

Article

Phytoplankton Diversity and Blooms in Ephemeral Saline Lakes of Cyprus

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Abstract: The ephemeral saline lakes of Cyprus in the Mediterranean, situated in close proximity to each other, demonstrate pronounced seasonal and interannual fluctuations in their environmental conditions. Despite their extreme saline conditions, these lakes support phytoplankton diversity and bloom-forming species. Anthropogenic activities, particularly urban and artificial land uses within their catchments, contribute to eutrophication, warranting conservation attention within the context of European legislation. Over two years (2018–2019), we examined phytoplankton abundance and diversity alongside salinity in six lakes, with samples collected every three weeks. Chlorophytes were the dominant and most diverse group, followed by cyanobacteria and diatoms. Increasing salinity correlated with reduced compositional diversity and species richness. The proximity of lakes to each other suggested airborne microbe colonization from one lake to another as a significant factor in shaping these communities, while similar land use within each lake's catchment impacted bloom formation. The highly halotolerant chlorophyte *Dunaliella* frequently dominated phytoplankton blooms, occasionally coexisting with other taxa in less saline lakes. Our findings provide insight into the phytoplankton community dynamics in temporal saline lakes, essential for developing effective conservation strategies and sustainable management practices.

Keywords: phytoplankton; temporal saline lakes; diversity; blooms; land use; *Dunaliella*



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1. Introduction

Saline lakes (salinity > 3 g L⁻¹) are significant components of the biosphere [1] since they account for almost half (~44%) of the volume of inland waters on the planet [2]. These lakes are associated with numerous ecosystem services, as documented by Williams [1]. They serve as vital resting and wintering grounds for migratory birds, provide habitats for distinctive yet often overlooked micro- and macro-organisms and serve as locales for cultural and recreational activities. Yet, their economic and ecosystem values have been either underestimated or neglected [3]. In Europe, saline and hypersaline lakes are mainly located in arid and semi-arid areas and are diverse [2]. Many of these lakes are very shallow, and due to enhanced evaporation exceeding precipitation, they are usually ephemeral and/or hypersaline [4]. As a consequence of their temporary nature, they exhibit high seasonal and interannual variability in their physical, chemical and biological characteristics driven by the hydrological budget and timing of precipitation [4]. Notably, the composition of their biota uniquely distinguishes them from other aquatic environments [5].

In such extreme systems, biotic interactions are of minor importance in shaping community structure, and environmental pressures predominantly drive community dynamics [4]. Thus, biodiversity and food web structure are highly variable and depend strongly on salinity [3]. The biota of moderately saline lakes ($<10 \text{ g L}^{-1}$) mostly include halotolerant taxa of freshwater environments, but with increasing salinity, alkaliphilic and halophilic taxa thrive [6,7]. In hypersaline conditions, diversity is largely limited by the ability of each species to tolerate salinity stress [8]. While increasing salinity usually leads to a biodiversity decrease, the pattern of decrease is by no means regular [9]. Although the harsh living conditions are adverse for many organisms and require specialized physiological adaptations to osmotic stress [10], these lake systems may support high primary productivity and dense phytoplankton blooms. The phytoplankton community is usually characterized by unexpected shifts in species composition and abundance, with chlorophytes, cyanobacteria and diatoms being the main functional groups [10,11]. Chlorophytes (e.g., *Dunaliella* species and *Picocystis salinarum*) and cyanobacteria (e.g., *Arthospira fusiformis*, *A. platensis*, *Anabaenopsis arnoldii*, *Synechocystis* and *Synechococcus* species) have been reported to bloom in various saline lakes around the world, such as the Dead Sea, the Great Salt Lake, Urmia, Lake Tyrell, Mono lake, Chinese and Mongolian saline lakes, Lake Dziani Dzaha, Fuente de Piedra, Nakuru/Bogoria/Elmentaita Rift Valley lakes, Ethiopian Rift Valley lakes and Brazilian Pantanal saline lakes [4,10,12–18].

In saline lakes, resident phytoplankton species typically exhibit adaptations to cope with the significant fluctuations in physical parameters such as temperature and variations in water chemistry, including salinity and pH. Additionally, in temporary aquatic environments, they have evolved strategies to endure desiccation [5]. Consequently, the underlying factors influencing seasonal phytoplankton dynamics in these ecosystems may differ substantially from those in freshwater lakes, as discussed in Salm et al. [19]. In particular, changes in salinity may directly and indirectly influence phytoplankton species richness and abundance [20], most notably *Dunaliella* sp. (in the Great Salt Lake) [8], leading to the extinction of some species and the appearance of other salt-tolerant species [21]. For example, in 14 saline lakes in northeastern Mongolia, cyanobacteria such as *Spirulina major* and *Oscillatoria* sp. were the main components of the phytoplankton community in polyhaline lakes, whereas lakes with medium mineralization were dominated by chlorophytes, diatoms and cyanobacteria (e.g., *Anabaenopsis elenkinii*, *Merismopedia elegans*, *Tetrastrum komarekii*, *Lyngbya* sp., *Oocystis* sp., *Diatoma* spp., *Navicula* spp.). Since the adapted tolerant species are usually few, these may reach high biomass in the absence of competitors and top-down pressures [22]. Such shifts in shallow systems may also be driven by the resuspension of bottom sediments due to wind-driven mixing replacing planktonic species with benthic forms (e.g., *Diatoma* and *Navicula* spp.) and/or increasing the contribution of certain green algae [23].

Across the globe, saline lakes are highly threatened by climate change, water diversions for domestic or agricultural use, catchment changes and other human activities that critically affect fundamental lake attributes [24]. While they constitute unique biodiversity hotspots, no official policies/directives at local, national or international levels have yet been developed to achieve environmentally sustainable management of these systems [25]; an exception is the European Union, where the Water Framework Directive obliges Member States to implement environmentally sustainable management in such systems, when they are designated as water bodies under the Directive. Seasonally filled aquatic environments such as the Mediterranean temporal lakes, where enhanced evaporation and decreased precipitation are expected as a result of global warming by the end of this century [26], are likely to be drier for longer periods [5].

Cyprus' saline lakes are the only natural lake assets of the homonymous island; they are athalassohaline with salinities often exceeding that of seawater. They are ephemeral, and dry phases alternate with hydroperiods of varying duration. In these systems, the flooding period is observed in winter and rarely in spring, whereas the summer and autumn periods represent the dry phase. Some of the lakes may still hold water for more

than one year, while others may remain dry for more than one season, depending on the inflows [27]. These small shallow saline lakes of varying salinity are located in close proximity to each other, and have been declared protected areas for their vegetation and bird fauna [28,29]. In the last decades, freshwater Mediterranean lakes have been subjected to progressive eutrophication due to various human activities in their catchment (e.g., elevated agricultural and urban land use) [30]. Like most saline lakes around the globe, studies on their biota and water chemistry are rather limited [31,32]. Mediterranean temporary saline lakes have been included in Europe's conservation plans (Habitats Directive, Water Framework Directive 2000/60/EC) [28,33]; however, the majority of them are designated neither as 'habitats' according to the Habitats Directive nor 'waterbodies' according to the Water Framework Directive (WFD), as their surface areas rarely exceed the 50 ha (0.5 km²) threshold for designation. Consequently, an integrated adaptive management strategy of saline lakes and their catchments is still lacking.

In this study, we aim to explore phytoplankton community composition and structural shifts in the changing environment of the ephemeral saline lakes of Cyprus (Eastern Mediterranean) for the first time. We intend to investigate emerging phytoplankton variability in terms of species composition, diversity, abundance, biomass and bloom occurrence in these highly dynamic systems under the prevailing environmental conditions.

2. Materials and Methods

2.1. Study Area and Field Work

Phytoplankton samples were collected from six lakes located in the southern and southeastern part of Cyprus (Eastern Mediterranean) (Figure 1, Table 1) between February 2018 and July 2019. Samples were collected at inshore sites located at the deepest lake points every three weeks, using a plastic container, from the surface down to a 30–50 cm depth. The deepest sampling station depth ranged from 10 to 100 cm. In situ measurements of physico-chemical parameters (water level, water temperature, salinity, conductivity, dissolved oxygen (DO) and pH) were conducted using portable instruments (calibrated monthly; SD 320 Con—Lovibond, YSI ProODO, WTW Profiline pH 3110).

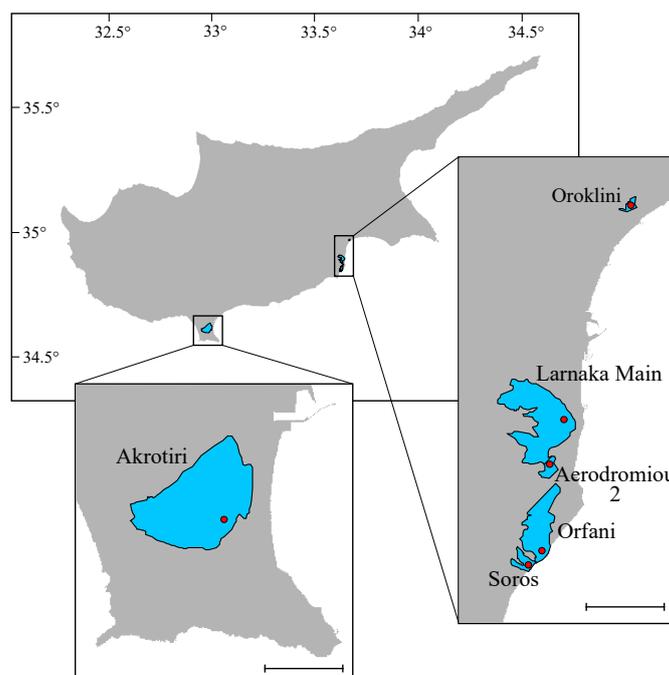


Figure 1. Locations of the studied lakes in Cyprus (Akrotiri, Larnaka Main, Aerodromiou 2, Orfani, Soros and Oroklini). The sampling sites are indicated with red dots. Scale bars: 3 km.

Table 1. Morphometric and topographic features of Cyprus' saline lakes.

