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Research article

Salinity-induced succession of phototrophic communities in a southwestern Siberian soda lake during the solar activity cycle

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ABSTRACT

A variety of lakes located in the dry steppe area of southwestern Siberia are exposed to rapid climatic changes, including intra-century cycles with alternating dry and wet phases driven by solar activity. As a result, the salt lakes of that region experience significant fluctuations in water level and salinity, which have an essential impact on the indigenous microbial communities. But there are few microbiological studies that have analyzed this impact, despite its importance for understanding the functioning of regional water ecosystems. This work is a retrospective study aimed at analyzing how solar activity-related changes in hydrological regime affect phototrophic microbial communities using the example of the shallow soda lake Tanatar VI, located in the Kulunda steppe (Altai Region, Russia, southwestern Siberia). The main approach used in this study was the comparison of hydrochemical and microscopic data obtained during annual field work with satellite and solar activity data for the 12-year observation period (2011–2022). The occurrence of 33 morphotypes of cyanobacteria, two key morphotypes of chlorophytes, and four morphotypes of anoxygenic phototrophic bacteria was analyzed due to their easily recognizable morphology. During the study period, the lake surface changed threefold and the salinity changed by more than an order of magnitude, which strongly correlated with the phases of the solar activity cycles. The periods of high (2011–2014; 100–250 g/L), medium (2015–2016; 60 g/L), extremely low (2017–2020; 13–16 g/L), and low (2021–2022; 23–34 g/L) salinity with unique biodiversity of phototrophic communities were distinguished. This study shows that solar activity cycles determine the dynamics of the total salinity of a southwestern Siberian soda lake, which in turn determines the communities and microorganisms that will occur in the lake, ultimately leading to cyclical changes in alternative states of the ecosystem (dynamic stability).

1. Introduction

The southwestern Siberian steppes, with their extreme continental climate, host a large number of endorheic salt lakes of variable

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chemical composition and salinity [1]. These lakes are subject to climatic changes on different time scales. Being located in the zone of arid continental climate, they are exposed to seasonal fluctuations of air temperature, atmospheric precipitation, and surface runoff, which result in annual hydrological cycles [2]. In addition, endorheic lakes in this region are characterized by long-term fluctuations in the water level since they are subject to explicit intra-century climatic cycles of various durations (within 20–47 years), which manifest themselves in the alternation of wet and dry periods [3]. In particular, relatively short-term cyclic climate changes in this region occur within the 11-year Schwabe-Wolf cycles of solar activity (actually 9–14 years) [4,5]. In the case of salt lakes in southwestern Siberia, the solar activity cyclicity results in a significant salinity change, which, in turn, strongly affects resident halophilic microbial communities. However, little is known about how this influence manifests itself during long-term climatic cycles.

There are few observations of the succession of eukaryotic and prokaryotic microbial communities in the Siberian salt lakes in long-term periods, although such studies are important for understanding the functioning of ecosystems "pulsating" in time and the possibility of their use [6]. The targeted observations relevant to this topic have been carried out in the Transbaikal area of the south-eastern Siberia at the sites of large soda lakes of the Torey group [7–10] and a small chloride-sulfate lake Khilganta [11,12]. Observations were also made for a soda lake Bitter-1 in the Kulunda Steppe of the southwestern Siberia [13,14]. Phytoplankton succession during the dry-refilling cycles was studied in Torey lakes. The salinity state of these lakes varied from oligo- (0.7–3.7 g/L) to hypersaline (58.1–81.4 g/L). *Chlorophyta* and *Bacillariophyta* dominated in phytoplankton, with *Cyanobacteria* being in third place [7,8]. The hypersaline state of the lakes was characterized by monospecific phytoplankton communities (often cyanobacterial). At maximum salinity (up to 400 g/L), eukaryotes practically disappear, and prokaryotic communities acquire a key functional role [15,16]. Phototrophic microbial communities with an emphasis on cyanobacteria and anoxygenic phototrophic bacteria were morphologically analyzed in Khilganta and Bitter-1 lakes; the molecular biological analyses, used in parallel, were consistent with morphological observations and confirmed and strengthened the results obtained. For lower salinities, a diversity of moderately salt-tolerant, unicellular, filamentous, and heterocystous cyanobacteria was obvious, while at hypersaline conditions, extremely halophilic unicellular green algae *Dunaliella* sp., anoxygenic purple sulfur bacteria *Ectothiorhodospira* sp., and (optionally) unicellular cyanobacterium *Euhalothece* sp. became the dominant phototrophs. Thus, in all cases, a change in the studied phyto- and microbial communities associated with the long-term salinity changes was shown. Therefore, it is clear that the unstable hydrological regime of southern Siberia dramatically affects the phototrophic communities that develop in the local salt lakes. In the context of global climate change, further aridization of southern Siberia will lead to a sharp change in the microbial diversity of local salt lakes, which may affect their functional potential and possibility of use. But long-term studies focusing on prokaryotes are very rare.

