *Pr. Cordatum*, *Pr. Micans*, and benthic *Pr. Lima*, were found (Table A1).

In all ecotopes on the farm, benthic species predominated (76%), but planktonic species (17%) inhabiting seafloor substrates were also noted. In relation to species to water salinity and phytogeography, marine (65%), brackish–marine (25%), cosmopolite (30%), boreal–tropical (24%), and arctical–boreal–tropical (16%) groups, including notal species, prevailed. Forty-four indicator species characterized by different degrees of saprobity were detected (Table A1). Images of some typical microalgae species from different ecotopes taken with light and scanning electron microscopes are presented in Figures 2 and 3.

For the mussel shells, epiphyton and sediments in 37 diatom species were common. These are mainly benthic species widespread in the microphytobenthos in the Black Sea coastal waters of Crimea. The analysis of the Sörensen–Dice similarity coefficient of the species composition of microalgal communities from the three ecotopes showed that the mussel shells and sediment microalgae have the closest similarity values (79%), the epiphyton and sediment microalgae have the least similar composition (43%), and the mussel shells and epiphyton species composition similarity was 51% (Figure 4).
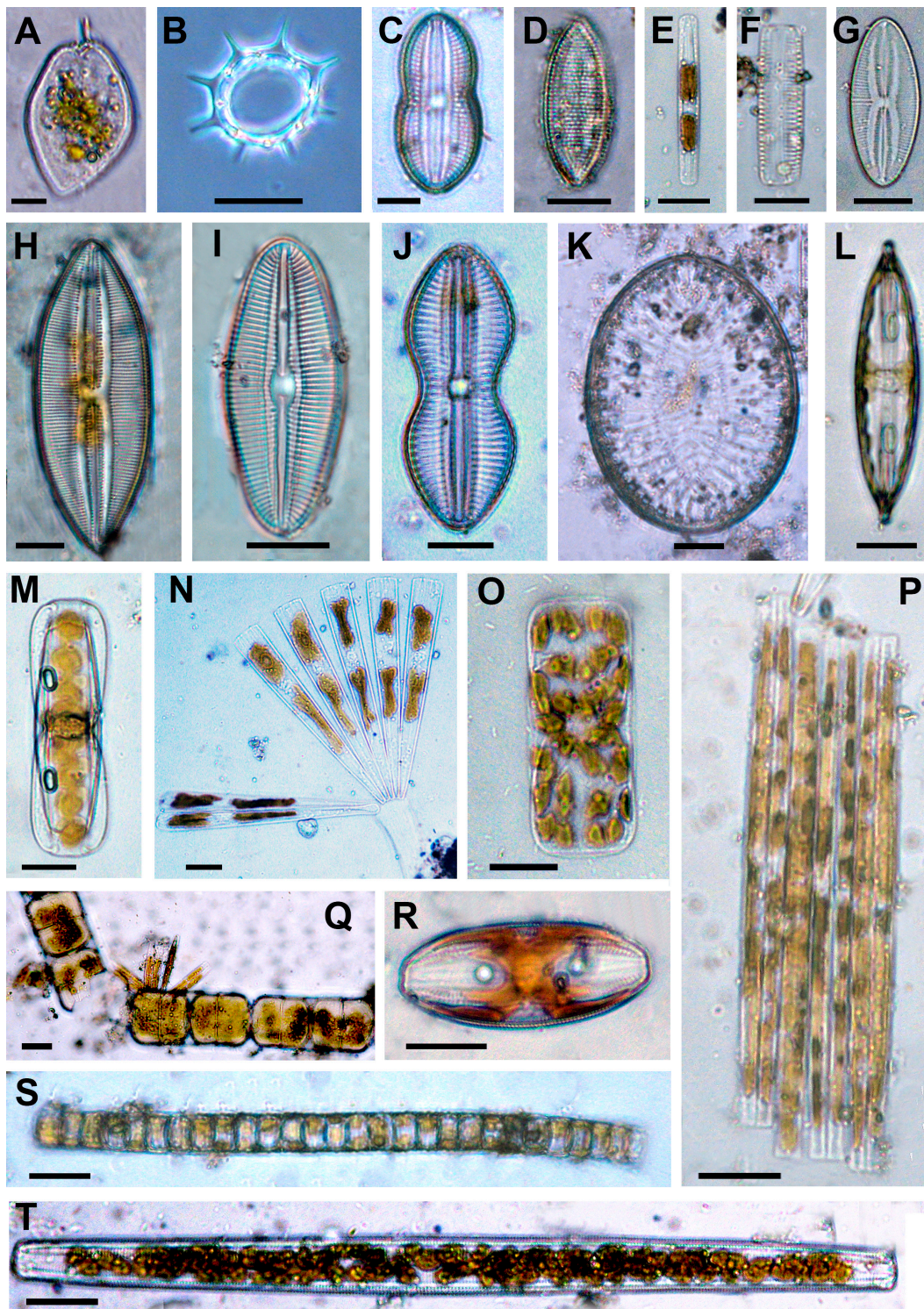
Figure 2. LM. Typical species of microalgae found on the farm: Dinoflagellata *Prorocentrum micans* (**A**), Ochrophyta *Octactis octonaria* (**B**), Bacillariophyta *Diploneis bombus* (**C**), *Tryblionella punctata* (**D**), *Nitzschia distans* (**E**), *Hantzschia marina* (**F**), *Lyrella abrupta* (**G**), *Lyrella lyroides* (**H**), *Diploneis smithii* (**I**), *Diploneis crabro* (**J**), *Campylodiscus neofastuosus* (**K**), *Plagiotropis lepidoptera* (**L**) valve view and (**M**) girdle view, *Licmophora flabellata* colony (**N**), *Undatella quadrata* (**O**), *Bacillaria paxillifer* colony (**P**), *Melosira moniliformis* and *Tabularia fasciculata* colonies (**Q**), *Amphora proteus* (**R**), *Paralia sulcata* colony (**S**), and *Ardissonea crystallina* (**T**). Living cells (**A**,**E**,**L–T**); frustules without chloroplasts (**B–D**,**F–K**). Scale bar: (**C**) = 10 μm; the rest of the images = 20 μm.
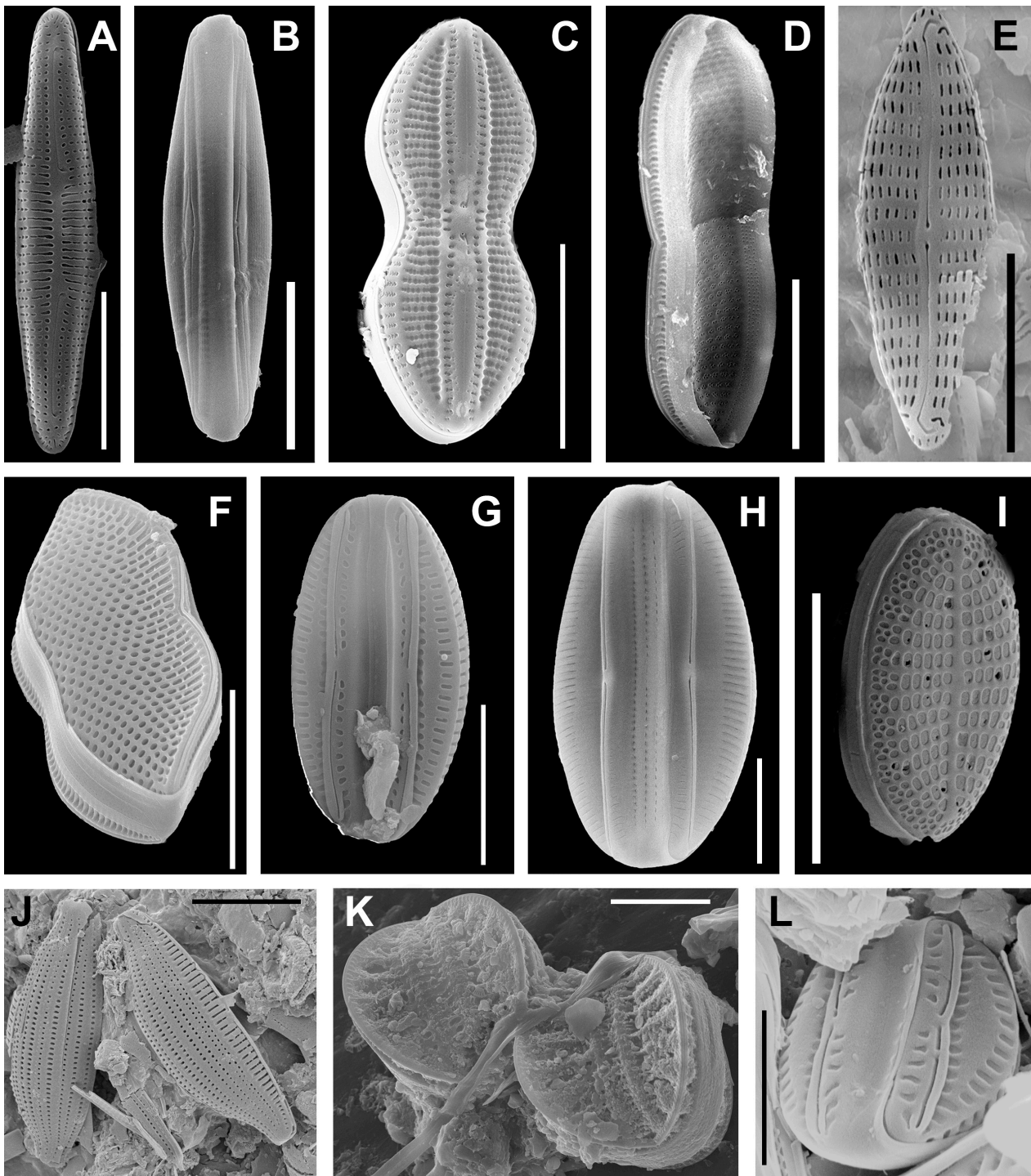
Figure 3. SEM. Acid-cleaned valves of the typical species of diatoms on the farm: *Berkeleya rutilans* (**A**), *Amphora angusta* (**B**), *Diploneis chersonensis* (**C**), *Tryblionella coarctata* (**D**), *Navicula antonii* (**E**), *Psammodyction panduriforme* var. *minor* (**F**), *Amphora proteus* (**G**), *Halamphora hyalina* (**H**), *Cocconeis scutellum* (**I**), *Halamphora coffeiformis* (**J**), *Campylodiscus thuretii* (**K**), and *Amphora ovalis* (**L**). Scale bar (**A**,**G**,**H**) = 5 µm; (**B**,**D**,**F**,**I**,**J**,**K**) = 10 µm; (**C**) = 50 µm; (**E**) = 4 µm; and (**L**) = 3 µm.
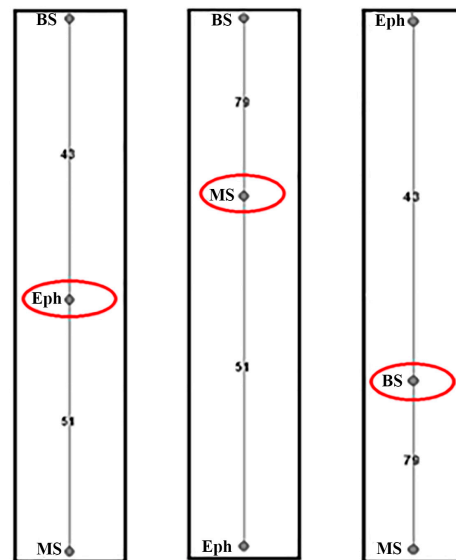
Figure 4. Similarity between microalgal communities from three ecotopes according to the Sörensen–Dice coefficient: %: MS = mussel shells, Eph = epiphyton, BS = bottom sediments on the mussel farm.