Lake	Altitude (m a.s.l.)	Latitude (N)	Longitude (E)	Area (km ²)	Catchment Area (km ²)
Aerodromiou 2	−1.0	34.878997	33.620442	0.31	1.84
Akrotiri	−6.0	34.619061	32.976002	11.90	91.52
Larnaka Main	−1.6	34.894315	33.622746	4.81	58.73
Orfani	−0.5	34.860969	33.619213	2.24	10.09
Oroklini	3.1	34.969443	33.654534	0.15	2.77
Soros	−0.5	34.845219	33.613079	0.38	10.62

Akrotiri Lake, the largest of the studied lakes, is located at the southern part of the island, close to Limassol city. It has a surface area of approximately 11.9 km². The area around the lake is particularly important as a refuge and resting place for migratory birds [1], as well as a wintering spot for many waterbirds [34]; the surrounding wetlands are designated sites of international importance under the Ramsar Convention [29,35]. Akrotiri Lake is considered especially important for aquatic species, notably flamingos, more so since it is one of the continuously decreasing (and already small) number of natural wetlands still left in the eastern Mediterranean [1]. The second largest lake, Larnaka Main Salt Lake is located at the southwest part of Larnaka city and has a surface area of approximately 4.8 km². It is the largest of a network of salt lakes known as Larnaka's salt lakes (Figure 1). Larnaka's salt lakes are Sites of Community Importance (SCI) due to their halophytic marsh vegetation, among other characteristics, and one of the most important bird migratory passages in Cyprus [29,34,36,37]. They have been declared protected areas under Cypriot law, and have been designated European Ramsar [29] and Natura 2000 sites since 2001. The network also comprises Lake Orfani (surface area 2.2 km²), and the saline Lakes Soros and Aerodromiou 2, which are smaller in size (0.4 km² and 0.3 km² surface areas). The smallest of the studied lakes, Lake Oroklini, originally a wetland that was drained and impounded, is part of another network of shallow lakes, known for its rich biodiversity [37,38]. This lake has the lowest salinity range (from 3.0 to 20.4), a surface area of 0.15 km² and maximum depth of 0.7 m (Table 1). It is one of the most important shelters for the migratory birds of the island and it is designated as a Special Protection Area (SPA) for nesting species and for species that stage during migration or overwinter at the site [38]. The lake is also a Site of Community Importance under the Habitats Directive 92/43/EEC due to its halophytic marsh vegetation [28].

2.2. Microscopic Analysis

Live and preserved samples were examined in sedimentation chambers using inverted microscopes (Carl Zeiss Axio Observer.A1/Nikon Eclipse TE 2000-S) with phase contrast. Species identification was carried using appropriate taxonomic keys and papers (e.g., [39–45]). Phytoplankton enumeration was performed using Utermöhl's sedimentation method [46–48]. At least 400 individuals were counted in each sample. Species cell volume was estimated according to the water quality standard CEN/EN 16695 [47]. For biomass (biovolume) estimation, dimensions of 30 individuals of each species were measured using digital microscope cameras and the relevant software (Canon Power Shot A640 and Carl Zeiss AxioVision Rel. 4.7/Nikon DS-L1). Phytoplankton species which exhibited a significant population increase (high cell density in relation to cell volume) were considered bloom-forming species.

2.3. Land Use Coverage

Land use coverage of lake catchments (provided by the Cyprus Water Development Department, Ministry of Agriculture, Rural Development and Environment) was calculated using the CORINE Land Cover 2018 database for Cyprus [49]. The CORINE Land Cover 2018 database represents the only land use type database validated at national level. Land use types are grouped into three levels, with increasing details on the spatial elements of

the land use types presented. For this study, we used the third level of land use data for our analysis. Land-use cover proportions were calculated at the scale of the entire lake catchment using analytical tools of ArcMap 10.5.1 (ArcGis Desktop 10.5.1 software). Basic land use types identified within our study areas include the following land use categories: agricultural (non-irrigated arable land, permanently irrigated land, vineyards, fruit trees and berry plantations, annual crops associated with permanent crops, complex cultivation patterns, land principally occupied by agriculture, with significant areas of natural vegetation), artificial (continuous/discontinuous urban fabric, industrial/commercial units, road and rail networks and associated land, airports, mineral extraction sites, construction sites, green urban areas, sport and leisure facilities), wetland (inland and salt marshes, waterbodies), forest and semi-natural (broad-leaved forest, natural grasslands, sclerophyllous vegetation, transitional woodland-shrub, beaches, dunes, sands, sparsely vegetated areas).

2.4. Data Analysis

Simpson (1-D), Shannon (H) and Evenness (eH/S) alpha diversity indexes of the phytoplankton community were calculated based on species abundances using the PAST3 software [50]. To compute the beta diversity of the phytoplankton community for each sample, we used the 'betapart' R package version 1.5.1 [51]. Baselga's [52] approach suggests that Sorensen multiple-site dissimilarity (bSOR) is partitioned into two components: spatial turnover in species composition, measured as Simpson dissimilarity (bSIM), and variation in species composition due to nestedness (bNES), measured as the nestedness-resultant fraction of Sorensen dissimilarity. The above analyses were run in R environment version 3.5.3 [53].

Phytoplankton communities of each sample were compared using the Plymouth routines in the multivariate ecological software package PRIMER v.6 [54]. The Bray–Curtis similarity coefficients were calculated based on untransformed phytoplankton species biomass to identify interrelationships between samples and construct a nonmetric multidimensional scaling (nMDS) plot.

The correlation between phytoplankton communities (species/group abundance and biomass) and environmental parameters (water level, water temperature, salinity, DO, pH) as well as and land use coverage was explored through ordination analysis, using R software (R Core Team 2021) with the packages 'data.table' [55] and 'vegan' [56]. Multivariate model selection was based on detrended correspondence analysis (DCA), an unconstrained ordination able to estimate the heterogeneity in the data (i.e., if too many variables deviate from the assumed model of linear response) and suggest which group of ordination methods (linear, e.g., RDA, or unimodal, e.g., CCA) is more suitable for the specific data. As a rule of thumb [57], when the gradient of the longest axis in the DCA is <3 SD, then a linear response is inferred, and when it is >4 SD, then a unimodal response is assumed. There is no significance test in DCA, and no data transformation is needed because the ordinal transformation has a logarithmic nature with respect to cover and provides reasonable weighting of species dominance [57]. A Monte Carlo permutation test ($n = 999$) was implemented to identify the set of parameters that significantly explained $>80\%$ of the variation in the first two axes. Explanatory variables that exhibited an inflation factor >10 were excluded from further analysis as this suggested collinearity between them.

3. Results

3.1. Environmental Factors and Catchment Land Use Coverage

During the study period, the mean water temperature was similar (19–20 °C) in all the lakes, with maximum values in early summer (June) and minimum values in winter (January) (Table S1). The mean water temperature was 19.4 ± 5.3 °C in Lake Aerodromiou 2, 19.2 ± 5.5 °C in Lake Akrotiri, 19.8 ± 5.6 °C in Lake Larnaka Main, 19.2 ± 6.0 °C in Lake Orfani, 19.3 ± 6.3 °C in Lake Oroklini and 19.8 ± 5.5 °C in Lake Soros. The mean DO concentrations on the surface layer of the six lakes ranged from 6.8 to 8.7 mg L⁻¹ during the study period; the DO values exhibited a decrease from winter to summer following

the increase in water temperature (Table S1). The mean pH values were similar across the lakes, ranging between 8.1 and 8.7. Salinity exhibited substantial variability in all the lakes during the study period (Figure 2). The highest values of salinity were recorded in Larnaka Main (mean salinity: $114 \pm 87\text{‰}$) (Figure 2). Mean salinity values of $>50\text{‰}$ were measured in lakes Larnaka Main, Soros (mean salinity: $54 \pm 47\text{‰}$) and Orfani (mean salinity: $51 \pm 31\text{‰}$). Lakes Aerodromiou 2 and Akrotiri exhibited mean salinity values between 30‰ and 50‰ (mean salinity: $39 \pm 33\text{‰}$ and $31 \pm 17\text{‰}$, respectively) whereas in Lake Oroklini, salinity did not exceed 20‰ (mean salinity: $7.4 \pm 5.0\text{‰}$) during the study period. The water level was constantly <1 m in all the lakes (Figure 2).

Regarding land use coverage, all the studied lakes belong to catchments with a high percentage ($>50\%$) of artificial or/and agricultural land use coverage (Table 2, Figure S1). In particular, regarding Larnaka’s network of salt lakes, the catchment of Aerodromiou 2 is dominated exclusively by artificial areas (83%), whereas $>70\%$ of the area of the catchments of Larnaka Main, Lake Orfani and Lake Soros are covered by both artificial and agriculture sites, while forests/semi-natural areas occupy $<10\%$. The catchments of Lake Oroklini and Lake Akrotiri are also dominated by artificial land use (56% and 22%, respectively), and agricultural areas (27% and 36%, respectively) with forest/semi-natural areas following with a percentage coverage of 12% and 27%, respectively (Table 2).