In this paper, we consider the small shallow soda lake Tanatar VI, located in the Kulunda steppe (southwestern Siberia, Altai Region, Russia), as a model object for studying climate-induced long-term succession of microbial communities. This lake differs from

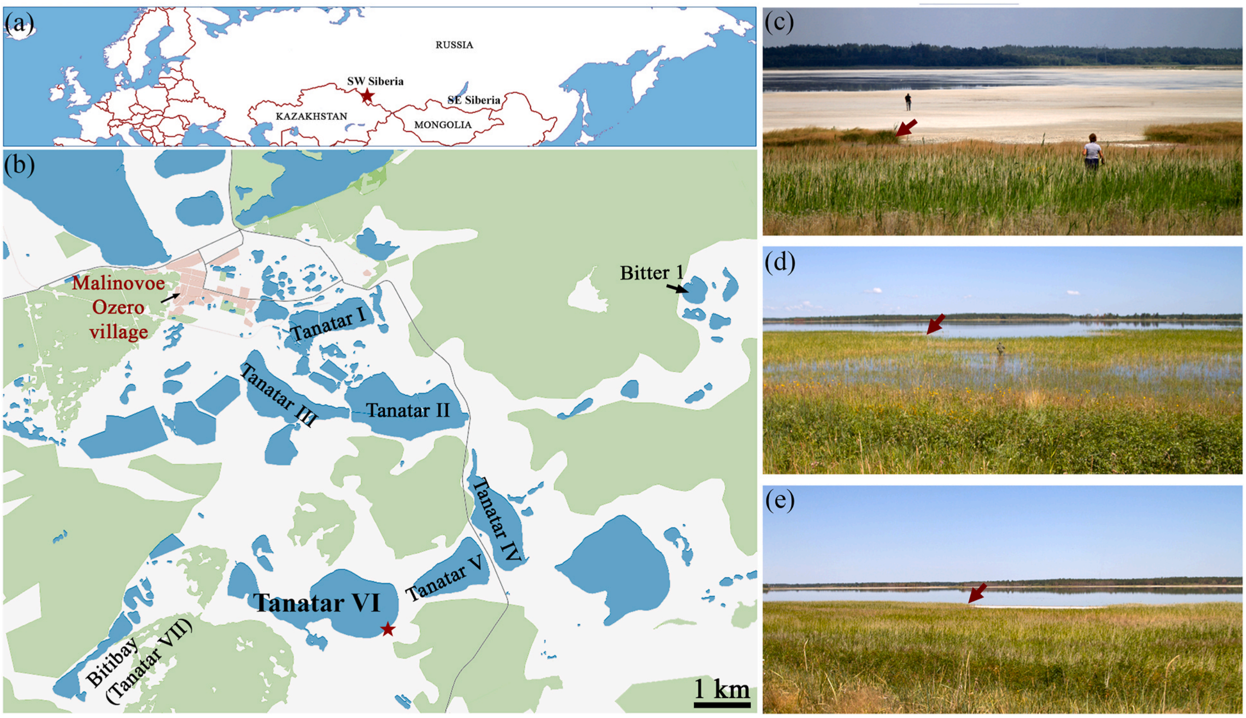

Fig. 1. Geographical location and the general view of the soda lake Tanatar VI: (a) approximate territories of southwestern (SW) and southeastern (SE) Siberia in the map of Eurasia; (b) Tanatar group of lakes (*the grey line* indicates the asphalt road); (c–d) general view of the sampling site in 2014 (c), 2018 (d), and 2022 (e). *The red asterisk* indicates the sampling site; *the red arrow* points to the same point in different years. (For interpretation of the references to color in this figure legend, the reader is referred to the Web version of this article.)

the lake Khilganta in its hydrochemical composition and from the soda lake Bitter-1 in the range of salinity changes. This lake was first studied in 2011–2012, when it was hypersaline (160–250 g/L) [17]. More recent published observations included data for 2015 and 2018, when salinity dropped to 60 g/L and to its lowest of 13 g/L, respectively [14,18]. The purpose of this work was to analyze the relationship between changes in solar activity, surface area, and lake salinity and to analyze the impact of these changes on the succession of phototrophic microbial communities, with a focus on cyanobacteria and some other phototrophs (key chlorophytes and anoxygenic phototrophic bacteria). The objectives included a detailed description of observations made over a 12-year (2011–2022) period of research on lake Tanatar VI. The main approach used in this study was the retrospective comparison of hydrochemical and microscopic data obtained during annual summer field work with satellite and solar activity data for the same period.

2. Materials and methods

2.1. Study site

Lake Tanatar VI is a part of the Tanatars soda lakes group located in Mikhailovsky district, Altai Region (Russia), to the south of the Malinovoe Ozero village (51°37′08.4″N, 79°48′53.0″E) (Fig. 1 a, b). The southern branch consists of the lakes Thanatar V and VI. They are adjoined from the west by a group of moderately saline lakes under the common name Tanatar VII (Lake Bitibay and others). The southern group of Tanatar lakes is connected by the south-to-north elongated hyposaline lake Tanatar IV, with a northern branch consisting of Tanatar II and III and the northernmost lake Tanatar I. All lakes are drainless. They are fed mainly by groundwater [2,19]. The lakes Tanatars I–III are industrially exploited for the production of soda and some other salts. To our knowledge, lake Tanatar VI has never been industrially exploited and therefore may represent a model ecosystem convenient for studying unaltered natural processes.

