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INFLUENCE OF ENVIRONMENTAL FACTORS ON MICROALGAE IN MARINE COASTAL SALINE SOIL

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Abstract

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This study analyzes the influence of abiotic factors on the microalgae in marine coastal saline soils. The analysis revealed 38 species of microalgae in the studied area. Cyanobacteria comprised the largest proportion of the found species. The species richness and biodiversity indicators depend on soil moisture, while relative abundance negatively correlates with chloride content. The results of permutational multivariate analyses of variance showed a marginal influence of moisture and sodium on the structure of microalgal communities. The factors beyond chemical properties and soil moisture (e.g. surge-related (tidal) phenomena) explain the observed microalgal quantitative and qualitative features. *Leptolyngbya foveolarum* and *Micractinium* sp., owing to their high values of occurrence frequency and relative abundance, may hold potential for the biological optimization of saline soils.

Key words: algae, Cyanobacteria, species richness, relative abundance, soil moisture, chemical composition.

Introduction

Soil microalgae play a crucial role in ecosystem functioning (hereafter, we will refer to both eukaryotic microscopic algae and cyanobacteria). The species richness and structure of microalgal communities depends on soil abiotic factors (Alghanmi, Muttar, 2018), and the algae themselves influence the soil by changing its quality (Chamizo et al., 2018; Afify et al., 2023; Young et al., 2024). Using different strategies of adaptation and due to the excretion of exopolymeric substances, microalgae can inhabit various habitats, including extreme ones (Rossi et al., 2018; Gunde-Cimerman et al., 2018). An example of such a habitat could be saline soils and hyperhaline water bodies, where organisms have an adverse effect due to osmotic and desiccation stress (Ruhl et al., 2018). Water or soil moisture in this case is a factor that reduces the impact of such stress (Karsten, Holzinger, 2012).

Recent papers confirm that salinity is one of the strongest environmental drivers of microbial evolution and community composition, which is very clearly noticeable in hyperhaline reservoirs (Kimbrel et al., 2018; Solonenko, Bren, 2020; Bren et al., 2022). Experimental studies have proved that among different chemical compounds, chlorides and sulfates can inhibit algal growth in an aquatic environment (Mera et al., 2015; Sikorski, 2021). A similar trend is observed for saline soils of continental areas—among individual ions, the greatest limiting effect on the microalgal communities is exerted by Na^+ and Cl^- (Sommer et al., 2020; Wu et al., 2022). Another article reveals the peculiarities of the influence of sodium, which can have both a stimulating and an inhibitory effect in different cases (Matos et al., 2024).

Coastal saline soils (salt marshes, solonchak) differ from continental soils due to the presence of surge processes and, therefore, the variability in water regime. This may determine the corresponding influence and differences in biota. However, these publications provide similar data on the negative effects of salinity on microorganisms. An overall trend was observed in the cyanobacterial communities where genetic diversity increased with rising salinity, while relative abundance was higher under lower-salinity conditions (Li et al., 2015). In coastal estuarine wetlands, a similar situation is observed—a higher relative abundance of cyanobacteria is observed in low salinity. It has also been established that soil salinity acts as a critical inhibitor in the soil biogeochemical processes in estuary ecosystems (Zhang et al., 2020). Investigation of microalgae from soils of the sea coast demonstrates that there is a positive effect of salinity and conductivity on the quantitative characteristics of some halotolerant algae (Morkoyunlu, Altundağ, 2020).

Microorganisms (including microalgae) can disperse widely (Fontaneto, 2011; Martiny, 2015), staying in an active vital or a dormant state (Stenström et al., 2001; Locey, 2010; Greening et al., 2019). When conditions match the species niche, such organisms can actively grow, coming out of dormancy (Lennon et al., 2012). In the first case, the lower influence of the environmental

factor allows the species to grow stronger and increase quantitatively. In another situation, the conditions in areas with lower influence of factors would be such that the dormancy of some organisms would be interrupted, and then more species would be observed in the samples; therefore, the species richness in such samples would be higher. It is possible for both events to occur simultaneously. A suitable hypothetical scenario for coastal marine soils has not been established. It also remains unclear which environmental factors influence species richness, relative abundance, occurence frequency and biodiversity of microalgae

Considering the possibility of using microalgae for the bioindication of saline biotopes, as well as in eliminating soil erosion and salinization (Song et al., 2022; Jebin, George, 2024), it is important to understand the influence of abiotic factors on the development of microalgae, such as chemical properties, pH, and soil moisture. Here, it is important to understand which factors predominate in influencing the existence of microalgae in extreme habitats, which in turn can indicate the most viable and suitable species for further practical use. With high soil salinity, higher plants in most cases stop their growth and distribution, while some microalgal species remain viable, which further determines the importance of their study and practical application. The purpose of this research was to establish the most essential physical and chemical characteristics of saline soils of the marine coast on the quantitative and qualitative parameters of microalgae and find microalgal species for further testing and practical use in the biological optimization of saline soils.

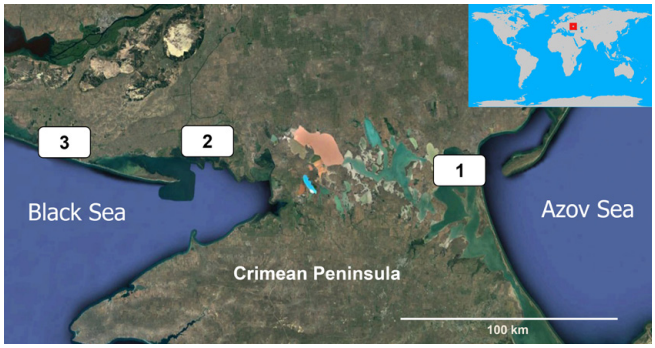

Fig. 1. Map of sampling sites on the coasts of the Azov and Black seas. The numbers indicate sampling locations.