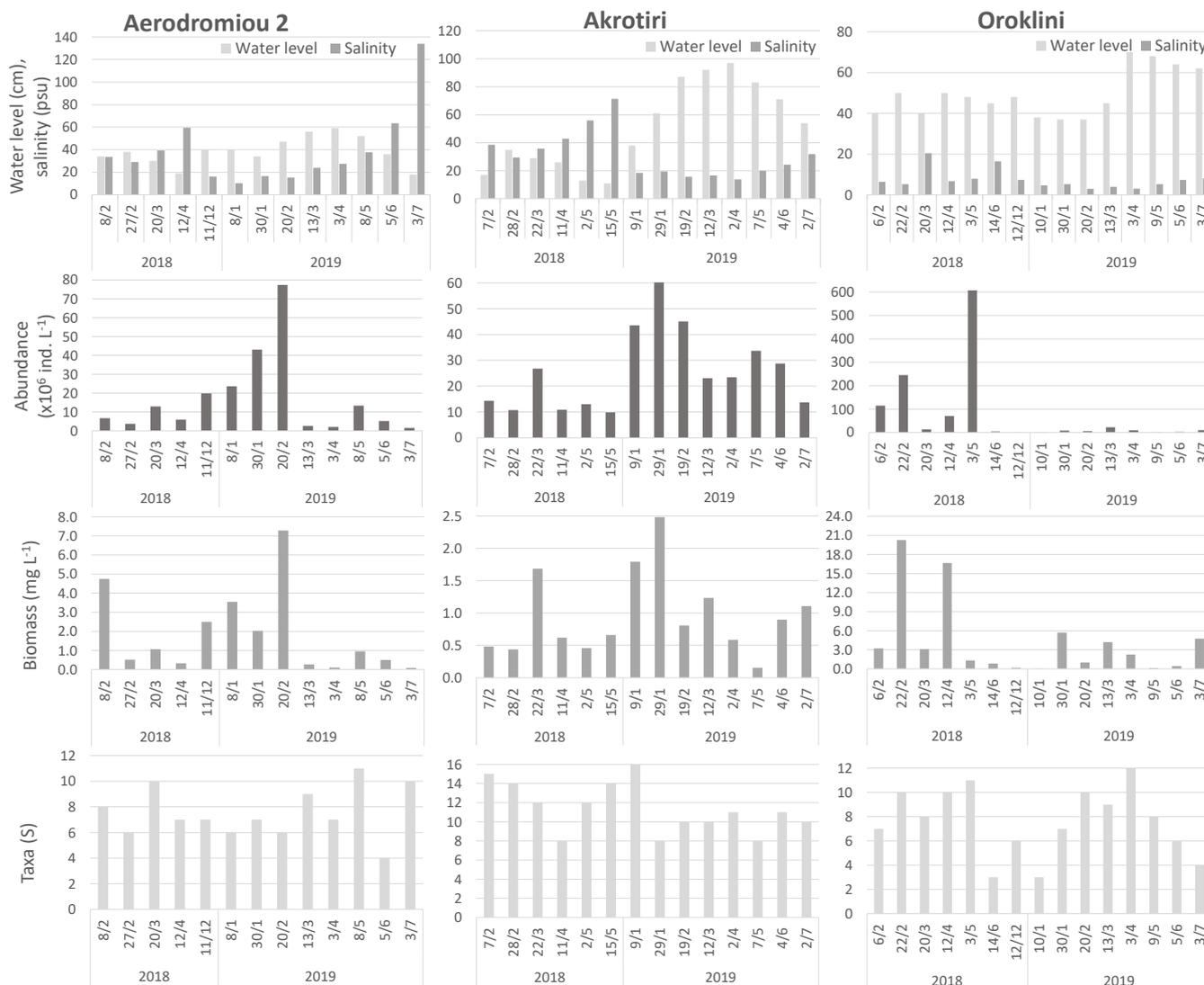


Figure 2. Cont.

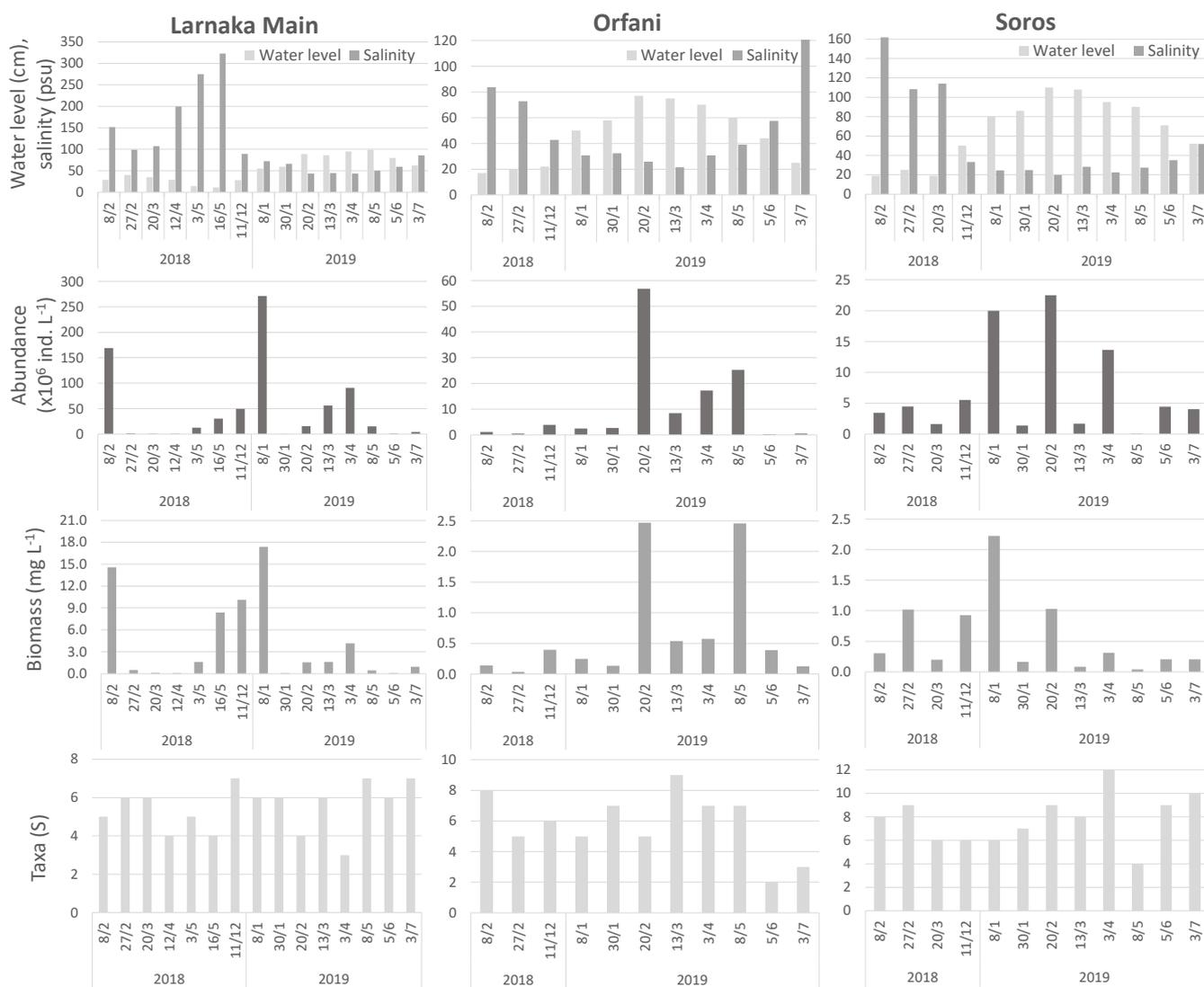


Figure 2. Water level (m), salinity (‰), abundance (individuals L⁻¹), biomass (mg L⁻¹) and phytoplankton species number in the six lakes during the study period.

Table 2. Land use coverage (%) of the respective lake catchments.

Factor/Lake	Aerodromiou 2	Akrotiri	Larnaka Main	Orfani	Oroklini	Soros
Artificial surfaces (%)	83	22	28	45	56	19
Agricultural areas (%)	0	36	57	26	27	77
Forest and semi-natural areas (%)	0	28	7	7	12	0
Wetlands	17	14	8	22	5	4

3.2. Phytoplankton Community Dynamics

3.2.1. Composition, Abundance and Biomass

A total of 40 phytoplankton taxa were identified in the studied lakes, including some species typical of saline environments (Table 3). Only eight of these taxa were recorded in all lakes. Chlorophyta was the taxonomic group with the highest taxon richness (12 taxa) followed by cyanobacteria and diatoms (9 and 7 taxa, respectively). The highest number of phytoplankton taxa (27 taxa) was recorded in the brackish Lake Oroklini (salinity of 3–20.4‰), while the lowest number (15 taxa) was recorded in the hypersaline Lake Larnaka Main (salinity: 43.3–323‰) (Table 1). In lakes Akrotiri, Soros and Oroklini, Chlorophyta was

the most diverse group in terms of species richness, with diatoms being the most diverse group in Lake Aerodromiou 2, and cyanobacteria in lakes Akrotiri, Aerodromiou 2 and Larnaka Main (Table 3). The rest of the taxonomic groups contributed ≤ 5 taxa each to the total phytoplankton richness. The recorded phytoplankton taxa (40) are given in Table 3.

Table 3. List of recorded phytoplankton taxa in the six saline lakes in Cyprus during 2018–2019 (dots). Bloom-forming taxa at various dates during the study period are represented by black dots. Genera or species are classified under Phylum (in bold) followed by Class (in bold), with authorship after genus or species.

	Aerodromiou 2	Akrotiri	Larnaka Main	Orfani	Oroklini	Soros
BACILLARIOPHYTA						
(DIATOMS)						
Bacillariophyceae						
<i>Cylindrotheca closterium</i> (Ehrenberg) Reimann & J.C.Lewin	●	●	○	○	○	○
<i>Fragillaria</i> (Lyngbye) sp.	○	○	○		○	
<i>Nitzschia</i> (Hassal) sp.	●	○	○	○	●	●
Mediophyceae						
<i>Chaetoceros</i> (Ehrenberg) sp.	○				○	
<i>Cyclotella</i> [(Kützing) Brébisson] sp.	●	●	○	○	○	○
Unidentified centric diatom	○			○		
Unidentified pennate diatom	○			○		
CHLOROPHYTA						
Chlorodendrophyceae						
<i>Tetraselmis</i> (F.Stein) sp.					○	
Chlorophyceae						
<i>Ankyra</i> (Fott) sp.	○	○			○	○
<i>Chlamydomonas</i> (Ehrenberg) sp.	○	○			●	
<i>Dunaliella</i> (Teodoresco) spp.	●	○	●	●	●	●
<i>Kirchneriella</i> (Schmidle) sp.					○	○
<i>Monoraphidium</i> (Komárková-Legnerová) sp.		○				○
<i>Schroederia</i> (Lemmermann) sp.	○	○	●	○	●	○
Pyramimonadophyceae						
<i>Pseudosourfieldia marina</i> (J.Thronsen) Manton	●	●		●	●	●
Trebouxiophyceae						
<i>Crucigeniella</i> (Lemmermann) sp.		○				
<i>Didymocystis</i> (Korshikov) sp.		●				
<i>Oocystis</i> (Nägeli ex A. Braun) sp.		●		○		
<i>Planctonema lauterbornii</i> (Schmidle)		○				
Unidentified coccoid microeukaryotes	○	●	●	○	●	○
CRYPTISTA						
Cryptophyceae						
<i>Rhodomonas</i> (G.Karsten) sp.					○	
<i>Cryptomonas</i> (Ehrenberg) sp.	○	○	○	●	●	○
CYANOBACTERIA						
Cyanophyceae						
<i>Anabaena</i> (Bory ex Bornet & Flahault) sp.	○	○	○		○	○
<i>Aphanizomenon</i> (Morren ex Bornet & Flahault) sp.	○	○	○			
<i>Chroococcus</i> (Nägeli) sp.	○	○			○	
<i>Jaagenima?</i> (Anagnostidis & Komarek) sp.	○	○	○	○	○	○

Table 3. Cont.