2.2. Sampling and field measurements

The samples were collected during summer periods (usually in July) from 2011 until 2022, excluding 2017. Sampling dates are shown in Table 1. The sampling site was located in the southeastern part of the lake and was the same each year. It is indicated by an asterisk in Fig. 1b. The connection of the lakes Tanatar VI and V, starting in 2017, didn't lead to a change in the sampling site or methodology.

Samples of phototrophic biomass were collected from the brine and littoral zone (water column, lake bottom, and submerged plants), as well as from the surface of the soil surrounding the lake. Water samples were collected in 0.5-liter bottles, separately water with blooms at a distance of several meters from the shore and an accumulation of phototrophic biomass near the shore. Samples of submerged stems of higher plants with green fouling were collected in quantities of about 10 specimens, which were placed in vials partially filled with lake water. Small floating or bottom biofilms were collected separately in 50-ml sterile vials. Subaerial biofilms were also collected in 50-ml sterile vials. If phototrophic communities from the same biotope differed in color or other macromorphological characteristics, then they were selected separately. On average, 5 to 15 specimens of each type were collected. For further studies, the samples were transported to the laboratory at ambient temperature (maximum storage time: 5 days).

Total salinity and pH were measured with an Atago ATC-S/Mill-E refractometer (Japan) and/or a WTW field potentiometer-conductometer (Germany). Control of the salinity of soda brines by the gravimetric method showed a high degree of agreement between the values obtained by these devices and the total content of dissolved salts (TDS) in grams per liter. Therefore, in this work, we express the total salinity in g/L. The pH was measured twice for each sample: native (undiluted) and diluted 1:5 with distilled water. The average value was taken into account since an extremely high sodium concentration interfered with the measurements. The soluble carbonate alkalinity (total alkalinity, or TA) was determined by a two-step titration with 1 M HCl, as described earlier [18].

Table 1
Some hydrochemical and hydrological parameters of the soda lake Tanatar VI during 2011–2022 summer periods.

Year	Sampling date (dd/mm)	Salinity (g/L)	Total alkalinity (mol-eq/L)	pH	Approximate surface area (km^2)	Salinity period
2011	09/07	160	1.7	10.0	1.36	High
2012	30/06	250	3.4	9.8	1.18	
2013	29/06	100	1.1	9.8	1.48	
2014	07/07	105	0.8	9.6	1.41	
2015	04/07	60	0.6	10.2	1.74	Medium
2016	01/07	60	0.6	9.9	2.08	
2017	–[a]	–[a]	–[a]	–[a]	3.19	?
2018	29/07	13	–[a]	10.1	3.53	Extremely low
2019	06/07	14	0.13	9.7	3.58	
2020	17/07	16	0.16	9.8	3.30	
2021	07/07	23	0.2	9.9	3.00	Low
2022	26/07	34	0.35	9.8	2.49	

[a] No data.

2.3. Microscopic analysis of the phototrophic microorganisms

The diversity of phototrophic microorganisms was examined in wet mounts under a Jenaval light microscope equipped with a Zeiss Bundle Canon PS G9 digital camera (Germany). The main focus of our work was on the cyanobacteria, although we also took into account key morphotypes of anoxygenic phototrophic bacteria and chlorophytes. Diatoms were also an important component of phototrophic communities in the Kulunda steppe soda lakes [14,17], and their abundance and diversity varied significantly during the study period. However, a systematic annual identification of diatoms was not carried out, so their use in the current analysis turned out to be impossible.

On average, 25–35 examinations of each sample were carried out to determine the community composition. Identification of cyanobacteria and algae in environmental samples was performed according to determination manuals [20–22], previous studies [13,