3.1. Mussel Shells

On the shells of farmed mussels, 102 taxa of microalgae belonging to Bacillariophyta (87 taxa), Dinoflagellata (6), Ochrophyta (2), Haptophyta (4), and Cyanobacteria (3) were found (Table A1). Benthic (79%), marine (59%), brackish–marine (34%), *β*-mesosaprobic (63%), cosmopolite (37%), and boreal–tropical (28%) species of microalgae dominated. Diatoms were the most abundant microalgae on the mussel shells. Among them, the taxonomically richest genera were *Nitzschia* (8 taxa) and *Navicula* (6). The seasonal dynamics of diatom average abundance and biomass vs. water temperature are presented in Figure 5. The maximum abundance (N = 119 $\times$ 10^3 cells/cm^2) and biomass (B = 0.0489 mg/cm^2) were recorded at low temperatures (9.7 °C) in February, whereas the minimum (N = 6 $\times$ 10^3 cells/cm^2 and B = 0.001 mg/cm^2) was reached in August at the highest water temperature of 25.6 °C. During periods with the increased amounts of diatoms on the mussel shells at water temperatures below 12 °C (February–April and December 2015–February 2016), the following colonial species thrived: *Bacillaria socialis* var. *baltica*, *Licmophora abbreviata*, *L. flabellata* (Figure 2O), *Melosira moniliformis* (Figure 2R), and potentially toxic *Pseudo-nitzschia calliantha*, as well as the solitary species *Cylindrotheca closterium*, *Halamphora coffeiformis* (Figure 3K), *Nitzschia* spp., and *Pleurosigma* spp. In terms of abundance, the dominant species were the colonial *Navicula ramosissima* and *Tabularia fasciculata* (Figure 2R), *Ardissonea crystallina* (Figure 2T), *Bacillaria paxillifer* (Figure 2Q), *Berkeleya rutilans* (Figure 3A), *Neosynedra provincialis*, *Striatella unipunctata*, and the solitary *Cocconeis scutellum* (Figure 3J). At a water temperature of 15 °C or higher (May–October 2015), the quantitative characteristics of the mussel shell diatoms significantly decreased, with the high biodiversity being maintained.

The average values of the diatom species richness (R) on the mussel shells were less variable than their abundance and biomass; the maximum (24 species) was observed in February 2015 and the minimum (4 species) was in August (Figure 6). The Shannon index values were mostly large (i.e., >1.5), and the Pielou index varied throughout the year within a rather narrow range (0.57–0.88, with a minimum in March and October and a maximum in September), which is due to a relatively uniform distribution of species in the community in terms of abundance.
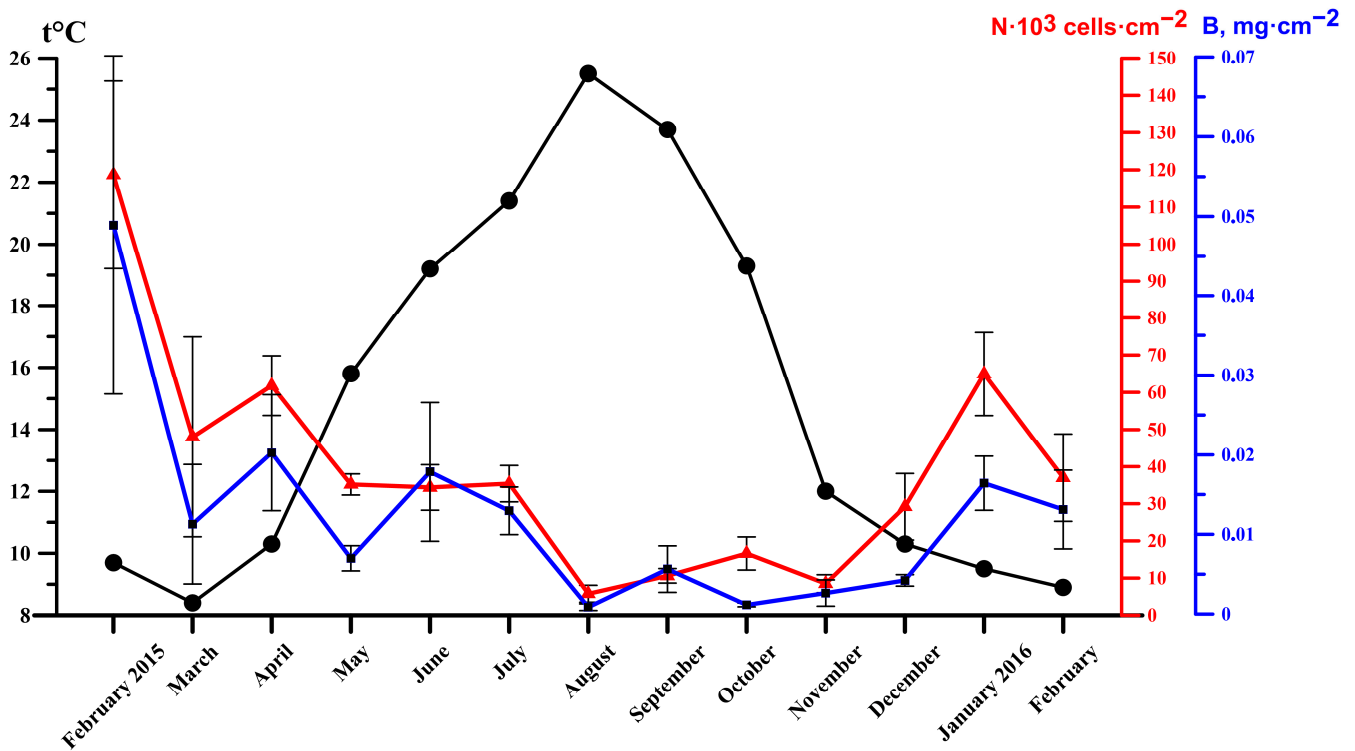
Figure 5. Seasonal dynamics of abundance (N, red plot) and biomass (B, blue plot) of the diatom communities of mussel shells and the water temperature (t °C, black plot) on the mussel farm.

Figure 6. Seasonal dynamics of species richness (R), Shannon index (H), and Pielou index (e) of the diatom communities of mussel shells on the mussel farm.

3.2. Sediments

A total of ninety-seven microalgal taxa were found in the sediments, and ninety-one belonged to Bacillariophyta, two species in each group were from Dinoflagellata and Cyanobacteria, and there was one Haptophyta and Ochrophyta species (Table A1). The diatoms included fifty-five genera, the richest of which were *Nitzschia* (eight species), *Diploneis* (6), *Amphora* (5), and *Navicula* (5). Many of them are typical for these substrates. Benthic (81%), marine (66%), brackish–marine (25%), β-mesosaprobic (61%), cosmopolite (31%) and boreal–tropical (29%) microalgae were predominant (Table A1). The abundance of diatom communities varied from 4×10^3 to 104×10^3 cells/cm^3, and the biomass was 0.003–0.046 mg/cm^3 at a depth of 17 m (Figure 7).
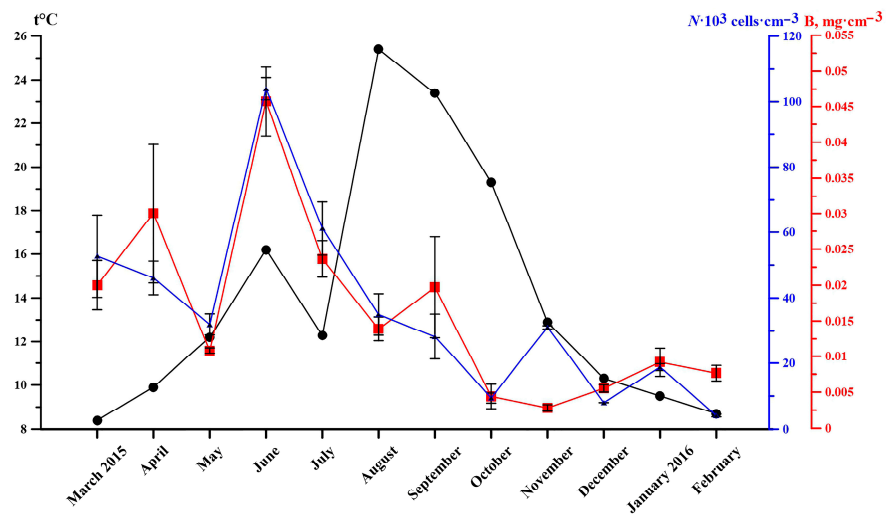
Figure 7. Seasonal dynamics of abundance (N, blue plot) and biomass (B, red plot) of the diatom communities in the sediments and water temperature (t °C, black plot) on the mussel farm.