	Aerodromiou 2	Akrotiri	Larnaka Main	Orfani	Oroklini	Soros
<i>Euhalothece</i> (F.Garcia-Pichel, U.Nübel & G.Muyzer, 1998, non. inval.) sp.		•				
<i>Oscillatoria</i> (Vaucher ex Gomont) sp.	○	○	○	○		○
<i>Planktothrix</i> (Anagnostidis & Komárek) sp.			○			
<i>Pseudanabaena</i> (Lauterborn) sp.	○	○	○	○	•	○
Unidentified coccoid cyanobacteria		•			•	
EUGLENOZOA						
Euglenophyceae						
<i>Euglena</i> (Ehrenberg) sp.	○				•	○
Unidentified euglenophytes					○	
HAPTOPHYTA						
Coccolithophyceae						
<i>Prymnesium parvum</i> (N.Carter)					•	
CHAROPHYTA						
Closteriaceae						
<i>Closterium</i> (Nitzsch ex Ralfs) sp.					○	
MIOZOA						
Dinophyceae						
<i>Amphidinium</i> (Claperède & Lachmann) sp.				○		○
<i>Gymnodinium</i> (F.Stein) sp.	•	○		○	○	○
<i>Peridiniella</i> (C.A.Kofoed & J.R.Michener) sp.	•	○	○		○	○
<i>Peridinium</i> (Ehrenberg) sp.	○				○	
Unidentified dinoflagellate	•					

In the brackish Lake Oroklini, phytoplankton abundance varied between 0.035×10^6 individuals L^{-1} (in January 2019) and 607×10^6 individuals L^{-1} (in May 2018) (Figure 2). In the remaining saline/hypersaline lakes, phytoplankton abundance varied between 0.074×10^6 individuals L^{-1} (in May 2019, Lake Soros) and 271×10^6 individuals L^{-1} (in January 2019, Lake Larnaka Main). In the majority of the lakes, higher abundance values were recorded in January or February, usually when water level increased and salinity decreased (Figure 2). Species from several algal groups contributed to the maximum abundance values: the diatom *Cylindrotheca closterium* in Lake Aerodromiou 2, the pyramimonadophyte *Pseudoscurfieldia marina* and the chlorophytes *Oocystis* spp. in Akrotiri, the chlorophytes *Dunaliella* spp. in Lake Larnaka Main, two cyanobacteria species in Lake Oroklini (unidentified coccoid cyanobacteria and *Pseudanabaena* sp.), and both the pyramimonadophyte *Pseudoscurfieldia marina* and the chlorophyte *Dunaliella* spp. in Lakes Orfani and Soros were the most dominant in each system. Higher mean abundance values and higher variability were recorded at Lakes Oroklini and Larnaka Main (Figure 2). Phytoplankton biomass also varied substantially (from 0.03 to 20.27 mg L^{-1}) in and between the lakes during the study period (Figure 2). The highest biomass values were mostly recorded during the period of January–March. Lakes Oroklini (20.27 mg L^{-1}) and Larnaka Main (17.37 mg L^{-1}) exhibited the highest biomass values in February 2018 and January 2019, respectively, and also the highest variability (Figure 2). This high biomass was dominated in both lakes by the chlorophyte *Dunaliella* at 5.3 and 72.0‰ salinity values, respectively. The lowest phytoplankton biomass (0.03 mg L^{-1}) was recorded in Lake Orfani (February 2019). The taxa of phytoplankton that contributed substantially to the maximum biomass values were the diatom *Cylindrotheca closterium* (6.25 mg L^{-1}) in Lake Aerodromiou 2, the chlorophytes *Planktonema* sp. (1.12 mg L^{-1}) and *Dunaliella* (0.74 mg L^{-1}) in Lake Akrotiri and the chlorophyte *Dunaliella* sp. in Lakes Larnaka Main (17.32 mg L^{-1}), Orfani (2.01 mg L^{-1}),

Soros (2.07 mg L^{-1}) and Oroklini (19.66 mg L^{-1}). Higher mean biomass values and higher variability were also recorded at Lakes Oroklini and Larnaka Main (Figure 2).

Phytoplankton blooms represented by various taxa were recorded in all the lakes during the study period (Table 3), under a wide range of salinity values. In Lake Oroklini, representative taxa from seven out of the eight recorded phytoplankton groups were found to form blooms, whereas in Lake Larnaka Main, only blooms of chlorophytes were recorded (Table 3). The most common of all were *Dunaliella* (Chlorophyceae) and *Pseudoscurfieldia marina* (Pyramimonadophyceae) blooms. *Dunaliella* blooms (17 blooms in total in Aerodromiou 2, Larnaka Main, Orfani, Oroklini and Soros) occurred in all salinity ranges (3 to 323‰) (Figure 3) at several times during the year, regardless of the season. Most of them were observed in Lake Larnaka Main with high abundance values ($271 \times 10^6 \text{ ind. L}^{-1}$). In these blooms, *Dunaliella* was not the sole primary producer. *Pseudoscurfieldia* blooms were recorded in a salinity range of 5.3 to 38.6‰. Blooms of mainly coccoid cyanobacteria were observed in lakes Akrotiri and Oroklini (Table 3) under brackish conditions (8 to 15.8‰), and the harmful haptophyte *Prymnesium parvum* was found to dominate in Lake Oroklini at lower salinities (<8‰). Species of dinophytes were recorded in high abundances only in Lake Aerodromiou 2, and a bloom of *Euglena* sp. was observed only in Lake Oroklini.

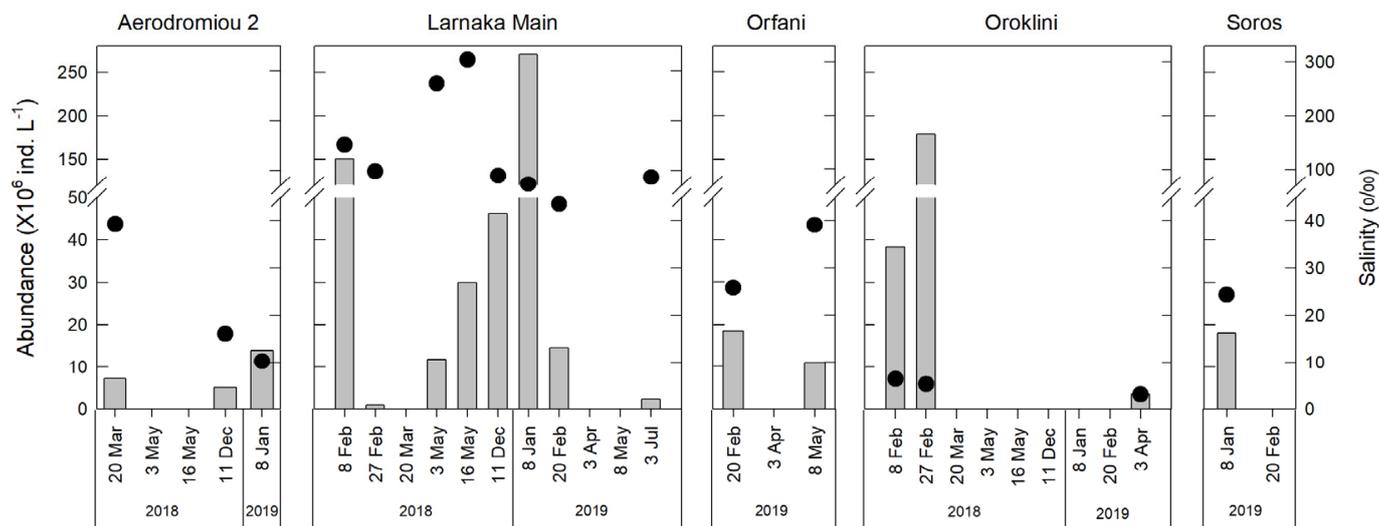


Figure 3. *Dunaliella* blooms [mentioned as abundance values, $\times 10^6 \text{ ind. L}^{-1}$ (bars)] and corresponding salinity (black dots) values (‰) in the lakes during the study period.

3.2.2. Composition, Abundance and Biomass

Alpha Diversity

The number of phytoplankton taxa among samples varied between 2 in Orfani (June 2019, salinity: 57‰) and 16 in Akrotiri (January 2019, salinity: 18.5‰). Simpson's 1-D index was highly variable in all lakes (Figure S2), ranging from 0.01 (indicating dominance of one species) in several sampling events in Larnaka Main during the cold period and Akrotiri in May to 0.85 in Oroklini during February. Similarly, the Shannon's H and Evenness indices fluctuated in all cases.

Beta Diversity

Phytoplankton beta diversity (bSOR) remained quite low during the study period and ranged from 0.57 (February 2018) to 0.74 (July 2019) (Figure 4). Beta diversity did not display a seasonal pattern but exhibited some peaks in February 2019 and June–July 2019. Community compositional variation was mostly attributed to the species turnover ($0.55 \pm 0.08 \text{ SE}$), with low nestedness ($0.11 \pm 0.05 \text{ SE}$).