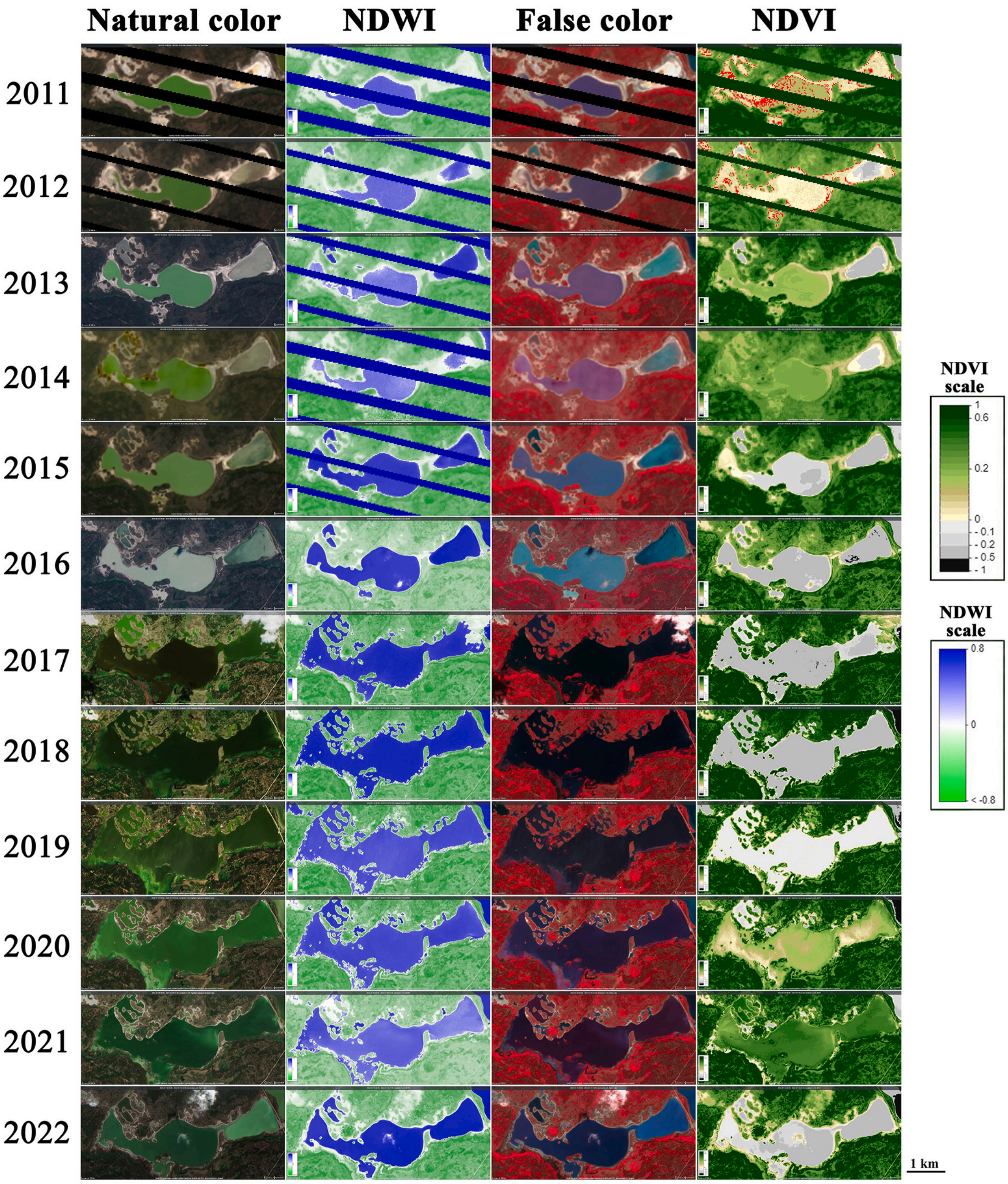

Fig. 2. Soda lakes Tanatar VI and Tanatar V in summer periods during 2011–2022. NDWI – normalized difference water index, NDVI – normalized difference vegetation index, False color – composite satellite image in near infrared, red and green bands. See Table S1 for more details on each image, and for a thorough explanation of the implications of the color scale, see Section 2.4. (For interpretation of the references to color in this figure legend, the reader is referred to the Web version of this article.)

14,17,23], and recent taxonomic papers [24–27].

2.4. Solar sunspot and satellite data

The data on the sunspot number were obtained from https://www.swpc.noaa.gov/products/solar-cycle-progression.

Satellite images were obtained using the web resource https://apps.sentinel-hub.com/. Images from 2011 to 2015 were obtained from Landsat 7, 8, and 9 satellites, and images from 2016 to 2022 were obtained from the Sentinel-2 satellite. The satellite images used in this work were chosen according to the following principle: they were taken in cloudless weather in July of each year (or in late June or early August, if there were no high-quality July images). The exact data on satellite images is given in Table S1.

The *Normalized Difference Water Index* (NDWI) was used for water body mapping (values of water bodies are >0.5 and blue color; vegetation has negative values and green color). The False color composite was used to assess plant and phytoplankton density, which appears shades of red (since chlorophyll reflects near infrared and green light while absorbing red); exposed ground is grey or tan; and water appears blue or black. The *Normalized Difference Vegetation Index* (NDVI) was used for quantifying green vegetation. Negative values approaching −1 (grey to black color) correspond to water; values close to zero (−0.1 to 0.1, or light grey to yellow brown color) generally correspond to barren areas of exposed ground; positive values and shades of green color correspond to green vegetation (water blooms, shrubs, grassland, and pine forest).

The approximate surface area was calculated using NDWI satellite images (Fig. S1). At the first stage, manual digitization of the lake boundaries was carried out using the online service https://automeris.io/WebPlotDigitizer/. The result of digitization was the coordinates of the lake boundaries in the pixel reference system relative to the upper left corner of the jpg image containing the NDWI map. Only the main part of the lake was contoured, without taking into account occasional bridges with the water areas of neighboring small water bodies. The presence of small islands was also not taken into account. The digitized pixel coordinates of the lake boundaries were then converted to meters using the scale bar found on NDWI maps. Further, polygons were built according to the coordinates, and their area was calculated using the standard function ‘polyarea’ of the Matlab programming environment. The calculated areas of the lake in the years from 2011 to 2022 are highlighted in red in Fig. S1.