Table 1. Coordinates and brief description of the sample sites.

Sampling site	Brief description	Sample	Coordinates	
1	Kherson region, Arabat spit	1	46°07‘22.86“N	34°48‘49.20“E
		2	46°02‘33.78“N	34°49‘26.17“E
		3	45°56‘22.94“N	34°51‘27.12“E
2	Kherson region, Tarasovka vicinity	4	46°08‘16.09“N	33°06‘14.30“E
		5	46°08‘06.15“N	33°06‘37.89“E
		6	46°07‘38.74“N	33°07‘16.07“E
		7	46°07‘31.21“N	33°08‘04.55“E
		8	46°07‘48.79“N	33°08‘34.84“E
		9	46°08‘07.47“N	33°08‘39.40“E
3	Kherson region, Lazurne vicinity	10	46°06‘03.46“N	32°29‘19.98“E
		11	46°05‘32.54“N	32°28‘05.26“E
		12	46°05‘15.12“N	32°26‘55.33“E
		13	46°05‘25.43“N	32°29‘18.46“E
		14	46°04‘54.38“N	32°29‘30.72“E
		15	46°04‘10.83“N	32°32‘17.80“E
		16	46°04‘03.79“N	32°32‘26.42“E
		17	46°04‘00.99“N	32°32‘34.18“E

Material and methods

Study area and data collection

This study was conducted in the Kherson region using the expeditionary route method during the summer of 2018. For the current study, we collected 17 composite soil samples (each sample consisted of 10–15 individual ones within one facies) from three sample sites (Fig. 1, Table 1). The soil was not flooded during sampling. The sampling sites were devoid of higher vegetation and visible algal crusts.

Cultivation and identification

Samples were studied by direct microscopy; during cultivation, they were studied using microscope Olympus BX51. For cultivation, we used agar solidified and liquid Bold's basal medium with single and triple nitrogen content (1N and 3N) with and without addition of the soil extract (Bold, 1949; Bischoff, Bold, 1963). The cultures were grown in a light stand with fluorescent lamps at 12:12 h dark and light phases with an intensity of 20 μmol photons m^{-2} s^{-1} at a temperature of 23–25 °C. The cultures were examined under a microscope for 30 days. The organisms were determined to be in the living state. Bacillariophyta representatives have also been identified on permanent microslides (Hasle, Heimdal, 1970).

Identification of species was performed using guides for each phylum: for Cyanoprokaryota (Komárek, Anagnostidis, 1998, 2005; Komárek, 2013), Chlorophyta (Ettl, Gärtner, 1988; Tsarenko, 1990; Andreieva, 1998), and Bacillariophyta (Krammer, Lange-Bertalot, 1986-2004). The names of phyla, classes, orders, families, genera, and species are given in accordance with the current nomenclature changes of individual species and intraspecific taxa (Guiry, M.D., Guiry, G.M., 2023). The relative abundance of microalgae in each sample was estimated using the following scale: 0 = absent, 1 = observed once, 2 = rare, 3 = occasionally, 4 = frequent, 5 = abundant (Schulz et al., 2016). The frequency of occurrence was determined as the quotient of the number of observations of a certain species from the total number of samples studied. We considered those species dominant whose frequency of occurrence was above a threshold value and was defined as the quotient of the total number of observations of microalgae during the microscopical examination of samples divided by the number of observed species.

Chemical analysis

The soil samples were dried at 105 °C to a constant weight and then analyzed. pH was measured in 1 M KCl by pH-meter Ulab MP 512 (PRC). Soil moisture was estimated by gravimetric method (State standards of Ukraine 11465:2001, 7908:2015, 7943:2015, 7945:2015). Electrical conductivity was determined

using a dried soil sample placed and mixed in deionized water (mass ratio- 1:5) using the EC800 laboratory benchtop conductivity meter. The sulfate content (SO_4^{2-}) was estimated spectrophotometrically using a Thermo Scientific GENESYS 10S ultraviolet–Vis spectrophotometer (Waltham, USA). The chlorides and hydrocarbonates were determined using Mohr's method and acid titration, respectively. Ca^{2+} and Mg^{2+} levels were determined in a complex manner. Na^+ and K^+ were analyzed using flame photometer Jenway PFP7 (Sheung Wan, Hong Kong).

Statistical analysis

Correlations between algal species composition, diversity indices, and environmental factors were assessed using Pearson's parametric correlation test. Biodiversity assessment was conducted using Simpson's 1-D and Shannon indices. To display the multidimensional data structure, non-metric multidimensional scaling (nMDS) was used in three-dimensional space for dissimilarity matrix (Bray–Curtis distance) of the microalgal presence/absence with log-transformed values for continuous numerical data. All the above-mentioned statistical analyses and calculations were performed using PAST 5.3 (Hammer et al., 2001). To assess the influence of environmental factors on a certain species composition in samples, we used one-way permutational multivariate analyses of variance (perMANOVA with Jaccard distance) (9999 permutations), which was performed using vegan package in R (Version 4.3.2) (Oksanen et al., 2017).