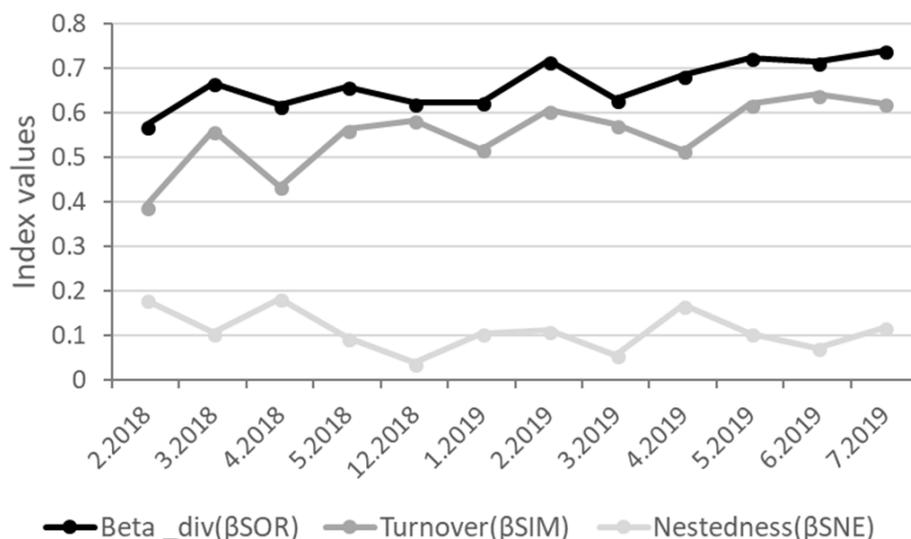


Figure 4. Phytoplankton beta diversity according to Sorensen similarity index (bSOR), turnover (bSIM) and nestedness (bNES) components values in the six saline lakes during the study period.

3.3. Environmental Effects on Phytoplankton Communities

NMDS analysis showed substantial similarity of phytoplankton community composition between the studied lakes. Although the Bray–Curtis dissimilarity index exhibited high 2D stress in the nMDS plot (0.22) (Figure 5), suggesting low confidence in the output, the results indicated overall high similarity (>40% similarity clustering) of most phytoplankton communities independent of spatial and seasonal variability.

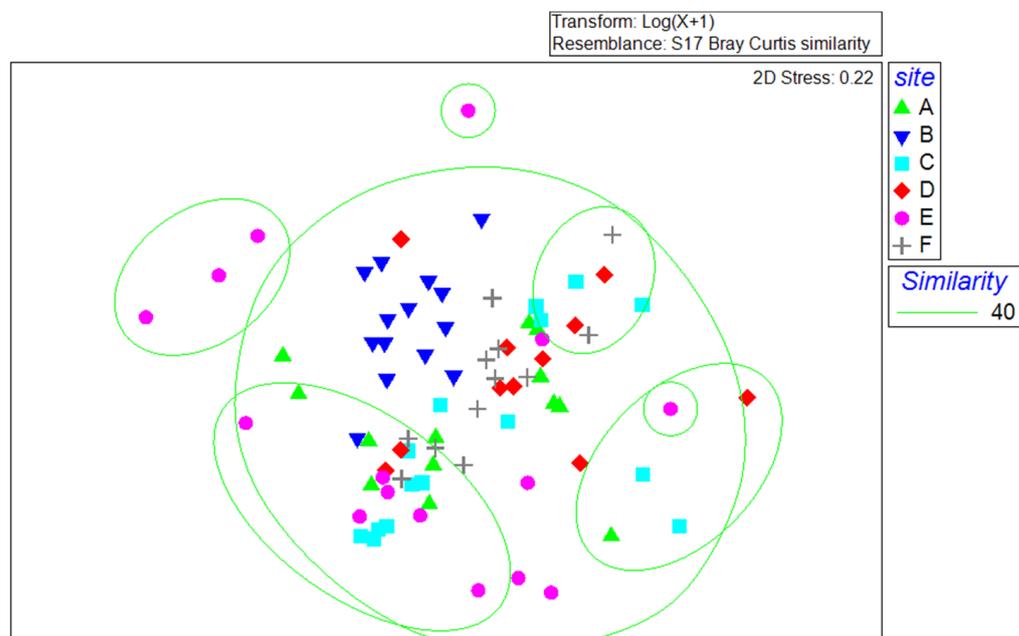


Figure 5. Multidimensional scaling plot (nMDS) of log(x+1)-transformed species biomass data in the samples, according to Bray–Curtis similarity index (A: Aerodromiou 2; B: Akrotiri; C: Larnaka Main; D: Orfani; E: Oroklini; F: Soros).

An RDA biplot (DCA longest axis < 3 SD) of environmental parameters and land use coverage over phytoplankton taxonomic groups biomass (all lakes combined) is shown in Figure S3. The permutation test indicated that the model was statistically significant ($p = 0.001$), explaining more species variance than expected by chance, and the constraints

explained 30% of the variance. The first axis was most positively correlated with salinity (RDA score = 0.51), pH (0.29) and most of the artificial land uses (0.44, 0.51, 0.55, −0.81). The second axis was most positively correlated with a number of artificial land uses (0.48, 0.45, 0.33) and salinity (0.38) and negatively with pH (−0.32). Artificial land use types were found to be the only significant basic type of land use coverage (artificial, agricultural, forests/semi-natural). Cyanobacteria biomass was positively correlated with most of the artificial urban land uses, salinity and water temperature. The biplot over group biomass indicated that most of the groups (except cyanobacteria, diatoms and Chlorophyceae) were negatively correlated with salinity and pH, as well as artificial areas. Ordination analyses did not reveal a clear pattern between phytoplankton species abundance/biomass and environmental factors/land use (not shown here).

A CCA biplot (DCA longest axis > 4 SD) of environmental parameters and land use coverage over phytoplankton dominant species biomass (all lakes combined) is shown in Figure S4. The permutation test indicated that the model was statistically significant ($p = 0.001$), explaining more species variance than expected by chance, and the constraints explained 24% of the variance. The first axis was most positively and negatively correlated with artificial land use types (RDA score = 0.46, 0.19, 0.18, −0.46). The second axis was most positively correlated with one artificial land use type (0.78) and negatively with salinity (−0.55), pH (−0.31) and other artificial land use types (−0.52, −0.43, −0.32). As previously shown in Figure S3, artificial land use types were found to be the only significant basic type of land use coverage (artificial, agricultural, forests/semi-natural). Bloom-forming cyanobacteria (like *Pseudanabaena* sp.), diatoms and most of the dinophytes' biomass were positively correlated with artificial land uses, salinity and water temperature. Unlike most of the chlorophytes, *Dunaliella salina* biomass was the only representative of this group positively correlated with salinity, pH, water temperature and artificial/urban land uses.

4. Discussion

Extreme environments are usually characterized by a key environmental variable driving species diversity, composition and dominance [8]. For aquatic environments of elevated salinity such as saline and hypersaline lakes, a number of studies support the significance of salinity in shaping the composition and diversity of the encountered microbial communities (e.g., [14,58,59]). This study investigates the characteristics of the phytoplankton communities found in six lakes in Cyprus, encompassing a salinity spectrum from brackish to hypersaline. We explored the potential relationship between salinity and other pivotal environmental factors and phytoplankton dynamics. Many of the studied systems are terminal basins and are thus affected by activities in their upstream catchments [2]. All of the studied lakes belong to catchments with a high percentage of artificial or/and agricultural land use coverage which may drive the decline of water quality [60]. According to LAWA [61], when agricultural and artificial land use types exceed 40 and 15% of the catchment area, respectively, they are considered significant pressures. Thus, we expected to observe a significant effect of land uses on phytoplankton community, since the studied salt lakes are subjected to a variety of anthropogenic impacts [62].

Although the lakes are all temporary, shallow and saline, they had marked differences in the range of their abiotic parameters (period of inundation, water level and salinity), but nevertheless, did not exhibit marked differences among one another regarding species composition, as has been shown in other Mediterranean saline lakes (e.g., Spain) [63]. The nMDS results indicated overall high similarity (>40% similarity clustering) of most phytoplankton communities of salt lakes in Cyprus, independent of spatial and seasonal variability. The most diverse groups in terms of species richness were chlorophytes, followed by cyanobacteria and diatoms; this pattern is typical in many eutrophic lakes in the Mediterranean [64,65], and these groups have also been found to be important in salt lakes in other climate zones (e.g., Uldza-Torey saline lakes (Central Asia), Ethiopian and Kenyan Rift Valley lakes (Africa), Great Salt Lake (USA), Rauer Island lakes (East Antarctica) [23,66–68]. The common feature of Cyprus' saline lakes phytoplankton community

was the low compositional diversity (low species number) as a result of the harsh environmental conditions [10] compared to the rich phytoplankton communities of large freshwater lakes (e.g., [69,70]). Furthermore, the observed decrease in the number of phytoplankton species (highest species number in the brackish Lake Oroklini, lowest species number in the hypersaline Lake Larnaka Main) with increasing salinity is typical for saline and hypersaline lakes (e.g., [8,23]). The highest species diversity in Lake Oroklini is probably due to its close proximity (<30 km distance) to other lakes which may favour increased species dispersal [71,72], while bottom-up forcing of similar land uses in the catchment promoted similar taxon dominance and bloom formation [30]. Genitsaris et al. [73] suggested that colonization of inland waters by air-dispersed microbes is driven by the salinity of the target habitats, exhibiting clustering to similar bottom-up forcing. Also, the connectivity among lakes and catchment-scale processes might influence phytoplankton richness and the encourage transport of materials and organisms through immigration [74].

The analysis of alpha and beta diversity revealed low and highly variable biodiversity (Simpson's 1-D) both temporally and spatially (among lakes), revealing the dominance of one species (especially in the hypersaline Lake Larnaka Main) and coexistence of more than one species in the other lakes. Low Simpson's values in Lake Larnaka Main were expected since phytoplankton diversity is very low in systems with high salinity and an ephemeral regime [63]. Other indices also fluctuated in all cases (Shannon's H and Evenness), suggesting alternations in species distribution homogeneity patterns/dynamics, and the presence of skewed communities in terms of species abundance (i.e., lower Shannon and Evenness indices) in several cases. The same is true for evenness: when one or a small number of species are highly dominant, diversity is also low. In such environments, with reduced hydroperiod or a complete dry out, major implications for species diversity are expected [75].

The phytoplankton abundance and biomass values in Cyprus' saline lakes were similar to those reported for other saline lakes (e.g., [23,63,76]). In the majority of the lakes, higher abundances were recorded in January or February, usually when water levels increased due to increased water inputs and a subsequent decrease in salinity. The same relationship between total abundance and salinity has been described in other salt lakes, where total abundance and biomass decrease as salinity increases [63], since most phytoplankton species are eliminated at very high salinity levels due to osmotic stress [59]. Higher mean abundance values and higher variability were recorded at Lakes Oroklini and Larnaka Main. It is known that eutrophication and salinization both have major effects on aquatic ecosystems, and their combined effects are expected to affect phytoplankton abundance cumulatively and to promote large algal blooms and poor water quality [20]. Since the two above-mentioned lakes belong to catchments with very high percentages of artificial and agricultural land use coverage, higher mean abundance and biomass values were expected.