2.5. Statistical and cluster analysis

The Pearson’s correlation coefficients (*R*) and two-tailed *p*-values were performed using the standard program MS Excel 2010. To assess the strength of correlations, the Chaddock scale was used: weak, from 0.1 to 0.3; moderate, from 0.3 to 0.5; noticeable, from 0.5 to 0.7; high, from 0.7 to 0.9; very high (strong), from 0.9 to 1.0 [28]. Positive values mean a positive correlation; negative values mean a negative correlation.

Cluster analysis was performed by the Ward’s method with a Euclidean distance measure using the Past 4.03 software package (Multivariate → Clustering → Classical clustering → Algorithm Ward’s method) [29] and morphotype presence/absence matrices (Tables S4 and S5). Matrices were compiled separately for phototrophic communities developing directly in water (Table S4) and subaerially (Table S5). If a morphotype was detected in a certain year in at least one of the studied samples, then this morphotype was assigned a value of 1 (presence); if it was not detected, then a value of 0 (absence) was assigned.

3. Results

3.1. Hydrological, hydrochemical, and hydrobiological features of soda lake Tanatar VI and their relationship with solar activity

During the 12-year period (2011–2022), the salinity range in lake Tanatar VI varied from hypersaline values of 160–250 g/L in 2011–2012 to hyposaline values of 13–14 g/L in 2018–2019. Related changes in total alkalinity were observed in the range from 1.7 to 3.4 to 0.13 mol-eq/L, while the pH remained stable with highly alkaline values around 10 (Table 1).

An analysis of satellite images taken during the 2011–2022 summer periods revealed significant changes in the surface area and the vegetation status of the lake (Table 1, Fig. 2). From 2011 to 2014, the approximate surface area of the lake varied between 1.18 and 1.48 km^2, with the minimum area in July 2012 (Table 1). The false color and NDVI satellite images indicate blooms in the lake water from 2011 to 2014 (Fig. 2), and field observations confirmed these data. The vast “littoral” zone was exposed to the air during this period (Fig. 1c), and rare thickets of *Suaeda* sp. grew in this zone.

During 2015–2016, the surface area increased to 2.08 km^2, the water level rose, and the “littoral” zone with the thickets of *Suaeda* sp. was partially flooded. No green vegetation in the lake water was detected in false color and NDVI satellite images (Fig. 2), although during field observations water bloom was noted in 2015.

Natural color and NDWI images clearly show that there was a sharp increase in the surface area of the lake in 2017, which led to the formation of a water connection between Tanatar VI and Tanatar V (Fig. 2). Unfortunately, field observations were not carried out this year. A further increase in the area of the lake (with the maximum calculated area of 3.58 km^2 observed in July 2019) led to partial flooding of the floodplain, where *Phragmites* sp. grew (Fig. 1d). During field observations, water blooms were noted in 2018–2020, although false color and NDVI satellite images indicate blooms only in 2020 (Fig. 2).

In 2021, the reverse salinization of the lake began: the salinity increased and the surface area of the lake decreased to 3.00 km^2 (Table 1). Both field observations and satellite images indicated a water bloom this year (Fig. 2). The partial flooding of the floodplain with *Phragmites* sp. remained, although its area was visually reduced. In 2022, the salinization of the lake and the reduction of its surface area continued (Table 1). Floodplain with *Phragmites* sp. dried up (Fig. 1 e). Both years were characterized by the precipitation of carbonate minerals at the bottom, which was not previously observed in this lake.

Based on the analysis of satellite and hydrochemical data, as well as the field observations described above, we distinguished high (100–250 g/L in 2011–2014), medium (60 g/L in 2015–2016), extremely low (13–16 g/L in 2017–2020), and low (23–34 g/L in 2021–2022) salinity periods (Table 1, Fig. 2). It is important to note that the salinity ranges were identified by us empirically and don't exactly correspond to any classifications of lakes by salinity.

Changes in salinity and surface area were negatively correlated ($R = -0.8238$, $p = 0.0087$) and showed signs of long-term dynamics. It might seem that the lake's fullness is related to the amount of precipitation falling in the area. However, analysis of the surface area of Tanatar VI with respect to the annual precipitation at four nearby meteorological stations (Rubtsovsk, Klyuchi, Uglovskoe, and Volchiha) didn't show a direct relationship: $R = -0.1360$, $R = -0.1203$, $R = -0.0974$, and $R = 0.1104$ ($p < 0.0001$) for the listed stations, respectively (Fig. S2, Table S2). To test the assumption that the cyclicity of lake fullness is linked to solar activity, we compared the surface area of Tanatar VI with the number of sunspots for the study period 2011–2022 (Fig. 3). It turned out that these parameters have a high or very high degree of negative correlation: $R = -0.8807$, $p = 0.0021$ (if the monthly values of sunspot numbers are used as the second dataset) and $R = -0.9002$, $p = 0.0009$ (if the smoothed monthly values are used as the second dataset) (Table S2). A period of high salinity was observed during the years of maximum solar activity of the 24th cycle; a period of medium salinity occurred at the decline in solar activity during the 24th cycle; a period of extremely low salinity occurred at a minimum of solar activity at the border of the 24th and 25th cycles; and the period of low salinity began with the beginning of the rise in solar activity in the 25th cycle.