Results

The content of chlorides and sulfates indicates the predominance of chloride salinity in the studied soils. Chlorides vary in a significantly wide range from 150.4 ± 0.6 to 2125.1 ± 0.5 mg/kg of soil, while the content of sulfates ranges from 21.0 ± 0.3 to 340.5 ± 0.6 mg/kg of soil. The studied soils are characterized by pH ranging from close to neutral (7.15 ± 0.06) to alkaline (9.10 ± 0.02). The content of hydrocarbonates is not very high (from 4.0 ± 0.2 to 8.0 ± 0.4 mg/kg), with the exception of one sample (17), where their concentration is 61.0 mg/kg. There are variations in the calcium, magnesium, and sodium content of the soils. The potassium content is consistently low (1.8 ± 0.5 to 40.1 ± 0.4 mg/kg of soil) (Appendix 1).

Among the analyzed chemical compounds, the highest values of the Pearson correlation index were observed between chloride ions and Mg^{2+}, K^+, and Na^+ (0.82, 0.63, and 0.66, respectively; $p < 0.01$), as well as in pairs between the cations themselves: K^+ with Na^+ ($r = 0.61$, $p < 0.05$), Mg^{2+} with Na^+ ($r = 0.58$, $p < 0.05$), and Mg^{2+} with K^+ ($r = 0.55$, $p < 0.05$). The highest correlation of pH values was observed with K^+ ($r = 0.51$, $p < 0.05$). High and statistically reliable values between other abiotic factors were not established in the study for hydrocarbonates, sulfates, and calcium ions (Appendix 1).

In the studied coastal soil, we identified 38 algal species, represented by three phyla, among which the majority were representatives of Cyanobacteria. The second and third places in terms of the number of species were held by Chlorophyta and Bacillariophyta (Table 2). The leading families were: Bacillariaceae and Leptolyngbyaceae (six species each), Oscillatoriaceae (five species), and Trichocoleusaceae, Nostocaceae, Aphanizomenonaceae, and Ctenocladaceae (two species each). *Phormidium*, *Leptolyngbya* (five species), and *Nitzschia* (three species) are among the leading genera. The prevalence of Cyanobacteria is notable at the level of dominant families and genera, which is typical for saline soils on the Azov–Black Sea coast. Low species richness combined with low species richness of genera (1.52) can be explained by the extreme conditions of salt marshes. All identified species were typical for the algal flora of the region, and no new or previously undescribed taxa were found during our study.

Five species had the highest frequency of occurrence: *Leptolyngbya foveolarum* (58.8%), *Parietochloris pseudoalveolaris*, *Hantzschia amphioxys* (both 29.4%), *Trichormus thermalis*, and *Ctenocladus* sp. (both 17.6%) (Appendix 2). Other species had lower frequency values below the established limit.

The analysis of biodiversity based on Simpson's 1-D and Shannon indices revealed significant differences between the studied sites. In several locations (1, 2, 10, 11, and 14), minimal species richness was recorded, as indicated by zero values of Simpson's 1-D and Shannon indices, confirming the dominance of a single species. The highest biodiversity was observed at sites 4, 5, 12, 13, and 15, where Simpson's 1-D index approached 1 and Shannon index values were also high (>2.0), indicating an even distribution of species (Table 3).

Table 2. Taxonomic structure of microalgae in the studied salt marshes.

Phylum	Class	Order	Family	Genus	Species
Cyanobacteria	1	4	8	9	20 (52.6%)
Chlorophyta	3	5	7	8	8 (21.1%)
Bacillariophyta	1	4	5	8	10 (26.3%)
Total	4	13	20	25	38 (100%)

Table 3. List of microalgal species with frequency of their occurrence in the studied salt marshes.

Sampling sites	Indices	
	Simpson_1-D	Shannon
1	0	0
2	0	0
3	1	0.94
4	0.92	2.34
5	1	2.52
6	1	1.76
7	1	1.43
8	1	1.76
9	1	0.94
10	0	0
11	0	0
12	0.90	2.15
13	1	2.01
14	0	0
15	1	3.03
16	0.57	0.75
17	1	0.94