In most of the cases where exceptionally high phytoplankton biomass values were measured, this was attributed to the very high proliferation of one or two species. This aligns with findings from other studies (e.g., [8,23]), wherein an increase in salinity from oligo- and mesohaline to hyperhaline levels is associated with a notable decrease in the species diversity of planktonic algae, leading to the development of a monodominant community. Blooms and extremely high productivity seem to be common phenomena not only in Cyprus, but also in other salt/hypersaline lakes [2,66]. In our study, the highly halotolerant chlorophyte *Dunaliella* was the main contributor to this high biomass in most cases, blooming under a wide range of salinity values (3 to 323‰). *Dunaliella* is considered a key component of inland saline ecosystems [17] with its members occurring over a wide range of salinity (i.e., 9 to 250 g L⁻¹) [2,77–79]. Due to their ability to grow at salt concentrations up to saturation, *Dunaliella* species dominate ecosystems with the highest salinities where they lack competitors [10,17]. Since living conditions in saline lakes are often extreme and highly variable, organisms such as *Dunaliella* that have evolved dormant stages to counter the adverse environmental conditions, play an important role in such systems [17,25,80]

and have been termed “stress specialists” [8]. The highest values of *Dunaliella* abundance recorded in our study in Cyprus lakes were much higher than the bloom values recorded in the Dead Sea by Oren in 1964, 1980 and 1992 [17,81]. In few bloom cases, *Dunaliella* was not the sole primary producer coexisting with species belonging to Chlorophyceae, Bacillariophyceae (diatoms), Cyanobacteria, Cryptophyceae, Dinophyceae and Pyramimonadophyceae, even though bloom species may create adverse physiological conditions for their competitors [82]. Also, in the Great Salt Lake (USA), along with *Dunaliella*, other Chlorophyceae (*Tetraselmis contracta*) and Cyanobacteria species (*Coccochloris elabens*) were capable of withstanding the highest salinities and were abundant [8]. In Australian salt lakes, cyanobacteria (like *Anabaena spiroides*, *Nodularia spumigena*) were observed to form blooms along with *Dunaliella salina* blooms [83]. The halotolerant cyanobacterium of the order Chroococcales *Euhalothece* sp., which formed blooms in Lake Akrotiri, has also been found and isolated from a hypersaline estuary of South Africa and grew at a temperature range of 25–45° C and salinity of 120 g/L [84]. We also observed that during *Dunaliella* blooms, at lower salinity levels (3–35 psu), a higher number of other coexisting species were recorded (4–11), whereas at higher salinity levels (>35 psu), this number was found to be lower (3–6). This was expected since, according to Rad et al. [16], only a few organisms can survive in high-saline conditions and against intense light and osmotic pressure. Species of green algae, cyanobacteria and diatoms have also been found to be dominant in other saline lakes [13,21], while in similar coastal lagoons of North Africa, a phytoplankton community was also dominated by chlorophytes; in the more saline lagoons, diatoms often predominated in the phytoplankton during the summer period [60]. Finally, chlorophytes and diatoms have been found to play a major role in solar saltworks’ population densities in northern Greece, especially in spring and throughout the summer [78].

The composition and diversity of phytoplankton communities have been thoroughly explored in this study, with conventional microscopy strategies showing, as expected, poorer communities in terms of species richness found in the studied Mediterranean temporal saline lakes, compared to the large freshwater lakes. However, the application of robust high-throughput sequencing technologies can offer enhanced insights into the phytoplankton communities, potentially leading to a substantial increase in the detection of phytoplankton taxa, including the identification of rare and cryptic species [85]. There has been increased interest in salt lakes across most parts of the world, stemming from their significant economic value [2,62,63], because of their biological components, some of which can be significant sources of food additives and other high-value products [83]. A typical example is the massive accumulation of β -carotene by some strains of *Dunaliella* under suitable growth conditions, which has led to interesting biotechnological applications [86]. The potential of the abundant *Dunaliella* in the studied hypersaline lakes, where it plays a major ecological role, is promising for biotechnological applications [87].

Since the studied lakes’ habitats have been designated as protected areas, it is important to understand their function as a first step toward their proper conservation and sustainable use. The rarity of saline/hypersaline systems, particularly the episodically inundated ones in arid regions, in a European context makes the assurance of their effective conservation even more important [63].

5. Conclusions

Here, a first attempt was made to elucidate the characteristics of the phytoplankton community inhabiting six Mediterranean lakes in Cyprus, encompassing a salinity range from brackish to hypersaline, and to investigate the possible impact of salinity and critical catchment factors on phytoplankton dynamics. Lakes seem to have high similarity of most phytoplankton communities, independent of spatial and seasonal variability. The common feature of Cyprus saline lakes’ phytoplankton community was their low compositional diversity as a result of the extreme environmental conditions. In fact, the observed decrease in the number of phytoplankton species with increasing salinity is typical for saline and hypersaline lakes. The most diverse groups in terms of species richness were chlorophytes,

followed by cyanobacteria and diatoms. Species of these groups have also been found to be dominant in terms of abundance and biomass. Blooms and extremely high biomass seem to be common phenomena in Cyprus' saline/hypersaline lakes. The highly halotolerant chlorophyte *Dunaliella* was the main contributor to high biomass in most of the cases, blooming under a wide range of salinity values. Our results provide useful information that could (i) serve as a basis for future monitoring of water quality and the ecological status assessment and management of the studied lakes and (ii) contribute to the restoration efforts in the region, aiming to recover the natural status of these lakes, specifically those facing eutrophication problems.

Supplementary Materials: The following supporting information can be downloaded at: <https://www.mdpi.com/article/10.3390/d15121204/s1>, Figure S1: Land use coverage of Akrotiri, Larnaka's network of lakes and Oroklini lake catchments; Figure S2: Boxplots of the number of taxa (S), and the Simpson (1-D), Shannon (H) and Evenness (eH/S) indices in the lakes throughout the study; Figure S3: Constrained ordination plot (linear RDA) of explanatory variables (environmental factors and land use coverage) over phytoplankton taxonomic group biomass; Figure S4: Constrained ordination plot (unimodal CCA) of explanatory variables (environmental factors and land use coverage) over phytoplankton dominant species biomass; Table S1: In situ measurements of physico-chemical parameters.

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References

1. Williams, W.D. Conservation of salt lakes. *Hydrobiologia* **1993**, *267*, 291–306. [[CrossRef](#)]
2. Saccò, M.; White, N.E.; Harrod, C.; Salazar, G.; Aguilar, P.; Cubillos, C.F.; Meredith, K.; Baxter, B.K.; Oren, A.; Anufrieva, E.; et al. Salt to conserve: A review on the ecology and preservation of hypersaline ecosystems. *Biol. Rev.* **2021**, *96*, 2828–2850. [[CrossRef](#)] [[PubMed](#)]
3. Zadereev, E.; Lipka, O.; Karimov, B.; Krylenko, M.; Elias, V.; Pinto, I.S.; Alizade, V.; Anker, Y.; Feest, A.; Kuznetsova, D.; et al. Overview of past, current, and future ecosystem and biodiversity trends of inland saline lakes of Europe and Central Asia. *Inland Waters* **2020**, *10*, 438–452. [[CrossRef](#)]
4. García, C.M.; García-Ruiz, R.; Rendón, M.; Niell, F.X.; Lucena, J. Hydrological cycle and interannual variability of the aquatic community in a temporary saline lake (Fuente de Piedra, Southern Spain). *Hydrobiologia* **1997**, *345*, 131–141. [[CrossRef](#)]
5. Williams, W.D. Environmental threats to salt lakes and the likely status of inland saline ecosystems in 2025. *Environ. Conserv.* **2002**, *29*, 154–167. [[CrossRef](#)]
6. Hammer, U.T. *Saline Lake Ecosystems of the World*; Springer Science & Business Media: Berlin/Heidelberg, Germany, 1986; Volume 59.