In March–April at a water temperature of 8.4–9.9 °C, the abundance and biomass of diatoms were large (Figure 7), with *B. paxillifer* (Figure 2Q) and *U. lineolata* (Figure 2P) dominating in terms of abundance. In May, when the water temperature increased to 12 °C, the abundance, biomass, and number of species decreased. However, in June, with a further temperature increase to 16 °C, the abundance and biomass reached their maximum values for the entire period under study, with *T. fasciculata* and *B. paxillifer* dominating in terms of abundance.

The highest species diversity and evenness were observed from June to September (Figure 8). Since October, the species richness, abundance, and biomass decreased, while the values of the Shannon index remained quite high (1.9–3.2) against the high evenness (e = 0.94–1.0). The minimum values of abundance were in December at t = 10.3 °C, and the minimum biomass and number of the species were in November at t = 12.9 °C. The most frequently encountered species from October 2015 to February 2016 were *C. liber*, *C. scutellum*, *D. smithii* (Figure 2J), and some species of the genus *Navicula*. In general, sediments are characterized by high community diversity (H mostly takes values above 2.5, except in May and November) and high species evenness in terms of abundance (e = 0.63–1).
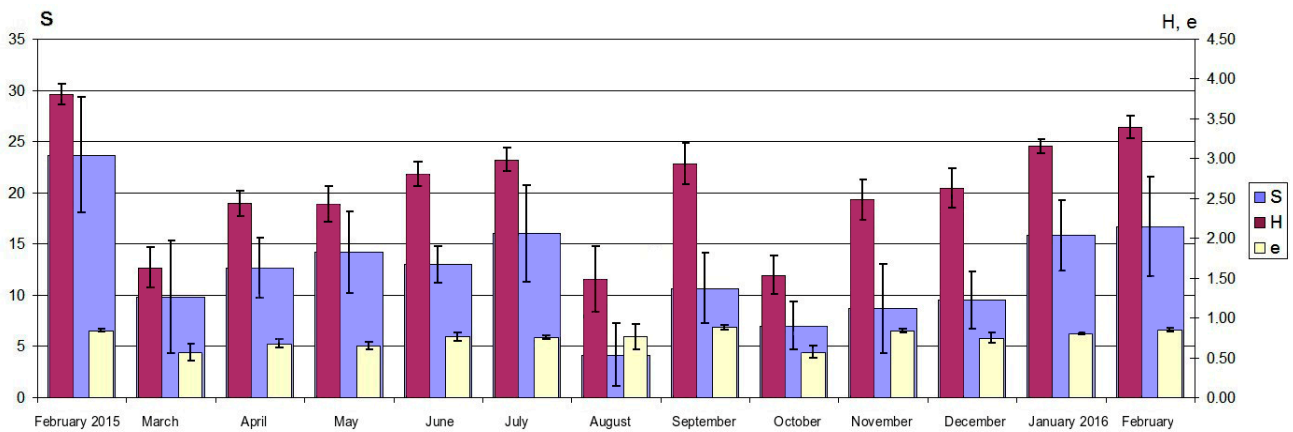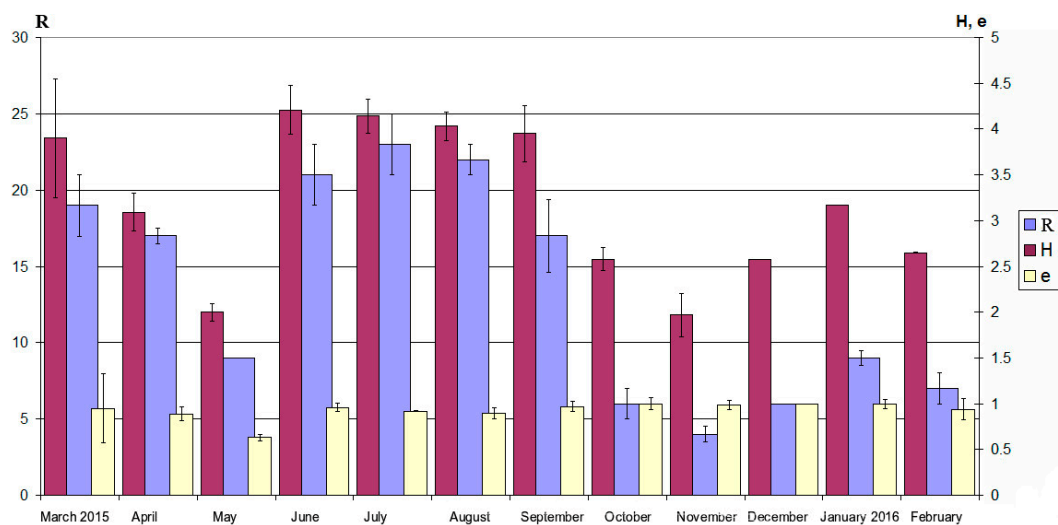

Figure 8. Seasonal dynamics of species richness (R), Shannon index (H), and Pielou index (e) of the diatom communities in the sediments on the mussel farm.

3.3. Epiphyton

A total of seventy-six taxa of Bacillariophyta and one taxon of Dinoflagellata were found on the twenty species of macroalgae. Of them, *Bryopsis adriatica* (J. Agardh) Frauenfeld 1854, *Ceramium virgatum* Roth 1797, *Codium vermilara* (Olivi) D. Chiaje 1829, *Cladophoropsis membranacea* (H. Bang ex C.A. Agardh) Børgesen 1905, and *Gongolaria barbata* (Stackhouse) Kunze 1891 were considered qualitatively. The following 15 species were treated quantitatively: the red algae *Callithamnion corymbosum* (Smith) Lyngbye 1819, *Laurencia coronopus* J. Agardh 1852, *Phyllophora crispa* (Hudson) P.S. Dixon 1964, *Ceramium arborescens* J. Agardh 1894, *Ceramium secundatum* Lyngbye 1819, the brown algae *Feldmannia paradoxa* (Montagne) Hamel 1939, *Nereia filiformis* (J. Agardh) Zanardini 1846, *Ericaria crinita* (Duby) Molinari et Guiry 2020, *Pyaiella littoralis* Kjellman 1872, and the green algae *Bryopsis plumosa* (Hudson) C. A. Agardh 1823, *Cladophora vadorum* (Areschoug) Kützing 1849, *Ulva clathrata* (Roth) C.A. Agardh 1811, *Ulva compressa* Linnaeus 1753, *Ulva rigida* C.A. Agardh 1823, and *Ulva torta* (Mertens) Trevisan 1842. Eight diatom species were dominant on them (Table A2).

The four epiphytic diatoms, *Anaulus maritimus* on the alga *E. crinita* at a depth of 6 m at the water temperature at 22 °C, *Licmophora hyalina* on *F. paradoxa* at a depth of 2 m at 15 °C, *Pleurosigma clevei* on *Ph. crispa* at a depth of 17 m at 18.0 °C, and *Pleurosigma inflatum* on *Ulva rigida* at a depth of 4.5 m at 8.6 °C, were noted in the coastal waters of Crimea and, in general, for the first time in the Black Sea [40]. Overall, thirty-nine genera of diatoms were found, the richest of which were *Navicula* (nine species), *Licmophora* (8), and *Nitzschia* (7) (Table A1).

The benthic (88%), marine (53%), brackish–marine (36%), β-mesosaprobic (59%), cosmopolite (33%), boreal–tropical (16%), and arctical–boreal–tropical (16%) species were predominant. The most abundant diatom species were *T. fasciculata, Gr. marina, L. abbreviata*, and the rare ones were *Hyalodiscus scoticus, B. socialis* var. *baltica, L. dalmatica*, and *L. gracilis*. For example, on *C. corymbosum* and *Br. plumosa*, the colonial diatom species *Gr. marina* was dominant with $N = 21 \times 10^3$ cells/cm^2 and 394×10^3 cells/cm^2, respectively. On *Ul. clathrata*, the dominant species was *L. abbreviata* with $N = 44.7 \times 10^3$ cells/cm^2.

The greatest abundance and biomass of diatoms were recorded on the alga *N. filiformis* in August 2018 at 26.6 °C with the maximum $N = 1001 \times 10^3$ cells/cm^2 and $B = 2.06$ mg/cm^2 and their average values $N = 472 \times 10^3$ cells/cm^2 and $B = 1.17$ mg/cm^2 with the dominance of *Pseudo-nitzschia seriata* (Table A2). Similarly, high values of diatoms were noted on *Ph. crispa* with the maximum $N = 1118 \times 10^3$ cells/cm^2 and $B = 3.24$ mg/cm^2 in July at 25 °C and the average $N = 436 \times 10^3$ cells/cm^2 and $B = 1.16$ mg/cm^2. The high abundance of diatoms on the seaweed in late summer can be explained by their decay, causing the increase in dissolved organics, which attracts microphytes. The Shannon index varied from 1.0 (March, *Ulva torta*, t = 8.1 °C) to 4.3 (*Phyllophora crispa*, October, t = 18.0 °C and *Ericaria crinita*, June, 22.0 °C).