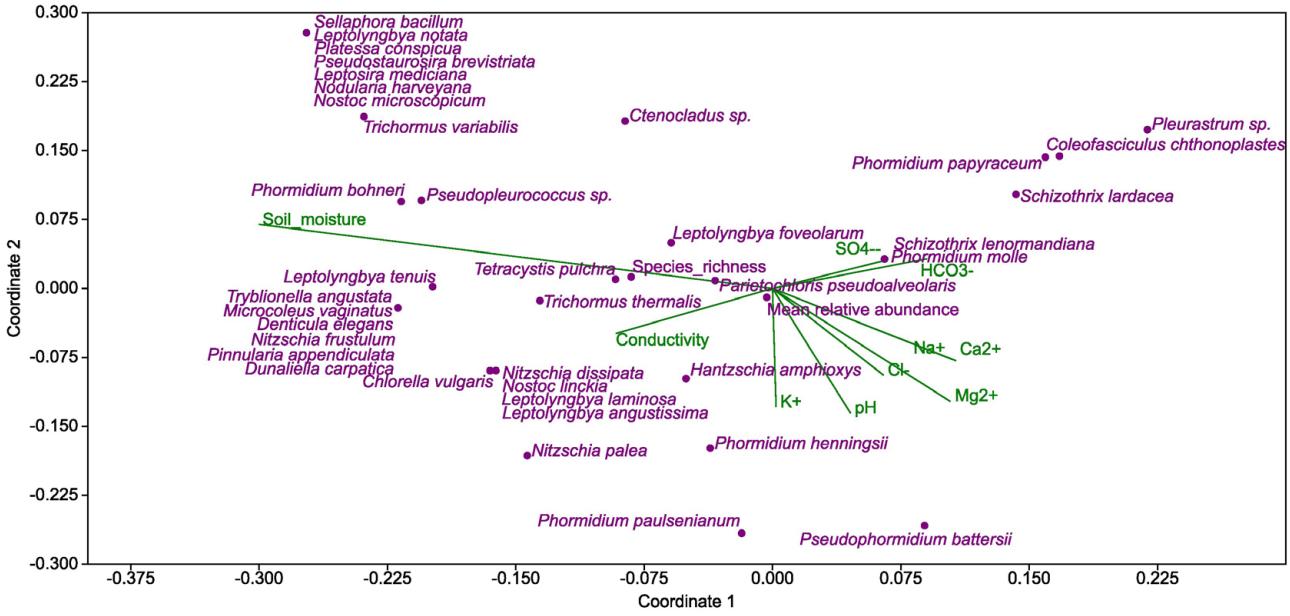

Fig. 2. The influence of environmental variables on the microalgal species, their species richness, and relative abundance (nMDS plot; stress = 0.15).

General trends in the impact of environmental factors on representatives of different phyla could be observed through nMDS. Soil moisture clearly stood out among other abiotic factors along the vector of which most microalgal species were located. Another important factor around the vector of which species were also located in the ordination field was conductivity, which also partially depends on soil moisture. In the lower right part of the plot, there is not a single species where the influence of the majority of ions is located, which may indicate the absence of influence or even a negative effect of these substances on the growth of certain microalgal species (opposite lower left and upper left parts of the plot consequently) (Fig. 2).

The results of perMANOVA showed a marginally significant relationship at the level of $p < 0.1$ between species structure on the sampling sites and only with factors such as Na^+ and soil moisture. However, the variance explained by these factors (within-group sum of squares) constituted a fairly small part of the total variance (total sum of squares), as observed by the coefficient of determination (R^2), which explains the variability in species composition only for 9.3% by the influence of Na^+ and for 8.6% by soil moisture of the total variance. For both these factors, F-values exceed 1, indicating that these two factors have an influence on the differences between groups of species at different sampling sites (Table 4).

The aspects of the influence of environmental factors on microalgae can be more clearly traced using correlation analysis. A correlation of medium strength was observed only between some species and several abiotic factors: *Leptolyngbya foveolarum* with Na^+ ($r = -0.54$, $p < 0.05$) and K^+ ($r = -0.50$, $p < 0.1$), *Coleofasciculus chthonoplastes* with $HCO3^-$ ($r = 0.65$, $p < 0.01$), *Parietochloris pseudoalveolaris* with Ca^{2+} ($r = -0.56$, $p < 0.05$), and *Pseudopleurococcus* sp. with Cl^- ($r = -0.61$, $p < 0.01$), Mg^{2+} ($r = -0.58$, $p < 0.05$), and Na^+ ($r = -0.66$, $p < 0.01$).

A strong negative correlation between chloride ions and average relative abundance was found ($r = 0.82$, $p < 0.01$). Among the analyzed data, the strongest correlation was found between soil moisture content and species richness in the samples ($r = 0.94$, $p < 0.01$), as well as between moisture and diversity indices ($r = 0.89$ for Shannon and $r = 0.73$ for Simpson 1-D, $p < 0.01$). However, no significant correlation was found between these parameters and other abiotic factors.

There was also a moderate correlation between soil moisture and the presence of certain species: *Phormidium bohneri* ($r = 0.57$, $p < 0.05$), *Trichormus variabilis* ($r = 0.62$, $p < 0.01$), *Leptolyngbya notata*, *Nostoc microscopicum, Nodularia harveyana*, *Leptosira mediciana, Pseudostaurosira brevistriata, Sellaphora bacillum*, and *Platessa conspicua* ($r = 0.51$, $p < 0.05$). A correlation was found between soil electrical conductivity and ions such as Na^+, Mg^{2+}, K^+, and Cl^-, as well as a moderate correlation with *Phormidium bohneri* ($r = 0.53$, $p < 0.01$) (Appendix 3).

Discussion

The coastal saline soil exhibited relatively low microalgal species richness, low frequency of occurrence for most species, and low values of relative abundance. Cyanobacteria dominated at all taxonomic levels. Such characteristics of partial algal flora are typical for the entire Azov–Black Sea coast, which has been reliably confirmed by earlier studies (Kostikov et al., 2001; Vinogradova, 2012; Arabadzhy-Tipenko et al., 2019).

Despite the lack of competition with higher plants on the highly saline marine coastal soils, we did not observe the same large species richness noted on the potash-tailings pile (Sommer et al., 2020). This may indicate the predominance of certain abiotic factors that influence microalgae over biotic ones. The absence of higher plants on such soils suggests that microalgae can

Table 4. Influence of abiotic conditions on species composition in the samples tested by perMANOVA; given in the table are df: degrees of freedom, F-value, R^2-value (the variation of species in the isolate composition explained by the respective factor), and *p*—level of significance ($p < 0.1$ is in bold).

	df	Total sum of squares	Within-group sum of squares	R^2	F	p-Value
pH	1	6.6206	0.2714	0.0410	0.6413	0.88
$HCO3^-$	1	6.6206	0.3218	0.0486	0.7663	0.83
Cl^-	1	6.6206	0.3018	0.0456	0.7164	0.80
$SO4^{2-}$	1	6.6206	0.4726	0.0714	1.1531	0.29
Ca^{2+}	1	6.6206	0.3684	0.0557	0.8839	0.60
Mg^{2+}	1	6.6206	0.3183	0.0481	0.7575	0.76
Na^+	1	6.6206	0.6186	0.0934	1.5460	**0.08**
K^+	1	6.6206	0.5699	0.0861	1.4129	0.12
Soil moisture	1	6.6206	0.6282	0.0861	1.5725	**0.08**
Conductivity	1	6.6206	0.4743	0.07165	1.1576	0.29

be used for quasi-natural optimization of saline coastal soils. The relatively small number of microalgae species we found narrows the search for candidates for such a task. Higher frequency and relative abundance scores for *Leptolyngbya foveolarum*, as well as high relative abundance scores for *Micractinium* sp. indicate their potential for this application.