3.2. Long-term variations in phototrophic communities of the soda lake Tanatar VI

The following types of phototrophic communities were found in Tanatar VI during the 2011–2022 summer periods (Fig. 4).

- bottom, floating, and epiphytic cyanobacterial (CB) biofilms were common throughout the study period. However, bottom and floating CB films occurred mainly during high salinity period, while epiphytic CB developed mainly on submerged stems of *Phragmites* sp. during low and extremely low salinity periods.
- blooms of the extremely salt-tolerant unicellular green algae *Picocystis salinarum* R.A.Lewin 2001 (*Picocystis*-bloom) were common during high and medium salinity periods.
- floating and epiphytic *Ctenocladus*-communities with filamentous chlorophyte *Ctenocladus circinnatus* Borzì 1883 and diverse cyanobacteria were common during medium and low salinity periods (although once recorded in a high salinity period);
- blooms of planktonic cyanobacteria (CB-blooms) were common during low and extremely low salinity periods.
- subaerial biofilms (SBF) developed on the shore of the lake (in the "littoral" zone) on the moist soil between thickets of *Suaeda* sp.; can be interpreted as biological soil crusts; were common throughout the study period except for the extremely low salinity period when the area of SBF development was flooded.

3.3. Diversity of key phototrophs in the soda lake Tanatar VI

Morphotypes of cyanobacteria and other key phototrophic microorganisms (algae and anoxygenic bacteria) identified in Tanatar VI during the 2011–2022 period are shown in Fig. 5.

Among eukaryotes, chlorophyta *Picocystis salinarum* and *Ctenocladus circinnatus* were the most abundant and played a key structural role in the phototrophic communities. Anoxygenic phototrophic bacteria were represented by morphotypes corresponding to the purple sulfur bacteria *Ectothiorhodospira* sp., *Chromatium* sp. and *Thiocapsa* sp. and filamentous "*Ca.* Viridilinea mediisalina", the latter

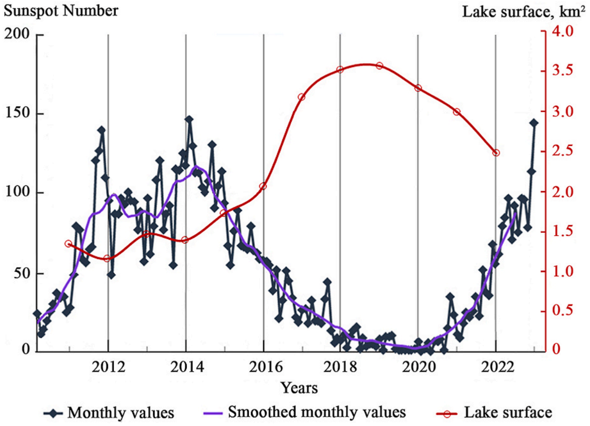

Fig. 3. Sunspot number progression and changes in surface area of the soda lake Tanatar VI for the study period 2011–2022. Smoothed monthly values are a 13-month weighted, smoothed version of the monthly averaged data.

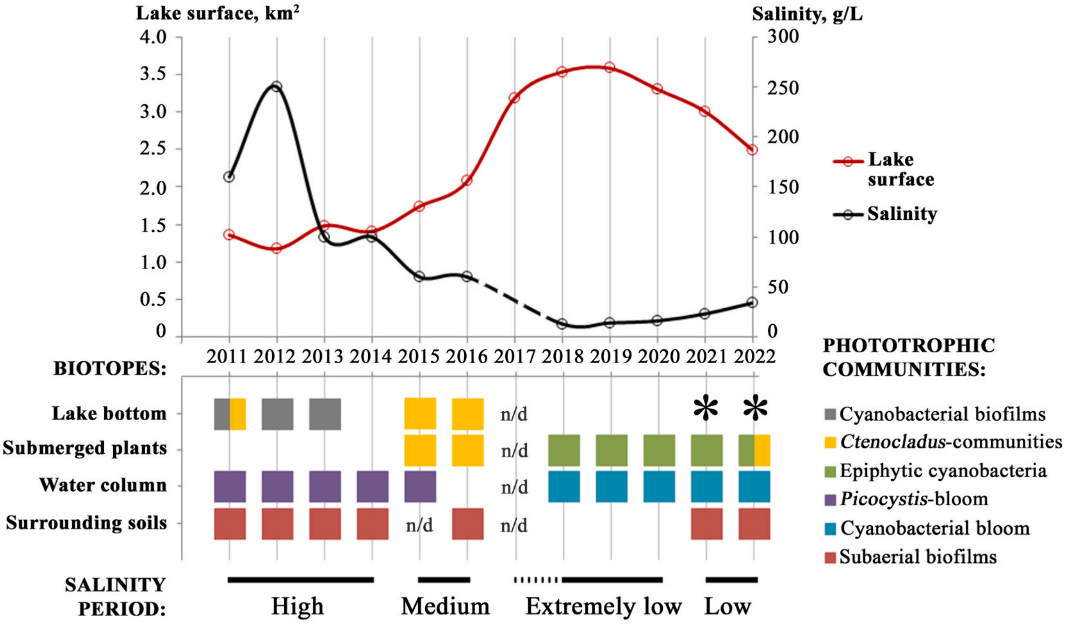

Fig. 4. Change in total salinity, surface area and microbial communities of the soda lake Tanatar VI during the summer periods from 2011 to 2022. * – cases of precipitation of carbonate minerals at the bottom of the lake in 2021–2022; n/d – no data.