3.4. Multivariate Analysis of Diatom Composition in Three Ecotopes

The Sörensen–Dice similarity coefficients were used to test the season- and substrate-related differences in the diatom composition. The significant differences in the ecotope and season groups are seen in the results of the two-way ANOSIM and PERMANOVA tests (Table 2). The cluster analysis coupled with the SIMPROF test (Figure 9a) demonstrates a tree of ten significantly different nested clusters, which include three clusters related mainly to sediment diatoms, one cluster of mussel shells diatoms, and six epiphyton clusters. The dendrogram shows progressively increasing similarity in the sequence from the sediment diatoms at low temperatures, with similarities 0–0.46, to the diatoms of mussel shells in all seasons (except in August 2015), with similarity coefficients of 0.44–0.67, and epiphytons of many macrophytes, with similarity coefficients of 0.21–0.80. The diatom composition in sediments was very sensitive to temperature changes in cold months. On the other hand, the composition of the mussel shell diatoms did not exhibit significant differences throughout the year, except in August, when it was closer to *Ceramium secundatum, Laurencia coronopus*,

and *Ulva torta* epiphyton. The deviation in August may be due to the low abundance and sharp decrease in species diversity (Figures 5 and 6). Close to the composition of the diatoms on mussel shells, when all quantitative indicators were low, there was a composition of sediment diatoms in warm months (from June to September).

Table 2. Results of two-way permutational global tests for comparing the Sørensen–Dice similarity in diatom communities from three ecotopes in different seasons.

PERMANOVA						
Source	df	SS	MS	Pseudo-F	P (perm)	Unique perms
Ecotope (Ec)	2	24,652	12,326	12.175	$<1 \times 10^{-5}$	91,759
Season (Se)	11	25,395	2308.6	2.2804	3×10^{-5}	86,913
Ec $\times$ Se	18	34,347	1908.1	1.8848	0.0002	85,893
Res	13	13,161	1012.4			
Total	44	1.05×10^{5}				

ANOSIM
Tests for differences between ecotope groups (across all season groups).
Sample statistic (Global R): 0.935. The significance level of the sample statistic: 0.0001%.
Number of permutations: 999,999 (random sample from 7,290,000).
Number of permuted statistics greater than or equal to Global R: 0.
Tests for differences between season groups (across all ecotope groups).
Sample statistic (Global R): 0.609. The significance level of the sample statistic: 0.0004%.
Number of permutations: 999,999 (random sample from a large number).
Number of permuted statistics greater than or equal to Global R: 3.

There were sporadic allocations of variables in foreign clusters, e.g., August 2015 diatoms of mussel shells in the epiphyton cluster; March 2015 sediment diatoms in the mussel shells cluster; a *Phyllophora crispa* diatom epiphyton in September 2018 assigned to the cluster of sediment diatoms in May and October 2015 and January 2016; and a *Nereia filiformis* epiphyton in October 2019 embedded in the cluster with the sediment diatoms in April and November–December 2015 and February 2016.

Canonical analysis of principal coordinates (CAPs) with an ecotope as the discriminant factor shows the separation of the similarity data in three distinct ecotope-related groups (Figure 9b). In this case, cross-validation allows us to correctly classify 92, 92, and 100% of the data in the sediment, mussel shells, and epiphyton groups, respectively, and the total correct classification percentage is 96% (45 out of 47 values). The permutation test yields the canonical trace statistic, $tr(\mathbf{Q_m'HQ_m}) = 1.67$, $p < 0.001$, and the first squared canonical correlation, $\delta_1^2 = 0.90$, $p < 0.001$. CAPs for groups within the season factor (Figure 9c) demonstrate much fewer correct classification results, 12 out of 47 values (26%), and, accordingly, a large misclassification error (74%), which is mainly due to the high similarity of diatom compositions in neighboring seasons (the permutation test results are $tr(\mathbf{Q_m'HQ_m}) = 1.76$, $p = 0.066$ and $\delta_1^2 = 0.74$, $p < 0.001$). Canonical axis 1 in this analysis has a large contribution to water temperature, as most of the observations in the positive half space are associated with low temperatures, and the negative half space contains data obtained mainly in the warm season.
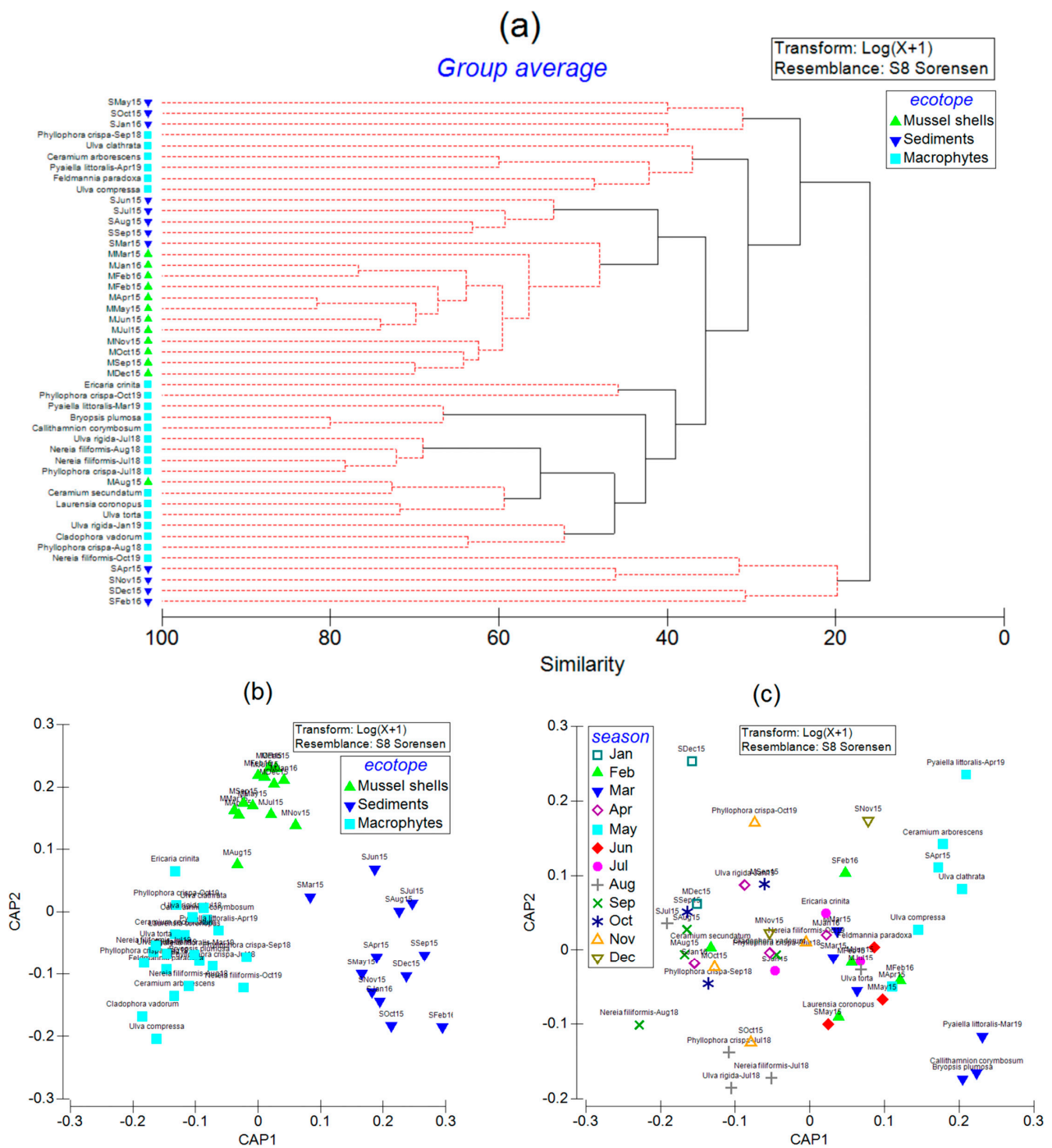
Figure 9. Multivariate analysis of the composition of diatom communities from three ecotopes in different seasons: (**a**) cluster analysis (M = mussel shell ecotope, S = sediments ecotope; significantly different clusters are marked by black solid lines); (**b**) canonical analysis of principal coordinates (CAPs) for groups within the ecotope factor and (**c**) CAPs for groups within the season factor.

Multivariate Analysis of Epiphyton Diatoms

The two-way PERMANOVA applied to the Bray–Curtis coefficients of the log-transformed epiphyton diatom abundances with the macrophyte and season factors shows the lack of differences in the macrophyte species group factor (*p* = 0.401) (Table 3). However, the result of this test could not be regarded as reliable because of the considerable probability of the type II error, as the numbers of possible permutations in each pair of groups were rather low. At the same time, the season season factor yielded significant

differences in the seasonal epiphyton distributions ($p = 0.044$). These results are confirmed by the results of one-way ANOSIM tests with the macrophyte and season group factors, which give significance levels of 24.3% (Global R = 0.134) and <0.1% (Global R = 0.598), respectively. These results suggest that temperature, rather than substrate macrophyte species identity, most strongly affects the epiphytic diatom communities.