According to the nMDS ordination, and as further supported by the correlation analysis, soil moisture is an important environmental factor influencing microalgal species richness. In addition, some individual species demonstrated a positive mid-strong significant correlation with soil moisture (Appendix 3).

Another strong correlation we found was a negative relationship between relative abundance and the content of chloride ions in the soil. A similar effect was noted in previous works (Li et al., 2015; Mera et al., 2015; Sikorski, 2021). At the same time, conductivity does not have such a pronounced correlation as chlorides. Considering that conductivity depends on both the ionic composition and water, moisture probably exerts the same effect of reducing osmotic stress (Karsten, Holzinger, 2012).

The results of the correlation analysis indicated a negative dependence of the medium strength between the ions and several species of microalgae. The only positive but medium-strong correlation was between hydrocarbonates and *Coleofasciculus chthonoplastes*. Among the species, we did not detect a strong stimulating effect of salinity (conductivity), as indicated for some species, for example, for *Hantzshia amphioxys* (Morkoyunlu, Altundağ, 2020), which was also present at our sample sites (Table 4).

It is also important to note that the vast majority of organisms in extreme habitats have a wide niche to a certain environmental factor (Coker, 2019; Sánchez-Otero et al., 2019). For this reason, even the high chloride content in the soil that we observed could be within the boundaries of the niches of the detected species. Therefore, the analyzed ions do not have a clear effect on their occurrence (except *Pseudopleurococcus* sp.) (Appendix 3).

The results of perMANOVA further confirmed the importance of soil moisture in the life of microalgae and qualitatively determined the species composition in the gradient of the environmental factor. In addition to soil moisture, the results for sodium were also significant in this analysis (Table 4). The effect of sodium on species composition was not observed by ordination and correlation methods. Such features of this ion indicate that it may not have a direct effect, but can be present in combination with other factors, which is consistent with the effects of sodium in different conditions and concentrations reported in the literature (Matos et al., 2024).

It should be noted that none of the statistical analyses we used in our study revealed a significant relationship between species richness and conductivity or content of chlorides, which was described previously (Li et al., 2015). Therefore, in the studied areas, we did not observe an impact of the reduced salinity content in the microalgal species richness. Nevertheless, we registered a strong correlation between chlorides and relative abundance, as also reported in scientific papers (Li et al., 2015; Zhang et al., 2020). Thus, we infer that the reduced content of chloride ions does not "open" a niche for introduction of new species or termination of dormancy for some organisms, but allows those species that are already present in a given facies to grow and increase in quantity.

The low perMANOVA determination coefficients for Na^+ concentration and soil moisture indicate that the distribution and species composition of microalgae in saline coastal soils are governed by additional factors beyond those analyzed in this study. A combination of factors such as surge processes, microrelief, and the presence of the waterproofing layer not only determine the heterogeneity of soil conditions at the facies level, but also influence the microalgae.

Conclusion

The species richness of microalgae in marine coastal saline soils is low, with cyanobacteria dominating at all taxonomic levels. Among all the analyzed abiotic factors, chloride ions and soil moisture had the strongest effects on the quantitative parameters of the microalgae.

We revealed the separate influence of the physical and chemical properties of soils on microalgae. Species richness and biodiversity depend on moisture availability, and relative abundance is negatively correlated with chlorides. Qualitative features, such as species structure in each sample (facies), depend on moisture and Na^+, although the latter likely acts in combination with other factors, rather than directly. This gives us reason to conclude that the qualitative and quantitative characteristics of microalgae in coastal saline soils depends on a combination of factors, among

which chemical composition and moisture are important, but not decisive.

Considering the variability of the water regime and microrelief of marine coastal areas, surge processes probably can be such another important factor. This finding underlines the importance of taking abiotic factors into account when selecting organisms for soil biological optimization. The main properties of suitable organisms include the ability to attach to the topsoil surface even under conditions of water movement, to survive unfavorable periods through dormancy, and to rapidly resume growth once conditions improve. Such traits enable them to quickly proliferate, stabilize the substrate, prevent erosion, and contribute to primary production.

A reasonable continuation of this work may be to determine the niche borders and optima of the identified microalgal species in relation to various abiotic factors. Further research may involve a more in-depth study of strains, the use of a polyphasic approach to determine taxonomic characteristics, as well as an experimental assessment of the potential application of the isolated strains for optimizing the properties of saline soils. Among the species we identified, our attention falls on *Leptolyngbya foveolarum* and *Micractinium* sp., which we propose for testing and use.

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Appendix 1. Results of chemical analysis of the studied saline soils (x ± SD), mg/kg of soil (the last column is in pH units).