7. Sorokin, D.Y.; Berben, T.; Melton, E.D.; Overmars, L.; Vavourakis, C.D.; Muyzer, G. Microbial diversity and biogeochemical cycling in soda lakes. *Extremophiles* **2014**, *18*, 791–809. [[CrossRef](#)] [[PubMed](#)]
8. Larson, C.A.; Belovsky, G.E. Salinity and nutrients influence species richness and evenness of phytoplankton communities in microcosm experiments from Great Salt Lake, Utah, USA. *J. Plankton Res.* **2013**, *35*, 1154–1166. [[CrossRef](#)]
9. Williams, W.D. Salinity as a determinant of the structure of biological communities in salt lakes. *Hydrobiologia* **1998**, *381*, 191–201. [[CrossRef](#)]
10. Padisak, J.; Naselli-Flores, L. Phytoplankton in extreme environments: Importance and consequences of habitat permanency. *Hydrobiologia* **2021**, *848*, 157–176. [[CrossRef](#)]
11. Alexe, M.; Șerban, G.; Baricz, A.; Andrei, A.; Cristea, A.; Battes, K.P.; Cîmpean, M.; Momeu, L.; Muntean, V.; Porav, S.; et al. Limnology and plankton diversity of salt lakes from Transylvanian Basin (Romania): A review. *J. Limnol.* **2017**, *77*, 17–34. [[CrossRef](#)]
12. Ballot, A.; Krienitz, L.; Kotut, K.; Wiegand, C.; Metcalf, J.S.; Codd, G.A.; Pflugmacher, S. Cyanobacteria and cyanobacterial toxins in three alkaline Rift Valley lakes of Kenya—Lakes Bogoria, Nakuru and Elmenteita. *J. Plankton Res.* **2004**, *26*, 925–935. [[CrossRef](#)]
13. Costa, N.B.; Kolman, M.A.; Giani, A. Cyanobacteria diversity in alkaline saline lakes in the Brazilian Pantanal wetland: A polyphasic approach. *J. Plankton Res.* **2016**, *38*, 1389–1403. [[CrossRef](#)]
14. Stefanidou, N.; Katsiapi, M.; Tsianis, D.; Demertzioglou, M.; Michaloudi, E.; Moustaka-Gouni, M. Patterns in alpha and beta phytoplankton diversity along a conductivity gradient in coastal mediterranean lagoons. *Diversity* **2020**, *12*, 38. [[CrossRef](#)]
15. Schagerl, M.; Oduor, S.O. Phytoplankton community relationship to environmental variables in three Kenyan Rift Valley saline-alkaline lakes. *Mar. Freshw. Res.* **2008**, *59*, 125–136. [[CrossRef](#)]
16. Rad, F.A.; Aksoz, N.; Hejazi, M.A. Effect of salinity on cell growth and β -carotene production in *Dunaliella* sp. isolates from Urmia Lake in northwest of Iran. *Afr. J. Biotechnol.* **2011**, *10*, 2282–2289.
17. Oren, A. The ecology of *Dunaliella* in high-salt environments. *J. Biol. Res. Thessalon.* **2014**, *21*, 23. [[CrossRef](#)]
18. Williams, W.D. Comments on the so-called salt lakes of Greenland. *Hydrobiologia* **1991**, *210*, 67–74. [[CrossRef](#)]
19. Salm, C.R.; Saros, J.E.; Martin, C.S.; Erickson, J.M. Patterns of seasonal phytoplankton distribution in prairie saline lakes of the northern Great Plains (USA). *Saline Syst.* **2009**, *5*, 1–13. [[CrossRef](#)]
20. Lind, L.; Schuler, M.S.; Hintz, W.D.; Stoler, A.B.; Jones, D.K.; Mattes, B.M.; Relyea, R.A. Salty fertile lakes: How salinization and eutrophication alter the structure of freshwater communities. *Ecosphere* **2018**, *9*, 1–19. [[CrossRef](#)]
21. Afonina, E.Y.; Tashlykova, N.A. Plankton community and the relationship with the environment in saline lakes of On-Torey plain, Northeastern Mongolia. *Saudi J. Biol. Sci.* **2018**, *25*, 399–408. [[CrossRef](#)]
22. Afonina, E.Y.; Tashlykova, N.A. Fluctuations in plankton community structure of endorheic soda lakes of southeastern Transbaikalia (Russia). *Hydrobiologia* **2020**, *847*, 1383–1398. [[CrossRef](#)]
23. Afonina, E.Y.; Tashlykova, N.A. Plankton of Saline Lakes in Southeastern Transbaikalia: Transformation and Environmental Factors. *Contemp. Probl. Ecol.* **2019**, *12*, 155–170. [[CrossRef](#)]
24. Moore, J.N. Recent desiccation of western Great Basin saline lakes: Lessons from Lake Abert, Oregon, USA. *Sci. Total Environ.* **2016**, *554*, 142–154. [[CrossRef](#)]
25. Shadrin, N.; Zheng, M.; Oren, A. Past, present and future of saline lakes: Research for global sustainable development. *Chin. J. Oceanol. Limnol.* **2015**, *33*, 1349–1353. [[CrossRef](#)]
26. Erol, A.; Randhir, T.O. Climatic change impacts on the ecohydrology of Mediterranean watersheds. *Clim. Chang.* **2012**, *114*, 319–341. [[CrossRef](#)]
27. Zacharias, I.; Dimitriou, E.; Dekker, A.; Dorsman, E. Overview of temporary ponds in the Mediterranean region: Threats, management and conservation issues. *J. Environ. Biol.* **2007**, *28*, 1–9.
28. Council of the European Commission. Council directive 92/43/EEC of 21 May 1992 on the conservation of natural habitats and of wild fauna and flora. *Off. J. Eur. Communities Bruss.* **1992**, *206*, 7–49.
29. Ramsar List. The List of Wetlands of International Importance. 2023. Available online: <https://www.ramsar.org/sites/default/files/2023-08/sitelist.pdf> (accessed on 30 August 2023).
30. Katsiapi, M.; Mazaris, A.D.; Charalampous, E.; Moustaka-Gouni, M. Watershed land use types as drivers of freshwater phytoplankton structure. In *Phytoplankton Responses to Human Impacts at Different Scales*, *Hydrobiologia*; Springer: Berlin/Heidelberg, Germany, 2012; pp. 121–131.
31. Christia, C.; Tziortzis, I.; Fyrtis, G.; Kashta, L.; Papastergiadou, E. A survey of the benthic aquatic flora in transitional water systems of Greece and Cyprus (Mediterranean Sea). *Bot. Mar.* **2011**, *54*, 169–178. [[CrossRef](#)]
32. Karagianni, A.; Stamou, G.; Katsiapi, M.; Polykarpou, P.; Dörflinger, G.; Michaloudi, E. Zooplankton communities in Mediterranean temporary lakes: The case of saline lakes in Cyprus. *Ann. Limnol. Int. J. Limnol.* **2018**, *54*, 14. [[CrossRef](#)]
33. European Commission. *Directive 2000/60/EC of the European Parliament and of the Council Establishing a Framework for Community Action in the Field of Water Policy*; European Commission: Brussels, Belgium, 2000.
34. Hadjisterkotis, E.; Charalambides, M. The first evidence for the breeding of the Greater Flamingo *Phoenicopterus ruber* on Cyprus. *Zeitschrift für Jagdwissenschaft.* **2002**, *48*, 72–76.
35. Ramsar Sites Information Service. Annotated List of Wetlands of International Importance: United Kingdom of Great Britain and Northern Ireland. 1999. Available online: https://rsis.ramsar.org/sites/default/files/rsiswp_search/exports/Ramsar-Sites-annotated-summary-United-Kingdom-of-Great-Britain-and-Northern-Ireland.pdf?1686509325 (accessed on 30 August 2023).

36. Ramsar Sites Information Service. Annotated List of Wetlands of International Importance: Cyprus. 2008. Available online: <https://rsis Ramsar.org/ris/1081> (accessed on 30 August 2023).
37. Giosa, E.; Mammides, C.; Zotos, S. The importance of artificial wetlands for birds: A case study from Cyprus. *PLoS ONE* **2018**, *13*, e0197286. [CrossRef] [PubMed]
38. Guçel, S.; Kadis, C.; Özden, O.; Charalambidou, I.; Linstead, C.; Fuller, W.; Kounnamas, C.; Öztürk, M. Assessment of biodiversity differences between natural and artificial wetlands in Cyprus. *Pak. J. Bot.* **2012**, *44*, 213–224.
39. Bold, H.C.; Wynne, M.J. *Introduction to the Algae*, 2nd ed.; Benjamin Cummings: San Francisco, CA, USA, 1984; 720p.
40. Canter-Lund, H.; Lund, J.W. *Freshwater Algae: Their Microscopic World Explored*; Biopress Limited: Bristol, UK, 1994; 360p.
41. Hallegraeff, G.M.; Bolch, C.J.S.; Hill, D.R.A.; Jameson, I.; Leroi, J.M.; McMinn, A.; Murray, S.; de Salas, M.F.; Saunders, K. *Algae of Australia: Phytoplankton of Temperate Coastal Waters (Algae of Australia Series)*; Canberra & Melbourne: ABRS; CSIRO Publishing, 2010. Available online: <https://hdl.handle.net/102.100.100/538278> (accessed on 30 August 2023).
42. Hoppenrath, M.; Elbrächter, M.; Drebes, G. *Marine Phytoplankton—Selected Microphytoplankton Species from the North Sea around Helgoland and Sylt*; Kleine Senckenberg-Reihr, Bd 49; Schweizerbart Sche Vlgsb.: Stuttgart, Germany, 2010.
43. Huber-Pestalozzi, G. Das Phytoplankton des Süßwassers. In *August Thienemann, Die Binnengewässer*; E. Schweizerbart'sche Verlagsbuchhandlung: Stuttgart, Germany, 1942; Volume 16/2, pp. 367–549.
44. Kraberg, A.; Baumann, M.; Dürselen, C.-D. *Coastal Phytoplankton: Photo Guide for Northern European Seas*; VerlagDr. Friedrich Pfeil.: Munchen, Germany, 2010.
45. Tikkanen, T. *Kasviplanktonopas. Suomen Luonnonsojelun Tuki Oy*; Forssan kirjapaino Oy, Forssa: Helsinki, Finland, 1986.
46. CEN 15204; Water Quality—Guidance Standard on the Enumeration of Phytoplankton Using Inverted Microscopy (Utermöhl Technique). European Committee for Standardization, Management Centre: Brussels, Belgium, 2006.
47. CEN/EN 16695; Water Quality—Guidance on the Estimation of Microalgal Biovolume. European Committee for Standardization (CEN): Brussels, Belgium, 2015.
48. Utermöhl, H. Zur Vervollkommnung der quantitative Phytoplanktonmethodik. *Mitteilungen Int. Ver. Theor. Angew. Limnol.* **1958**, *9*, 1–38.
49. European Environmental Agency. *Corine Land Cover Technical Guide; Addendum*; European Environmental Agency: Copenhagen, Denmark, 2000.
50. Hammer, Ø.; Harper, D.A. Past: Paleontological statistics software package for education and data analysis. *Palaeontol. Electron.* **2001**, *4*, 1.
51. Baselga, A.; Orme, C.D.L. betapart: An R package for the study of beta diversity. *Methods Ecol. Evol.* **2012**, *3*, 808–812. [CrossRef]
52. Baselga, A. Multiplicative partition of true diversity yields independent alpha and beta components; additive partition does not. *Ecology* **2010**, *91*, 1974–1981. [CrossRef] [PubMed]
53. R Core Team. *R: A Language and Environment for Statistical Computing*; R Foundation for Statistical Computing: Vienna, Austria, 2021.
54. Clarke, K.R.; Gorley, R.N. *Primer. PRIMER-e, Plymouth*; Plymouth Marine Laboratory: Plymouth, UK, 2006; 866p.
55. Dowle, M.; Srinivasan, A.; Gorecki, J.; Chirico, M.; Stetsenko, P.; Short, T.; Lianoglou, S.; Antonyan, E.; Bonsch, M.; Parsonage, H.; et al. Data. Table R Package, Version 1.14.0. 2021. Available online: <https://cran.r-project.org/web/packages/data.table/index.html> (accessed on 30 August 2023).
56. Oksanen, J.; Blanchet, F.G.; Friendly, M.; Kindt, R.; Legendre, P.; McGlinn, D.; Minchin, P.R.; O'hara, R.B.; Simpson, G.L.; Solymos, P.; et al. Vegan: Community Ecology Package; R Package Version 2.5-7. 2020. Available online: <https://cran.r-project.org/> (accessed on 30 August 2023).
57. Lepš, J.; Šmilauer, P. *Multivariate Analysis of Ecological Data Using CANOCO*; Cambridge University Press: Cambridge, UK, 2003; pp. 1–269.
58. Diego, F.; Yamila, B.; Gisela, M.; Patricia, M. Controlling factors in planktonic communities over a salinity gradient in high-altitude lakes. *Ann. Limnol. Int. J. Limnol.* **2015**, *51*, 261–272. [CrossRef]
59. Li, Z.; Gao, Y.; Wang, S.; Lu, Y.; Sun, K.; Jia, J.; Wang, Y. Phytoplankton community response to nutrients along lake salinity and altitude gradients on the Qinghai-Tibet Plateau. *Ecol. Indic.* **2021**, *128*, 107848. [CrossRef]
60. Ramdani, M.; Elkhiafi, N.; Flower, R.J.; Thompson, J.R.; Chouba, L.; Kraiem, M.M.; Ayache, F.; Ahmed, M.H. Environmental influences on the qualitative and quantitative composition of phytoplankton and zooplankton in North African coastal lagoons. *Hydrobiologia* **2009**, *622*, 113–131. [CrossRef]
61. LAWA. German Guidance Document for the Implementation of the EC Water Framework Directive. 2003. Available online: <http://www.lawa.de/Publikationen.html> (accessed on 30 April 2003).
62. Jellison, R.; Zadereev, Y.S.; DasSarma, P.A.; Melack, J.M.; Rosen, M.R.; Degermendzhy, A.G.; DasSarma, S.; Zambrana, G. Conservation and Management Challenges of Saline Lakes: A Review of Five Experience Briefs; Lake Basin Management Initiative: Thematic Paper. 2004. Available online: http://www.worldlakes.org/uploads/ISSLR_Review_of_Salt_Lakes.pdf (accessed on 30 August 2023).
63. Alvarez, S.; Diaz, P.; Lopez-Archilla, A.I.; Guerrero, M.C. Phytoplankton composition and dynamics in three shallow temporary salt lakes (Monegros, Spain). *J. Arid Environ.* **2006**, *65*, 553–571. [CrossRef]
64. Temponeras, M.; Kristiansen, J.; Moustaka-Gouni, M. Seasonal variation in phytoplankton composition and physical-chemical features of the shallow Lake Doirani, Macedonia, Greece. In *The Trophic Spectrum Revisited: The Influence of Trophic State on the*