Table 3. Results of permutational global tests for comparing the Bray–Curtis similarity of numerical structure in diatom communities of epiphyton in different seasons.

Two-way PERMANOVA						
Source	df	SS	MS	Pseudo-F	P (perm)	Unique perms
Macrophyte (Ma)	9	11,013	1223.7	1.0929	0.401	999
Season (Se)	5	10,631	2126.2	1.8989	0.044	996
Ma × Se excluded						
Res	2	2239.3	1119.7			
Total	21	43,354				

One-way ANOSIM

Macrophyte
Sample statistic (Global R): 0.134. The significance level of the sample statistic: 24.3%.
Number of permutations: 999 (random sample from a large number).
Number of permuted statistics greater than or equal to Global R: 242.

Season
Sample statistic (Global R): 0.598. The significance level of the sample statistic: <0.1%.
Number of permutations: 999 (random sample from a large number).
Number of permuted statistics greater than or equal to Global R: 0.

The cluster analysis runs along with the SIMPROF test and yields differences at a significance level of 5%, which allows discrimination in a hierarchy of significantly different clusters of macrophytes (Figure 10a). At the highest level, the singular cluster I (*Nereia filiformis* in October 2019) differs from clusters II-VII. One level lower, there is the cluster II of macrophytes sampled in cool water (9.8 °C), which differs significantly from the lower clusters III-VII. At the lowest level, cluster VI with the macroalgae sampled in warm water differs from cluster VII containing predominantly the macrophytes from cool water. All these clusters are easily identifiable in the 2D plot of canonical analysis of principal coordinates (CAPs) with the applied discriminant analysis within the temperature factor (Figure 10b). Permutation test results show that the allocation of temperature groups in this method is significant (for the canonical trace statistic, $tr(\mathbf{Q_m}'\mathbf{HQ_m}) = 4.60$, $p < 0.001$, and for the first squared canonical correlation, $\delta_1^2 = 0.98$, $p = 0.006$). However, the misclassification error is considerable (36.4%), and it is more typical for warm waters. For example, there were no correct classifications for the groups of 15, 18, 24.4, and 26.4 °C.

The results of the redundancy analysis (RDA) show that the response variables (log-transformed epiphytic diatom abundances) cannot be considered linearly correlated with the explanatory variables (water temperature and macrophyte species) of F = 0.943, $p = 0.546$, $R^2 = 0.702$, $R^2_{adj} = -0.0424$. The RDA plot (Figure 10c) shows that canonical axis I is associated with the temperature, abundance, and monospecificity factors, and close to this axis are the microalgal species, whose large abundances are related mainly to the warm or cold seasons. For example, species such as *Amphora proteus*, *Navicula menisculus*, *Navicula pennata*, and *Cocconeis costata* were found on only one macrophyte (*Phyllophora crispa*) and only in the warm season (July 2019). *Pleurosigma elongatum*, *Navicula* sp., and *Pseudo-nitzschia seriata*, which are closer to the origin, were also found only in warm water, but their occurrence is associated with more than one macrophyte species. At the extreme values in the opposite half space of canonical axis I, there are species that were encountered in large amounts only in cool water, e.g., *Licmophora oedipus*, *Licmophora paradoxa*, *Licmophora gracilis*, *Gyrosigma fasciola*, and *Camplopyxis garkeana*.
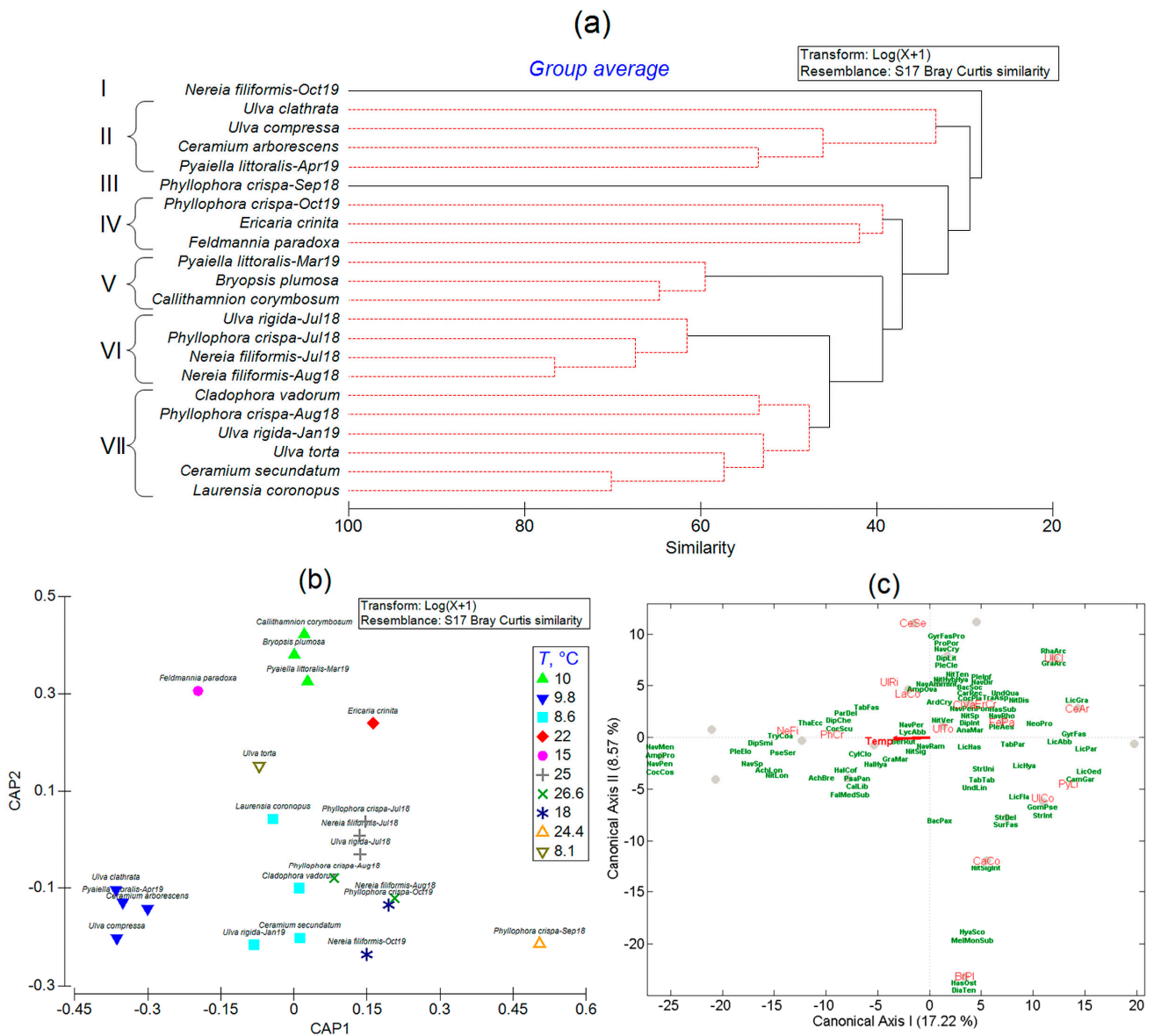
Figure 10. Multivariate analysis of the epiphyton with the group factors of temperature and macrophyte: (**a**) cluster analysis (significantly different clusters are marked by black solid lines), (**b**) canonical analysis of principal coordinates against groups in the temperature factor, and (**c**) redundancy analysis (RDA). In the RDA plot, the macrophyte (red color) and microalgae (green color) names are abbreviated, respectively, to the first two and three letters of the genus and epithet (and variety, where applicable). The explanatory variables (macrophyte and temperature) are shown as centroids (with the temperature vector added) and the response variables (log-transformed microalgae abundances) as their weighted average scores.

4. Discussion

Information on the seasonal and spatiotemporal distribution of marine microphytobenthos, especially in relation to marine farms, is scarce. The working hypothesis of our study was that the species composition and quantitative distribution of microphytobenthos depend on the season, ecotope, and substrate macrophyte species. A distinct effect of ecotope on the composition and quantitative distribution of microphytobenthos was revealed. The most pronounced effect of temperature is observed for the diatoms of mussel shells, in which the trend of an increase in abundance and biomass in winter and their decrease in summer is most noticeable. This may be due to the relative constancy of the diatom species composition throughout the year, with the abundance and biomass of

different species being affected almost equally by the seasonal temperature variations. In the Black Sea, species diversity and abundance tend to increase in the winter–spring season due to the intense diatom development and then decrease in summer and autumn due to the shallow water heating and grazing on microphytobenthos [7]. In addition, as shown earlier, an abundance of mussel shell diatoms demonstrated a strong negative correlation with temperature [31]. However, this pattern was not observed in sediments under the mussel farm collectors, where the correlation of microphytobenthos with water temperature was absent, and both the abundance and biomass of microalgae were affected mainly by variation in the species composition and richness throughout the year. The mussel shells and sediments are characterized by high diversity and species evenness throughout the year, as the Shannon and Pielou indices take mostly high values. For the mussel shell, the species evenness varies seasonally, in the sediments, the Pielou index remains high almost all year round (e = 0.9–1), indicating that all species are evenly distributed in terms of their abundance.

It is worthwhile to note that on *Mytilus galloprovincialis* shells from another Crimean farm in Kazachya Bay (Sevastopol), microalgae are also characterized by high diversity (H = 3.2–3.6), and the maximum of the quantitative parameters (R = 77, N = 830 × 10³ cells/cm², B = 3.26 mg/cm²) are in spring [23]. On the farm in Vostok Bay in the Sea of Japan, diatoms on *Mytilus trossulus* shells demonstrate low values of abundance (6.3 × 10³–63.3 × 10³ cells/cm²) and a low Shannon index (1.26–1.76), and these values also tend to increase in the winter–spring season and decrease in summer–autumn. Both in the Black Sea and the Sea of Japan, shallow waters typically warm up well in summer, and this leads to the fact that the diatom colonies are destroyed, more single cells are found, and the effect of increased grazing of invertebrates on diatoms is more pronounced [7,23]. Furthermore, some dominant and mass diatom species were the same on the mussel shells from the two seas: *T. fasciculata*, *C. scutellum*, *C. closterim*, and *L. abbreviata*.