Sample	HCO_3^-	Cl^-	SO_4^{2-}	Ca^{2+}	Mg^{2+}	Na^+	K^+	Soil moisture	Conductivity	pH
	mg/kg	mg/kg	mg/kg	mg/kg	mg/kg	mg/kg	mg/kg	%	µS/cm	
1	8.0 ± 0.4	2125.1 ± 0.5	55.1 ± 0.4	172.4 ± 0.7	650.2 ± 0.6	1326.2 ± 0.4	40.1 ± 0.4	7.1 ± 0.3	161.8 ± 7.9	8.80 ± 0.23
2	4.0 ± 0.2	312.9 ± 0.4	184.5 ± 0.3	61.3 ± 0.8	173.1 ± 0.4	2504.2 ± 0.4	8.4 ± 0.6	8.1 ± 0.2	132.4 ± 8.5	8.35 ± 0.12
3	8.9 ± 0.8	1555.2 ± 0.5	55.5 ± 1.0	253.2 ± 0.4	482.3 ± 0.7	850.4 ± 1.0	31.9 ± 0.8	19.3 ± 0.4	217.8 ± 5.0	7.66 ± 0.21
4	5.1 ± 0.2	509.9 ± 0.7	127.6 ± 0.5	50.0 ± 0.9	126.2 ± 0.5	456.3 ± 0.5	9.8 ± 0.6	38.8 ± 0.2	144.2 ± 8.9	8.65 ± 0.17
5	5.1 ± 0.7	640.1 ± 0.9	358.4 ± 0.4	235.2 ± 0.6	285.3 ± 0.8	481.6 ± 1.0	3.4 ± 0.3	27.4 ± 0.5	176.2 ± 10.3	7.45 ± 0.06
6	5.2 ± 0.7	765.3 ± 0.7	308.2 ± 0.4	147.1 ± 0.6	359.9 ± 0.6	565.2 ± 1.2	8.7 ± 0.5	12.5 ± 0.3	117.4 ± 11.1	9.10 ± 0.02
7	6.2 ± 0.4	1012.2 ± 0.8	340.5 ± 0.6	181.3 ± 1.0	325.2 ± 0.3	872.1 ± 0.9	31.5 ± 1.0	9.3 ± 0.2	120.6 ± 7.2	7.64 ± 0.05
8	6.1 ± 0.3	1096.5 ± 0.7	330.4 ± 0.8	91.9 ± 0.6	582.1 ± 0.4	740.5 ± 1.2	19.0 ± 0.5	11.8 ± 0.2	141.8 ± 5.6	7.02 ± 0.30
9	7.1 ± 0.5	1062.3 ± 0.4	25.8 ± 0.6	80.2 ± 0.8	161.8 ± 0.2	854.4 ± 0.8	4.3 ± 0.5	12.1 ± 0.2	113.2 ± 7.7	8.46 ± 0.34
10	6.1 ± 0.2	765.2 ± 0.4	264.6 ± 0.5	300.2 ± 0.6	430.1 ± 0.4	304.4 ± 0.7	1.8 ± 0.5	5.2 ± 0.2	61.2 ± 8.9	7.15 ± 0.06
11	7.2 ± 0.2	1275.3 ± 0.4	270.1 ± 0.3	140.3 ± 0.5	352.2 ± 0.6	1043.6 ± 0.9	19.1 ± 0.6	6.4 ± 0.2	109.2 ± 6.0	8.95 ± 0.23
12	5.1 ± 0.2	150.4 ± 0.6	56.3 ± 0.6	70.3 ± 0.5	50.1 ± 0.5	87.5 ± 0.4	3.4 ± 0.5	32.4 ± 0.5	38.8 ± 5.6	8.70 ± 0.46
13	5.9 ± 0.2	850.7 ± 0.9	217.3 ± 0.5	115.1 ± 0.2	345.3 ± 0.8	808.3 ± 0.5	5.2 ± 0.4	15.3 ± 0.3	142.4 ± 7.0	8.80 ± 0.10
14	5.8 ± 0.1	1360.6 ± 0.5	21.0 ± 0.3	250.2 ± 0.5	403.9 ± 0.3	720.4 ± 0.3	17.4 ± 0.8	11.2 ± 0.3	136.4 ± 12.2	7.65 ± 0.05
15	4.9 ± 0.3	1275.3 ± 0.5	76.3 ± 0.6	120.8 ± 0.8	313.1 ± 0.4	913.5 ± 0.3	13.4 ± 0.5	48.7 ± 0.3	346.2 ± 10.3	7.55 ± 0.05
16	4.9 ± 0.3	256.1 ± 0.5	247.6 ± 0.4	200.1 ± 0.4	110.3 ± 0.8	195.2 ± 0.6	3.1 ± 0.5	9.6 ± 0.2	57.2 ± 5.0	7.40 ± 0.28
17	61.0 ± 0.1	679.7 ± 1.0	138.4 ± 0.4	230.4 ± 0.5	89.9 ± 0.6	503.3 ± 0.9	6.1 ± 0.4	13.4 ± 0.3	96.2 ± 10.3	7.80 ± 0.42

Appendix 2. The list of abundance of soil microalgae and frequency of their occurrence in the sample sites.