- Assembly of Phytoplankton Communities, Proceedings of the 11th Workshop of the International Association of Phytoplankton Taxonomy and Ecology (IAP), Shrewsbury, UK, 15–23 August 1998*; Springer: Dordrecht, The Netherlands, 2000; pp. 109–122.
65. Katsiapi, M.; Moustaka-Gouni, M.; Michaloudi, E.; Kormas, K.A. Phytoplankton and water quality in a Mediterranean drinking-water reservoir (Marathonas Reservoir, Greece). *Environ. Monit. Assess.* **2011**, *181*, 563–575. [[CrossRef](#)] [[PubMed](#)]
 66. Belovsky, G.E.; Stephens, D.; Perschon, C.; Birdsey, P.; Paul, D.; Naftz, D.; Baskin, R.; Larson, C.; Mellison, C.; Luft, J.; et al. The Great Salt Lake Ecosystem (Utah, USA): Long term data and a structural equation approach. *Ecosphere* **2011**, *2*, 1–40. [[CrossRef](#)]
 67. Hodgson, D.A.; Vyverman, W.; Sabbe, K. Limnology and biology of saline lakes in the Rauer Islands, eastern Antarctica. *Antarct. Sci.* **2001**, *13*, 255–270. [[CrossRef](#)]
 68. Kebede, E.; Willén, E. *Phytoplankton in a Salinity-Alkalinity Series of Lakes in the Ethiopian Rift Valley*; Acta Universitatis Upsaliensis: Uppsala, Sweden, 1998; Volume 89, pp. 63–96.
 69. Moustaka-Gouni, M. Phytoplankton succession and diversity in a warm monomictic, relatively shallow lake: Lake Volvi, Macedonia, Greece. *Hydrobiologia* **1993**, *249*, 33–42. [[CrossRef](#)]
 70. Katsiapi, M.; Moustaka-Gouni, M.; Vardaka, E.; Kormas, K.A. Different phytoplankton descriptors show asynchronous changes in a shallow urban lake (L. Kastoria, Greece) after sewage diversion. *Fundam. Appl. Limnol.* **2013**, *182*, 219–230. [[CrossRef](#)]
 71. Chrisostomou, A.; Moustaka-Gouni, M.; Sgardelis, S.; Lanaras, T. Air-dispersed phytoplankton in a Mediterranean river-reservoir system (Aliakmon-Polyphytos, Greece). *J. Plankton Res.* **2009**, *31*, 877–884. [[CrossRef](#)]
 72. Genitsaris, S.; Moustaka-Gouni, M.; Kormas, K.A. Airborne microeukaryote colonists in experimental water containers: Diversity, succession, life histories and established food webs. *Aquat. Microb. Ecol.* **2011**, *62*, 139–152. [[CrossRef](#)]
 73. Genitsaris, S.; Stefanidou, N.; Beeri-Shlevin, Y.; Viner-Mozzini, Y.; Moustaka-Gouni, M.; Ninio, S.; Sukenik, A. Air-dispersed aquatic microorganisms show establishment and growth preferences in different freshwater colonisation habitats. *FEMS Microbiol. Ecol.* **2021**, *97*, fiab122. [[CrossRef](#)]
 74. Özkan, K.; Jeppesen, E.; Søndergaard, M.; Lauridsen, T.L.; Liboriussen, L.; Svenning, J.C. Contrasting roles of water chemistry, lake morphology, land-use, climate and spatial processes in driving phytoplankton richness in the Danish landscape. *Hydrobiologia* **2013**, *710*, 173–187. [[CrossRef](#)]
 75. Batanero, G.L.; León-Palmero, E.; Li, L.; Green, A.J.; Rendón-Martos, M.; Suttle, C.A.; Reche, I. Flamingos and drought as drivers of nutrients and microbial dynamics in a saline lake. *Sci. Rep.* **2017**, *7*, 1–13. [[CrossRef](#)]
 76. Alfonso, M.B.; Zunino, J.; Piccolo, M.C. Impact of water input on plankton temporal dynamics from a managed shallow saline lake. *Ann. Limnol. Int. J. Limnol.* **2017**, *53*, 391–400. [[CrossRef](#)]
 77. Olmos, J.; Ochoa, L.; Paniagua-Michel, J.; Contreras, R. DNA fingerprinting differentiation between β -carotene hyperproducer strains of *Dunaliella* from around the world. *Saline Syst.* **2009**, *5*, 1–10. [[CrossRef](#)] [[PubMed](#)]
 78. Dolapsakis, N.P.; Tafas, T.; Abatzopoulos, T.J.; Ziller, S.; Economou-Amilli, A. Abundance and growth response of microalgae at Megalon Embolon solar saltworks in northern Greece: An aquaculture prospect. *J. Appl. Phycol.* **2005**, *17*, 39–49. [[CrossRef](#)]
 79. Heidelberg, K.B.; Nelson, W.C.; Holm, J.B.; Eisenkolb, N.; Andrade, K.; Emerson, J.B. Characterization of eukaryotic microbial diversity in hypersaline Lake Tyrrell, Australia. *Front. Microbiol.* **2013**, *4*, 115. [[CrossRef](#)] [[PubMed](#)]
 80. Moscatello, S.; Belmonte, G. Egg banks in hypersaline lakes of the South-East Europe. *Saline Syst.* **2009**, *5*, 1–7. [[CrossRef](#)] [[PubMed](#)]
 81. Oren, A.; Gurevich, P.; Anati, D.A.; Barkan, E.; Luz, B. A bloom of *Dunaliella parva* in the Dead Sea in 1992: Biological and biogeochemical aspects. *Hydrobiologia* **1995**, *297*, 173–185. [[CrossRef](#)]
 82. Reid, A.J.; Carlson, A.K.; Creed, I.F.; Eliason, E.J.; Gell, P.A.; Johnson, P.T.J.; Kidd, K.A.; MacCormack, T.J.; Olden, J.D.; Ormerod, S.J.; et al. Emerging threats and persistent conservation challenges for freshwater biodiversity. *Biol. Rev.* **2019**, *94*, 849–873. [[CrossRef](#)] [[PubMed](#)]
 83. De Deckker, P. Australian salt lakes: Their history, chemistry, and biota—A review. *Hydrobiologia* **1983**, *105*, 231–244. [[CrossRef](#)]
 84. Mogany, T.; Swalaha, F.M.; Allam, M.; Mtshali, P.S.; Ismail, A.; Kumari, S.; Bux, F. Phenotypic and genotypic characterization of an unique indigenous hypersaline unicellular cyanobacterium, *Euhalothece* sp. nov. *Microbiol. Res.* **2018**, *211*, 47–56. [[CrossRef](#)]
 85. Bik, H.M.; Porazinska, D.L.; Creer, S.; Caporaso, J.G.; Knight, R.; Thomas, W.K. Sequencing our way towards understanding global eukaryotic biodiversity. *Trends Ecol. Evol.* **2012**, *27*, 233–243. [[CrossRef](#)]
 86. Oren, A. A hundred years of *Dunaliella* research: 1905–2005. *Saline Syst.* **2005**, *1*, 1–14. [[CrossRef](#)] [[PubMed](#)]
 87. da Silva, M.R.O.B.; Moura, Y.A.S.; Converti, A.; Porto, A.L.F.; Marques, D.D.A.V.; Bezerra, R.P. Assessment of the potential of *Dunaliella* microalgae for different biotechnological applications: A systematic review. *Algal Res.* **2021**, *58*, 102396. [[CrossRef](#)]

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