For epiphytons, it was shown that it is temperature, rather than substrate macrophyte species identity, that most strongly affects the epiphytic diatom communities. Furthermore, the microalgae distribution is most specific in the cold seasons, while in the warm seasons, this specificity becomes less distinct (Figure 10b). This can be explained by the fact that in summer, the toxic planktonic diatom *Pseudo-nitzschia seriata* settling from the water column to the surface of macrophytes dominated virtually all macrophyte species under consideration. Thus, our hypothesis of both temperature and substrate affecting the epiphyton community was only partially confirmed in relation to temperature. Furthermore, there is no linearity and additivity in the effect of temperature and substrate species on the numerical structure of epiphyton communities, as it follows from the RDA analysis, and these factors appear to interact in a complex non-linear manner throughout the year. In contrast to our findings, in a study of epiphytons in the Gulf of California, differences in the structure of diatom assemblages depended on the host macrophyte (*Codium*, *Ulva*, *Laurencia*, and *Ceramium*) [60]. On the other hand, in the epiphyton of *Ruppia maritima* in the Patos Lagoon estuary (Brazil), nutrient concentration and salinity were the main factors affecting diatom species richness and diversity on the macrophyte, and the temperature was the only factor that was associated with variations in the diatom species composition [61].

The species diversity index for epiphyton microalgae generally takes high values (2.8–4.4) on the farm. At the same time, in the epiphyton from Karantinnaya Bay, which is adjacent to the farm and where no mariculture facilities are located, the Shannon index also took high values (2.2–4.5), with the abundance varying from 4 × 10³ to 349 × 10³ cells/cm² [40]. The highest abundance of epiphyton microalgae in these two water areas was observed in summer. At the same time, the values of the Shannon index for the epilithon diatoms from the bay did not exceed 1.3 [7], which is lower than the values for all ecotopes on the farm. The abundance of epilithon diatoms in Karantinnaya Bay varied from 510 to 140 × 10⁴ cells/cm², with a maximum in April at a water temperature of 10 °C, and in summer, a decline in the quantitative characteristics was noted. The same seasonal pattern was noted for the diatoms of mussel shells on the farm.

In studies of microphytobenthos from the Mediterranean basin, which includes the Black Sea, researchers also noted seasonal changes in the quantitative characteristics of the microphytobenthic diatoms: the abundance of the most of diatom genera increased with rising temperature [62]. In the Baltic Sea, both spatial (i.e., site- and depth-related) and seasonal differences in the epiphyton and epipsammon diatoms were revealed [63]. These differences were attributed mainly to the varying proportions of taxa common in both sampling areas in three seasons rather than major taxonomic changes in the species present in the communities.

Although the use of indicator species in marine ecosystems is not yet as well developed as in freshwater ecosystems [64], it is worthwhile to note that among the organic pollution indicator species found on the farm, the majority in the three ecotopes were β-mesosaprobic indicators of moderate pollution. However, among the dominant species, there were also indicators of relatively clean waters (mesosaprobic *Bacillaria paxillifer*, xenosaprobic *Licmophora paradoxa*, and xenooligosaprobic *Tabularia fasciculata*), which do not survive in more polluted water areas. This fact and the high values of diversity indices (H, e) on the farm indicate that this area was relatively clean at the time of the study, which is consistent with the above-mentioned hydrochemical measurement results and the oligotrophic status of the water area. In addition, 10 potentially harmful algal species have been identified on the farm, most of which are planktonic and thus can be food for the cultivated mussel. For example, some species of diatoms of the genus *Pseudo-nitzschia* and strains of *H. coffeiformis* are known to produce domoic acid, which causes amnesic shellfish poisoning [15–17,19,65], and the Dinoflagellata of the genera *Dinophysis* and *Prorocentrum* produce hepatotoxins and bring about Diarrhetic Shellfish Poisoning [12–14,18,21]. Therefore, it is important not to overload the water area with cultivated mussels in order to prevent excessive metabolite excretion and, as a result, harmful algal blooms. As the farm is located in the open sea and its volume is small, potentially harmful algae do not grow to bloom levels and do not pose a threat to mariculture production and the water area in general.

5. Conclusions

The biodiversity of microphytobenthos (in 2015–2016 and 2018–2020) in different ecotopes (mussel shells, epiphyton, and sediments) of the mussel farm has been studied. The microphytobenthos list includes 150 microalgal taxa of which 135 are diatoms. The maximum values of abundance and biomass have been registered in winter for the diatoms of mussel shells and in summer for the epiphyton and sediments. The ecotope had the most pronounced effect on the composition and quantitative distribution of microalgae. The strongest effect of temperature is observed for the mussel shell diatoms, in which the trend of abundance and biomass increase in winter, and their decrease in summer is most noticeable. This trend has been noted in the literature for the mussel shell diatoms from other farms and is typical for the Black Sea. However, in sediments, the effect of the season is reflected only in the permanent changes in the microalgae species composition. For epiphyton, it was shown that it is temperature, rather than macrophyte species, that most strongly affects the diatom communities, and there is no linearity and additivity in the effect of these factors.

Institutional Review Board Statement: Not applicable.

Informed Consent Statement: Not applicable.

Appendix A

Table A1. Species composition, the ecological and phytogeographical characteristics of mussel shells, and epiphyton and sediment microalgae on the mussel farm at the entrance to Karantinnaya Bay (Black Sea).

	Taxon	MS	Eph	BS	H	RS	S	PhG
	CYANOBACTERIA							
1.	*Chamaecalyx swirenkoi* (Schirschoff) Komárek et Anagnostidis 1986	+	-	+	B	B	-	B
2.	*Phormidium nigroviride* (Thwaites ex Gomont) Anagnostidis et Komárek 1988	+	-	-	B	M	-	BT not
3.	*Spirulina tenuissima* Kützing 1836	+	-	+	B	M	-	BT
	DINOFLAGELLATA							
4.	*Dinophysis fortii* Pavillard 1924 **	+	-	-	P	M	-	ABT not
5.	*Phalacroma rotundatum* (Claparéde et Lachmann) Kofoid et Michener 1911 **	+	-	-	P	M	-	C
6.	*Prorocentrum compressum* (Bailey) T.H. Abé ex J.D. Dodge 1975 **	+	-	+	P	M	-	C
7.	*Prorocentrum cordatum* (Ostenfeld) J.D. Dodge 1976 **	+	-	+	P	BM	-	ABT not
8.	*Prorocentrum lima* (Ehrenberg) F. Stein 1878 **	+	+	-	B	M	-	C
9.	*Prorocentrum micans* Ehrenberg 1834 **	+	-	-	P	M	-	C
	HAPTOPHYTA							
10.	*Acanthoica acanthos* J. Schiller 1925	+	-	-	P	M	-	BT
11.	*Emiliania huxleyi* (Lohmann) W.W. Hay et H. Mohler 1967	+	-	+	P	M	-	C
12.	*Oolithotus fragilis* (Lohmann) Martini et Müller 1972	+	-	-	P	M	-	B
13.	*Rhabdosphaera hispida* Lohmann 1912	+	-	-	P	M	-	B
	OCHROPHYTA							
14.	*Octactis octonaria* (Ehrenberg) Hovasse 1946	+	-	-	P	M	-	B not
15.	*Octactis speculum* (Ehrenberg) Chang, J.M. Grieve et J.E. Sutherland 2017	+	-	+	P	M	-	AB not
	BACILLARIOPHYTA							
16.	*Achnanthes brevipes* C.A. Agardh 1824 var. *brevipes*	+	+	-	B	BM	β	C
17.	*Achnanthes brevipes* var. *intermedia* (Kützing) P.T. Cleve 1895	+	-	-	B	BM	-	C
18.	*Achnanthes brockmannii* Hustedt 1959	-	-	+	B	M	-	B
19.	*Achnanthes longipes* C.A. Agardh 1824	+	+	+	B	M	β	ABT
20.	*Amphora angusta* W. Gregory 1857	+	-	+	B	BM	β	C
21.	*Amphora arcus* W. Gregory 1855	+	-	+	B	M	-	AB
22.	*Amphora crassa* W. Gregory 1857	-	-	+	B	M	-	ABT
23.	*Amphora laevissima* W. Gregory 1857	-	-	+	B	M	-	ABT not
24.	*Amphora ovalis* (Kützing) Kützing 1844	-	+	-	B	BM	α-β	C
25.	*Amphora proteus* W. Gregory 1857	+	+	+	B	BM	β	C
26.	*Anaulus maritimus* Nikolaev 1969 *	-	+	-	B	M	β	B
27.	*Ardissonea crystallina* (C.A. Agardh) Grunow 1880	+	+	+	B	BM	β	BT
28.	*Auricula intermedia* (Lewis) P.T. Cleve 1894	-	-	+	B	M	-	B
29.	*Bacillaria paxillifer* (O.F. Müller) N. Hendey 1951	+	+	+	BP	BM	o-β	C
30.	*Bacillaria socialis* var. *baltica* (Grunow) De Toni 1892	+	+	+	BP	M	-	ABT
31.	*Berkeleya micans* (Lyngbye) Grunow 1880	+	-	-	B	BM	o	B not
32.	*Berkeleya rutilans* (Trentepohl ex Roth) Grunow 1880	+	+	+	B	BM	-	ABT not
33.	*Caloneis liber* (W. Smith) P.T. Cleve 1894	+	+	+	B	M	-	C
34.	*Campylodiscus neofastuosus* Ruck et Nakov 2016	+	-	+	B	M	-	ABT not
35.	*Campylodiscus thuretii* Brébisson 1854	+	-	+	B	M	-	ABT
36.	*Campylopyxis garkeana* (Grunow) Medlin 1985	-	+	-	B	M	-	AB
37.	*Carianosigma rectum* (Donkin) G. Reid 2012	+	+	+	B	M	-	BT not