Taxa	Sample sites																	Frequency of occurrence, %
	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	
Coleofasciculus chthonoplastes (Gomont) M. Siegesmund, J.R. Johansen & T. Friedl	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	1	11.8
Leptolyngbya angustissima	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	5.9
Leptolyngbya foveolarum (Gomont) Anagnostidis & Komárek	0	0	0	3	1	0	1	1	1	1	0	4	0	0	1	4	1	58.8
Leptolyngbya laminosa (Gomont) Anagnostidis & Komárek	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	5.9
Leptolyngbya notata (Schmidle) Anagnostidis & Komárek	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	5.9
Leptolyngbya tenuis (Gomont) Anagnostidis & Komárek	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	5.9
Microcoleus vaginatus Gomont	0	0	0	3	0	0	0	0	0	0	0	0	0	0	0	0	0	5.9
Nodularia harveyana Thuret ex Bornet & Flahault	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	5.9
Nostoc linckia Bornet ex Bornet & Flahault	0	0	0	0	0	0	0	0	0	0	0	3	0	0	0	0	0	5.9
Nostoc microscopicum Carmichael ex Bornet & Flahault	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	5.9
Phormidium bohneri Schmidle	0	0	0	0	1	0	0	0	0	0	0	0	0	0	1	0	0	11.8
Phormidium henningsii Lemmermann	0	0	0	0	1	1	0	0	0	0	0	0	0	0	0	0	0	11.8
Phormidium molle Lemmermann	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	5.9
Phormidium papyraceum Gomont	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	3	0	11.8
Phormidium paulsenianum J.B. Petersen	0	0	1	0	0	1	0	0	0	0	0	0	0	0	0	0	0	11.8
Pseudophormidium battersii (Gomont) Anagnostidis	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	5.9
Schizothrix lardacea Gomont 1892	0	0	0	0	0	0	0	1	0	0	0	0	1	0	0	0	0	11.8
Schizothrix lenormandiana Gomont	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	5.9
Trichormus thermalis (V.Vouk) Komárek & Anagnostidis	0	0	0	0	1	0	1	0	0	0	0	1	0	0	0	0	0	17.6
Trichormus variabilis (Kützing ex Bornet & Flahault) Komárek & Anagnostidis	0	0	0	0	0	0	0	0	0	0	0	2	0	0	1	0	0	11.8
Chlorophyta																		
Micractimium sp.	0	0	0	0	0	0	0	0	0	0	0	4	0	0	0	0	0	5.9
Ctenocladus sp.	0	0	0	0	0	0	0	0	0	0	0	3	1	0	1	0	0	17.6
Dunaliella salina (Dunal) Teodoresco 1905	0	0	0	3	0	0	0	0	0	0	0	0	0	0	0	0	0	5.9
Leptosira mediciana Borzì	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	5.9
Parietochloris pseudoalveolaris (T.R. Deason & Bold) Shin Watanabe & G.L. Floyd	1	3	0	3	0	0	0	0	0	0	1	3	0	0	0	0	0	29.4
Pleurastrum sp.	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	5.9
Pseudopleurococcus sp.	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	5.9
Tetracystis pulchra R.M. Brown & Bold	0	0	0	0	0	1	0	0	0	0	0	0	0	0	1	0	0	11.8
Bacillariophyta																		
Denticula elegans Kützing	0	0	0	2	0	0	0	0	0	0	0	0	0	0	0	0	0	5.9
Hantzschia amphioxys (Ehrenberg) Grunow	0	0	1	3	0	0	1	0	1	0	0	0	0	1	0	0	0	29.4
Nitzschia dissipata (Kützing) Rabenhorst	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	5.9
Nitzschia frustulum (Kützing) Grunow	0	0	0	2	0	0	0	0	0	0	0	0	0	0	0	0	0	5.9
Nitzschia palea (Kützing) W. Smith	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	5.9
Pinnularia appendiculata (C. Agardh) Schaarschmidt	0	0	0	2	0	0	0	0	0	0	0	0	0	0	0	0	0	5.9
Platessa conspicua (Ant. Mayer) Lange-Bertalot	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	5.9
Pseudostaurosira brevistriata (Grunow) D.M. Williams & Round	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	5.9
Sellaphora bacillum (Ehrenberg) D.G. Mann	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	5.9
Tryblionella angustata W. Smith	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	5.9

Appendix 3. Pearson correlation matrix between abiotic factors, species richness indices, species diversity indices, quantitative sample characteristics, and species occurrence ($p < 0.01$—values in bold; $p < 0.05$—values in italic).