with a confirmed phylogenetic affiliation [14].

Cyanobacteria reached the greatest morphological diversity among phototrophic microorganisms studied in the lake. In total, 33 morphotypes were identified during the observation period from 2011 to 2022. Among them are 9 heterocystous, 15 filamentous non-heterocystous, and 9 unicellular cyanobacteria.

Heterocystous cyanobacteria were represented by morphotypes corresponding to *Anabaenopsis issatschenkoi* Woronichin 1934, *Anabaenopsis nadsonii* Woronichin 1929, *Calothrix* cf. *elenkinii* Kossinskaja 1924, *Nodularia harveyana* Thuret ex Bornet & Flahault 1886, *Nodularia* cf. *sphaerocarpa* Bornet & Flahault 1888, *Nostoc* cf. *paludosum* (Kützing ex Bornet & Flahault) Elenkin 1936, *Nostoc* cf. *punctiforme* Hariot 1891, cf. *Trichormus variabilis* (Kützing ex Bornet & Flahault) Komárek & Anagnostidis 1989 and cf. *Trichormus* sp. Filamentous non-heterocystous cyanobacteria were represented by morphotypes corresponding to *Sodalinema* sp., *Nodosilinea* sp., cf. *Halomicronema* sp., *Phormidium* cf. *etoshii* Dadheech, Casamatta, P.Casper & Krienitz 2013, *Spirulina major* Kützing ex Gomont 1892, *Leptolyngbya tenuis* (Gomont) Anagnostidis & Komárek 1988, *Leptolyngbya* cf. *foveolarum* (Gomont) Anagnostidis & Komárek 1988, *Leptolyngbya* sp., *Pseudanabaena* sp., *Oscillatoria* cf. *tenuis* C.Agardh ex Gomont 1892, *Arthrospira maxima* Setchell & N.L.Gardner 1917, *Limnospira fusiformis* (Voronichin) Nowicka-Krawczyk, Mühlsteinová & Hauer 2019, *Leibleinia* sp.1, *Leibleinia* sp.2 and cf. *Jaaginema pseudogeminatum* (G.Schmid) Anagnostidis & Komárek 1988. Unicellular cyanobacteria were represented by morphotypes corresponding to *Chroococcus turgidus* (Kützing) Nägeli 1849, cf. *Chroococcus distans* (G.M.Smith) Komárková-Legnerová & Cronberg 1994, cf. *Synechocystis salina* Wisłouch 1924, cf. *Synechocystis minuscula* Woronichin 1926, cf. *Cyanobacterium stanieri* R.Rippka & G.Cohen-Bazire 2022, cf. *Merismopedia warmingiana* (Lagerheim) Forti 1907, cf. *Aphanocapsa salina* Woronichin 1929, cf. *Geminocystis* sp. and *Euhalothece* sp.

None of the studied morphotypes developed in the entire salinity range recorded in the lake during our study (13–250 g/L). The salinity limits were found for all morphotypes of phototrophs in Tanatar VI (Fig. 6). The data clearly demonstrated that the chlorophytes *Picocystis salinarum* and *Ctenocladus circinnatus* developed in wide ranges of salinity, with the former dominating in brine blooms and the latter mainly epiphytically, although it also occurred in bottom communities. Anoxygenic phototrophic bacteria were confined to low salinity (up to 34 g/L) with the exception of *Ectothiorhodospira* sp., which presence was limited to hypersaline conditions (160 g/L).

The development of heterocystous cyanobacteria in the brines was confined to low salinity (up to 34 g/L), with the exception of *Trichormus* spp., which were found in a wider range – up to 60 g/L. Interestingly, *Nodularia harveyana* and cf. *Trichormus variabilis* disappeared in the brines and reappeared in the SBFs at salinity levels that exceeded the upper limit for these morphotypes (Fig. 6). Filamentous non-heterocystous and unicellular cyanobacteria were present in a wide salinity range (13–160 g/L). Some filamentous morphotypes were also detected in the SBFs when the salinity of the brines became too high. But in addition to morphotypes restricted by the upper salinity limit (*Phormidium* cf. *etoshii*, cf. *Halomicronema* sp., *Leptolyngbya tenuis*, and others), there were morphotypes restricted by the lower salinity limit (non-heterocystous *Sodalinema* sp. and *Nodosilinea* sp.).