Table A1. *Cont.*

	Taxon	MS	Eph	BS	H	RS	S	PhG
38.	*Climaconeis inflexa* (Brébisson ex Kützing) E.J. Cox 1982	+	-	+	B	M	-	B not
39.	*Cocconeis costata* W. Gregory 1855	+	+	+	B	M	β	C
40.	*Cocconeis scutellum* Ehrenberg 1838	+	+	+	B	BM	β	C
41.	*Coscinodiscus jonesianus* (Greville) Ostenfeld 1915	+	-	+	P	M	-	B
42.	*Coscinodiscus radiatus* Ehrenberg 1840	+	-	+	B	M	-	B
43.	*Cylindrotheca closterium* (Ehrenberg) Reimann et Lewin 1964	+	+	+	BP	M	β	C
44.	*Cymbella helvetica* Kützing 1844	+	-	+	B	FW	χ-o	BT not
45.	*Diatoma tenuis* C.A. Agardh 1812	-	+	-	BP	B	α-β	C
46.	*Diploneis bombus* (Ehrenberg) Ehrenberg 1853	+	-	+	B	M	-	BT not
47.	*Diploneis chersonensis* (Grunow) P.T. Cleve 1892	-	+	+	B	M	-	ABT
48.	*Diploneis crabro* (Ehrenberg) Ehrenberg 1854	-	-	+	B	M	-	BT not
49.	*Diploneis didyma* (Ehrenberg) Ehrenberg 1845	+	-	+	B	BM	β	ABT not
50.	*Diploneis interrupta* (Kützing) P.T. Cleve 1894	-	+	-	B	B	-	AB not
51.	*Diploneis lineata* (Donkin) P.T. Cleve 1894	+	-	+	B	M	-	BT
52.	*Diploneis littoralis* (Donkin) P.T. Cleve 1894	-	+	-	B	M	-	AB not
53.	*Diploneis smithii* (Brébisson) P.T. Cleve 1894	+	+	+	B	BM	-	C
54.	*Entomoneis paludosa* (W. Smith) Reimer 1975	+	-	+	BP	BM	α-β	C
55.	*Falcula media* var. *subsalina* Proschkina-Lavrenko 1963	-	+	-	BP	M	o	B
56.	*Fallacia forcipata* (Greville) A.J. Stickle et D.G. Mann 1990	+	-	+	B	M	-	ABT not
57.	*Gomphonemopsis pseudexigua* (Simonsen) Medlin 1986	-	+	-	B	M	-	ABT not
58.	*Grammatophora arctica* P.T. Cleve 1867	-	+	-	B	M	-	AB
59.	*Grammatophora marina* (Lyngbye) Kützing 1844	+	-	+	B	M	β	C
60.	*Grammatophora serpentina* (Ralfs) Ehrenberg 1844	-	-	+	B	M	-	ABT not
61.	*Gyrosigma fasciola* (Ehrenberg) J.W. Griffith et Henfrey 1856 var. *fasciola*	-	+	-	B	M	o	C
62.	*Gyrosigma fasciola* var. *prolongatum* (W. Smith) P.T. Cleve 1894	+	+	+	B	M	-	AB
63.	*Gyrosigma littorale* (W. Smith) J.W. Griffith et Henfrey 1856	+	-	+	B	M	-	BT not
64.	*Gyrosigma tenuissimum* (W. Smith) J.W. Griffith et Henfrey 1856	+	-	-	B	M	-	BT not
65.	*Halamphora angularis* (W. Gregory) Levkov 2009	-	-	+	B	B	-	B not
66.	*Halamphora coffeiformis* (C.A. Agardh) Levkov 2009 **	+	+	+	B	BM	α	C
67.	*Halamphora hyalina* (Kützing) Rimet et R. Jahn 2018	+	+	+	B	BM	β	ABT not
68.	*Hantzschia marina* (Donkin) Grunow 1880	+	-	+	B	M	-	BT not
69.	*Haslea crystallina* (Hustedt) Simonsen 1974	+	-	+	B	M	-	B
70.	*Haslea ostrearia* (Gaillon) Simonsen 1974	-	+	-	B	M	-	BT
71.	*Haslea subagnita* (Proschkina-Lavrenko) Makarova et Karayeva 1985	-	+	-	B	B	-	C
72.	*Hyalodiscus scoticus* (Kützing) Grunow 1879	+	+	+	P	BM	β	C
73.	*Hyalosira delicatula* Kützing 1844	+	+	+	B	BM	-	AB
74.	*Licmophora abbreviata* C.A. Agardh 1831	+	+	+	B	M	β	C
75.	*Licmophora dalmatica* (Kützing) Grunow 1867	+	+	-	B	M	-	C
76.	*Licmophora flabellata* (Greville) C.A. Agardh 1830	+	+	+	B	M	β	BT not
77.	*Licmophora gracilis* (Ehrenberg) Grunow 1867	+	+	-	B	M	-	ABT
78.	*Licmophora hastata* Mereschkowsky 1902	-	+	-	B	M	-	B
79.	*Licmophora hyalina* (Kützing) Grunow 1867 *	-	+	-	B	M	-	AB
80.	*Licmophora oedipus* (Kützing) Grunow 1881	-	+	-	B	M	-	AB
81.	*Licmophora paradoxa* (Lyngbye) C.A. Agardh 1828	-	+	-	B	M	χ	C
82.	*Lyrella abrupta* (W. Gregory) D.G. Mann 1990	+	-	+	B	M	-	BT not
83.	*Lyrella hennedyi* (W. Smith) Stickle et D.G. Mann 1990	-	-	+	B	M	-	AB not
84.	*Lyrella lyroides* (Hendey) D.G. Mann 1990	+	-	+	B	M	-	BT
85.	*Melosira moniliformis* (O.F. Müller) C.A. Agardh 1824 var. *moniliformis*	+	-	+	P	BM	β	C
86.	*Melosira moniliformis* var. *subglobosa* Grunow 1878	-	+	-	P	BM	β	B
87.	*Microtabella interrupta* (Ehrenberg) Round 1990	-	+	-	B	M	-	BT
88.	*Navicula ammophila* var. *intermedia* Grunow 1862	-	+	-	B	BM	-	AB
89.	*Navicula antonii* Lange-Bertalot 2000	+	+	+	B	FW	-	BT not
90.	*Navicula cancellata* Donkin 1872	+	-	+	B	M	-	B
91.	*Navicula cryptocephala* Kützing 1844	+	+	-	B	B	α	ABT not
92.	*Navicula directa* (W. Smith) Ralfs ex Pritchard 1861	+	+	-	B	BM	-	C
93.	*Navicula menisculus* Schumann 1867	-	+	-	B	B	α	ABT not
94.	*Navicula palpebralis* Brébisson ex W. Smith 1853	-	-	+	B	M	-	ABT not