	pH	**HCO_3^-**	**Cl^-**	**SO_4^{2-}**	**Ca^{2+}**	**Mg^{2+}**	**Na^+**	**K^+**	**Soil moisture**	**Conductivity**
pH										
HCO_3^-	0.32									
Cl^-	0.30	0.18								
SO_4^{2-}	0.33	−0.09	−0.21							
Ca^{2+}	0.05	0.34	0.38	0.08						
Mg^{2+}	0.21	−0.20	0.82	**0.12**	0.40					
Na^+	0.06	0.00	**0.63**	−0.03	−0.08	*0.58*				
K^+	0.51	0.06	**0.66**	−0.18	0.03	*0.55*	*0.60*			
Soil_moisture	−0.20	−0.10	−0.22	−0.21	−0.36	−0.36	−0.29	−0.08		
Conductivity	0.00	−0.06	**0.68**	−0.12	0.02	*0.57*	*0.71*	*0.58*	0.33	
Species richness	−0.18	−0.23	−0.13	−0.04	−0.30	−0.18	−0.25	−0.04	**0.94**	0.40
Shannon index	−0.03	−0.21	−0.16	0.10	−0.29	−0.16	−0.30	−0.04	**0.89**	**0.34**
Simpson_1-D	0.07	−0.15	−0.18	0.18	−0.26	−0.18	−0.33	−0.06	**0.73**	**0.20**
Mean relative abundance	−0.23	−0.32	**−0.83**	0.07	*−0.45*	**−0.67**	−0.36	−0.35	0.11	−0.47
Leptolyngbya angustissima	−0.17	−0.11	−0.07	0.27	0.24	0.05	−0.09	−0.27	0.27	0.19
Phormidium bohneri	−0.40	−0.18	0.09	0.09	0.13	0.09	0.03	−0.12	*0.57*	**0.53**
Leptolyngbya foveolarum	−0.10	0.11	−0.36	0.15	−0.10	−0.46	*−0.54*	−0.45	*0.35*	−0.27
Phormidium henningsii	0.06	−0.16	−0.05	0.37	0.20	0.13	−0.09	−0.21	0.17	0.13
Leptolyngbya laminosa	−0.17	−0.11	−0.07	0.27	0.24	0.05	−0.09	−0.27	0.27	0.19
Phormidium molle	0.25	−0.04	0.13	0.26	−0.20	0.30	0.06	0.20	−0.07	0.08
Phormidium paulsenianum	0.26	0.01	0.19	0.00	0.22	0.26	0.06	0.24	0.07	0.21
Phormidium papyraceum	−0.19	−0.14	−0.27	0.23	0.05	−0.14	−0.22	−0.34	−0.07	−0.22
Leptolyngbya tenuis	−0.19	−0.01	0.33	−0.29	0.15	0.23	0.18	0.33	0.47	0.61
Microcoleus vaginatus	0.32	−0.11	−0.15	−0.01	**−0.48**	−0.25	−0.10	0.02	0.42	**0.09**
Coleofasciculus chthonoplastes	0.01	**0.65**	−0.01	0.11	0.10	−0.19	0.02	−0.20	0.02	−0.03
Schizothrix lardacea	0.06	−0.07	0.12	0.29	−0.21	0.30	0.11	0.03	−0.02	0.11
Schizothrix lenormandiana	0.25	−0.04	0.13	0.26	−0.20	0.30	0.06	0.20	−0.07	0.08
Pseudophormidium battersii	0.25	−0.11	−0.01	0.24	0.03	0.13	−0.03	−0.01	−0.04	−0.02
Leptolyngbya notata	−0.38	−0.13	0.19	−0.15	−0.07	0.08	0.13	0.11	*0.51*	*0.53*
Nostoc linckia	−0.04	0.00	−0.25	−0.35	−0.03	−0.26	−0.40	0.05	0.35	−0.20
Nostoc microscopicum	−0.38	−0.13	0.19	−0.15	−0.07	0.08	0.13	0.11	*0.51*	*0.53*
Trichormus thermalis	−0.05	−0.16	−0.35	0.19	0.03	−0.28	−0.39	−0.12	0.29	−0.24
Trichormus variabilis	−0.40	−0.18	−0.31	−0.28	−0.29	−0.37	−0.39	−0.12	**0.62**	−0.03
Nodularia harveyana	−0.38	−0.13	0.19	−0.15	−0.07	0.08	0.13	0.11	*0.51*	*0.53*
Dunaliella salina	0.32	−0.11	−0.15	−0.01	**−0.48**	−0.25	−0.10	0.02	0.42	0.09
Parietochloris pseudoalveolaris	0.21	−0.19	−0.27	−0.10	*−0.56*	−0.26	0.08	0.17	−0.01	−0.18
Micractinium sp.	−0.04	0.00	−0.25	−0.35	−0.03	−0.26	−0.40	0.05	0.35	−0.20
Tetracystis pulchra	−0.09	−0.17	0.14	0.06	−0.03	0.15	0.07	0.07	0.34	0.38
Ctenocladus sp.	−0.44	−0.19	−0.24	−0.15	−0.30	−0.24	−0.27	−0.20	*0.55*	0.02
Leptosira mediciana	−0.38	−0.13	0.19	−0.15	−0.07	0.08	0.13	0.11	*0.51*	*0.53*
Pleurastrum sp.	−0.17	−0.06	0.04	0.14	−0.09	0.11	0.09	−0.16	0.04	0.08
Pseudopleurococcus sp.	−0.17	−0.11	**−0.61**	−0.24	−0.32	*−0.58*	**−0.66**	−0.27	0.35	*−0.57*
Pseudostaurosira brevistriata	−0.38	−0.13	0.19	−0.15	−0.07	0.08	0.13	0.11	*0.51*	*0.53*
Sellaphora bacillum	−0.38	−0.13	0.19	−0.15	−0.07	0.08	0.13	0.11	*0.51*	*0.53*
Pinnularia appendiculata	0.32	−0.11	−0.15	−0.01	*−0.48*	−0.25	−0.10	0.02	0.42	0.09
Platessa conspicua	−0.38	−0.13	0.19	−0.15	−0.07	0.08	0.13	0.11	*0.51*	*0.53*
Denticula elegans	0.32	−0.11	−0.15	−0.01	*−0.48*	−0.25	−0.10	0.02	0.42	0.09
Hantzschia amphioxys	0.11	−0.04	0.28	−0.49	−0.04	0.04	0.15	0.35	0.13	0.21
Tryblionella angustata	0.32	−0.11	−0.15	−0.01	*−0.48*	−0.25	−0.10	0.02	0.42	0.09
Nitzschia dissipata	−0.17	−0.11	−0.07	0.27	0.24	0.05	−0.09	−0.27	0.27	0.19
Nitzschia frustulum	0.32	−0.11	−0.15	−0.01	*−0.48*	−0.25	−0.10	0.02	0.42	0.09
Nitzschia palea	−0.04	0.00	0.14	0.02	0.38	0.20	0.02	0.05	0.30	*0.36*