Table A1. *Cont.*

	Taxon	MS	Eph	BS	H	RS	S	PhG
95.	*Navicula pennata* A.W.F. Schmidt 1876	+	+	+	B	BM	-	BT not
96.	*Navicula perrhombus* Hustedt ex Simonsen 1962	-	+	-	B	BM	-	BT
97.	*Navicula ramosissima* (C.A. Agardh) P.T. Cleve 1895	+	+	+	B	BM	-	ABT not
98.	*Neosynedra provincialis* Williams et Round 1986	+	+	+	B	M	-	B
99.	*Nitzschia distans* (W. Smith) Ralfs ex Pritchard 1861	+	+	+	B	BM	-	BT not
100.	*Nitzschia hybrida* f. *hyalina* Proschkina-Lavrenko 1963	+	+	+	B	BM	β	B
101.	*Nitzschia longissima* (Brébisson) Ralfs 1861	+	+	+	BP	M	-	C
102.	*Nitzschia sigma* (Kützing) W. Smith 1853 var. *sigma*	-	+	-	B	BM	α	ABT not
103.	*Nitzschia sigma* var. *intercedens* Grunow 1878	+	+	+	B	M	α	B not
104.	*Nitzschia sigmoidea* (Nitzsch) W. Smith 1853	+	-	+	B	FW	o	BT not
105.	*Nitzschia spathulata* Brébisson 1853	+	-	+	B	M	-	BT
106.	*Nitzschia tenuirostris* Mereschkowsky 1902	+	+	+	BP	B	-	B
107.	*Nitzschia vermicularis* (Kützing) Hantzsch 1860	-	+	-	B	B	o	BT not
108.	*Nitzschia vidovichii* (Grunow) Grunow 1862	+	-	+	B	M	o	B
109.	*Paralia sulcata* (Ehrenberg) P.T. Cleve 1873	+	-	+	BP	M	-	C
110.	*Paraplaconeis placentula* (Ehrenberg) Kulikovskiy et Lange-Bertalot 2012	-	-	+	B	B	-	BT not
111.	*Parlibellus delognei* (Van Heurck) E.J. Cox 1988	+	+	+	B	M	-	C
112.	*Parlibellus rhombicus* (W. Gregory) E.J. Cox 1988	-	+	-	B	BM	-	BT
113.	*Petrodictyon gemma* (Ehrenberg) D.G. Mann 1990	-	-	+	B	M	-	BT not
114.	*Petroneis humerosa* (Brébisson ex W. Smith) Stickle et D.G. Mann 1990	-	-	+	B	M	-	BT not
115.	*Pinnularia quadratarea* (A.W.F. Schmidt) P.T. Cleve 1895	-	-	+	B	M	-	C
116.	*Plagiotropis lepidoptera* (W. Gregory) Kuntze 1898	+	-	+	B	M	o	ABT not
117.	*Pleurosigma aestuarii* (Brébisson ex Kützing) W. Smith 1853	-	+	-	B	M	-	AB
118.	*Pleurosigma angulatum* (J.T. Quekett) W. Smith 1852	+	-	+	B	M	β	C
119.	*Pleurosigma clevei* Grunow 1880 *	-	+	-	B	M	-	AB
120.	*Pleurosigma elongatum* W. Smith 1852	+	+	+	B	BM	β	C
121.	*Pleurosigma inflatum* Shadbolt 1853 *	-	+	-	B	M	-	BT not
122.	*Pleurosigma intermedium* W. Smith 1853	+	-	-	B	M	-	BT not
123.	*Proboscia alata* (Brightwell) Sundström 1986	+	-	+	P	M	-	C
124.	*Proschkinia poretzkiae* (Korotkevich) D.G. Mann 1990	-	+	-	B	M	-	AB
125.	*Psammodyction panduriforme* var. *minor* (Grunow) L.I. Ryabushko 2006	+	+	+	B	M	-	BT not
126.	*Pseudo-nitzschia calliantha* Lundholm, Moestrup et Hasle 2003 **	+	-	+	P	M	-	C
127.	*Pseudo-nitzschia delicatissima* (P.T. Cleve) Heiden 1928 **	+	-	+	P	M	-	C
128.	*Pseudo-nitzschia pungens* (Grunow ex P. Cleve) Hasle 1993 **	-	-	+	P	M	-	C
129.	*Pseudo-nitzschia seriata* (P.T. Cleve) H. Peragallo 1899 **	-	+	-	P	M	-	C
130.	*Pseudosolenia calcar-avis* (Schultze) B.G. Sundström 1986	+	-	+	P	M	-	BT
131.	*Ralfsiella smithii* (Ralfs) P.A. Sims, D.M. Williams et M. Ashworth 2018	-	-	+	P	M	-	B not
132.	*Rhabdonema arcuatum* (Lyngbye) Kützing 1844	+	+	+	B	M	-	C
133.	*Seminavis ventricosa* (Gregory) M. Garcia-Baptista 1993	+	-	+	B	M	β	C
134.	*Skeletonema costatum* (Greville) P.T. Cleve 1873	+	-	-	P	BM	α	C
135.	*Striatella unipunctata* (Lyngbye) C.A. Agardh 1832	+	+	+	B	M	-	BT not
136.	*Tabularia fasciculata* (C.A. Agardh) D. Williams et Round 1986	+	+	+	B	BM	χ-o	C
137.	*Tabularia parva* (Kützing) D. Williams et Round 1990	-	+	-	B	BM	α	ABT not
138.	*Tabularia tabulata* (C.A. Agardh) Snoeijs 1992	+	+	-	B	BM	α-β	C
139.	*Tetramphora ostrearia* (Brébisson) Mereschkowsky 1903	+	-	+	B	M	-	BT
140.	*Thalassionema nitzschioides* (Grunow) Mereschkowsky 1902	+	-	+	BP	M	-	C
141.	*Thalassiophysa hyalina* (Greville) Paddock et P.A. Sims 1981	+	-	+	BP	M	-	BT
142.	*Thalassiosira eccentrica* (Ehrenberg) P.T. Cleve 1904	+	+	-	P	M	-	C
143.	*Thalassiosira parva* Proschkina-Lavrenko 1955	+	-	+	P	BM	-	B
144.	*Toxonoidea insignis* Donkin 1858	-	-	+	B	M	-	B
145.	*Trachyneis aspera* (Ehrenberg) P.T. Cleve 1894	+	+	+	B	M	-	ABT not
146.	*Tryblionella coarctata* (Grunow) D.G. Mann 1990	+	+	-	B	BM	-	BT
147.	*Tryblionella granulata* (Grunow) D.G. Mann 1990	+	-	+	B	M	-	C
148.	*Tryblionella punctata* W. Smith 1853	-	-	+	B	B	-	C

Table A1. *Cont.*

	Taxon	MS	Eph	BS	H	RS	S	PhG
149.	*Undatella lineolata* (Ehrenberg) L.I. Ryabushko 2006	+	+	+	B	BM	β	ABT
150.	*Undatella quadrata* (Brébisson ex Kützing) Paddock et P.A. Sims 1980	+	+	+	B	BM	-	B
Total diatom species		87	76	91			44	
Total microalgae species		102	77	97				

Note: (-) species is absent; * new species in the Black Sea; (+) the species was present in the sample; ** potentially harmful species; H habitat: B benthos, P plankton, BP benthoplankton; ecotopes: mussel shells (MS), epiphyton (Eph), bottom sediments (BS); the relation of species to water salinity (RS): M marine, B brackish, BM brackish–marine, FW freshwater species; saprobity (S): α-mesosaprobic, β-mesosaprobic, α-β-mesosaprobic, o-β-mesosaprobic, o oligosaprobic, χ xenosaprobic, χ-o xenooligosaprobic; PhG phytogeographic elements: B boreal species, AB arctical–boreal, BT boreal–tropical, ABT arctical–boreal–tropical, C cosmopolite, not = notal species found in the northern and southern hemispheres.

Table A2. Species of macroalgae, sampling date, and water temperature at different depths, the number of diatoms and dominant species, mean ± SD of abundance (N), biomass (B), and Shannon index (H) of epiphyton diatoms on the mussel farm.

No.	Species of Macroalgae	Sampling Date and t °C	Depth, m	Number of Species	$N \times 10^3$, Cells/cm^2	H	B, mg/cm^2	Dominant Diatom Species
1	*Phyllophora crispa*	20 July 2018 (25 °C) 15 August 2018 (26.6 °C) 18 September 2018 (24.4 °C) 21 October 2019 (18.0 °C)	10.0 12.0 17.0 17.0	26 13 12 21	1118 ± 375 290 ± 45.6 103 ± 35.2 170 ± 8.0	4.2 3.3 3.5 4.3	3.24 ± 0.68 1.16 ± 0.17 0.041 ± 0.01 0.98 ± 0.1	*Tabularia fasciculata* *Pseudo-nitzschia seriata* *Tabularia tabulata* *Licmophora abbreviata*
		Total number of species		43				
2	*Ulva rigida*	20 July 2018 (25.0 °C) 17 January 2019 (8.6 °C)	12.0 4.5	16 10	58 ± 2.7 24 ± 6.4	2.6 3.1	0.1 ± 0.02 0.03 ± 0.002	*P. seriata* *L. abbreviata*
		Total number of species		21				
3	*Cladophora vadorum*	17 January 2019 (8.6 °C)	4.5	10	18 ± 12.0	2.9	0.02 ± 0.01	*L. abbreviata*
4	*Nereia filiformis*	20 July 2018 (25.0 °C) 15 August 2018 (26.6 °C) 21 October 2019 (18.0 °C)	12.0 12.0 17.0	20 14 14	368 ± 32.1 1001 ± 156.5 47 ± 21.7	3.2 2.5 3.7	1.1 ± 0.12 2.06 ± 0.53 0.36 ± 0.2	*P. seriata* *P. seriata* *L. abbreviata*
		Total number of species		29				
5	*Laurencia coronopus*	8 February 2019 (8.6 °C)	4.0	17	257 ± 53.0	3.7	1.08 ± 0.04	*L. abbreviata*
6	*Ceramium secundatum*	8 February 2019 (8.6 °C)	4.0	16	149 ± 19.6	3.4	0.37 ± 0.04	*Grammatophora marina*
7	*Callithamnion corymbosum*	4 March 2019 (10.0 °C)	6.0	20	21 ± 1.10	3.3	0.08 ± 0.008	*Gr. marina*
8	*Bryopsis plumosa*	4 March 2019 (10.0 °C)	6.0	20	394 ± 8.7	2.9	0.66 ± 0.03	*Gr. marina*
9	*Pyaiella littoralis*	4 March 2019(10.0 °C) 4 April 2019 (9.8 °C)	6.0 3.0	19 16	96 ± 15.2 173 ± 13.4	3.0	0.26 ± 0.03 0.53 ± 0.017	*T. fasciculata* *Licmophora oedipus*
		Total number of species		29				
10	*Ulva clathrata*	4 April 2019 (9.8 °C)	3.0	13	55 ± 2.8	1.3	0.08 ± 0.01	*L. abbreviata*
11	*Ceramium arborescens*	4 April 2019 (9.8 °C)	3.0	14	83 ± 22.0	2.9	0.28 ± 0.03	*Licmophora paradoxa*
12	*Ulva compressa*	4 April 2019 (9.8 °C)	3.0	16	179 ± 12.9	3.4	1.0 ± 0.07	*L. oedipus*
13	*Feldmannia paradoxa*	14 May 2019 (15.0 °C)	2.0	20	28 ± 4.3	3.0	1.3 ± 0.01	*L. abbreviata*
14	*Ericaria crinita*	14 June 2019 (22.0 °C)	6.0	27	19 ± 4.8	4.3	0.08 ± 0.01	*Navicula ramosissima*
15	*Ulva torta*	16 March 2020 (8.1 °C)	2.0	23	16 ± 2.0	1.0	0.08 ± 0.01	*L. abbreviata*

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