The number and diversity of phototrophic microorganisms differed at different salinities, both in the brine (Fig. 7 a) and in the SBFs (Fig. 7 b). Cluster analysis based on the presence/absence matrices confirmed the boundaries of salinity periods that we identified depending on the satellite and field observational data: extremely low, low, medium, and high salinity periods were characterized by

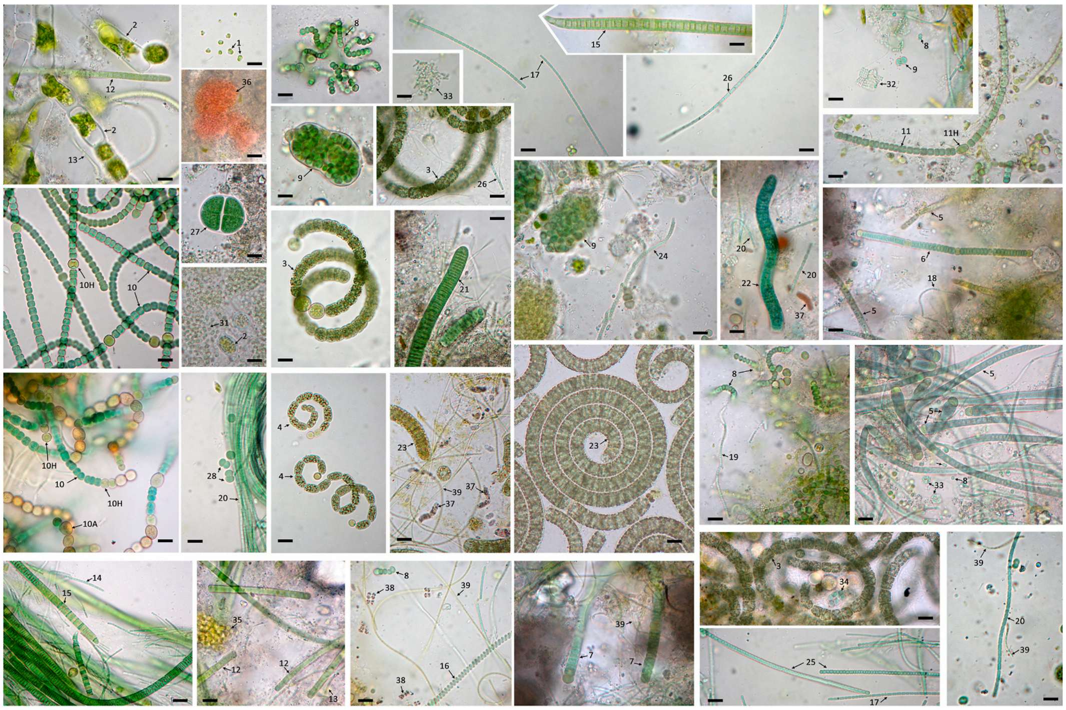

Fig. 5. Morphotypes of key phototrophs identified in the soda lake Tanatar VI (Kulunda steppe) during 2011–2022 study period. Eukaryotic algae: 1. *Picocystis salinarum*, 2. *Ctenocladus circinnatus*; Cyanobacteria: 3. *Anabaenopsis issatchenkoi*, 4. *Anabaenopsis nadsonii*, 5. *Calothrix* cf. *elenkinii*, 6. *Nodularia harveyana*, 7. *Nodularia* cf. *sphaerocarpa*, 8. *Nostoc* cf. *paludosum*, 9. *Nostoc* cf. *punctiforme*, 10. cf. *Trichormus variabilis*, 11. cf. *Trichormus* sp., 12. *Sodalinema* sp., 13. *Nodosilinea* sp., 14. cf. *Halomicronema* sp., 15. *Phormidium* cf. *etoshii*, 16. *Spirulina major*, 17. *Leptolyngbya tenuis*, 18. *Leptolyngbya* cf. *foveolarum*, 19. *Leptolyngbya* sp., 20. *Pseudanabaena* sp., 21. *Oscillatoria* cf. *tenuis*, 22. *Arthrospira maxima*, 23. *Limnospira fusiformis*, 24. *Leibleinia* sp.1, 25. *Leibleinia* sp.2, 26. cf. *Jaaginema pseudogeminatum*, 27. *Chroococcus turgidus*, 28. cf. *Chroococcus distans*, 29. cf. *Synechocystis salina*, 30. cf. *Synechocystis minuscula*, 31. cf. *Cyanobacterium stanieri*, 32. cf. *Merismopedia warmingiana*, 33. cf. *Aphanocapsa salina*, 34. cf. *Geminocystis* sp., 35. *Euhalothece* sp.; Anoxygenic phototrophic bacteria: 36. colonies of *Ectothiorhodospira* sp., 37. *Chromatium* sp., 38. *Thiocapsa* sp., 39. "*Cand.* Viridilinea mediisalina". The letter "A" next to the number indicates the akinetes of the morphotype indicated by this number, and the letter "H" indicates heterocysts. All images are at the same scale. Scale bar – 10 μm.

different complexes of phototrophic microorganisms. The transition of the lake from the period of medium salinity to the period of extremely low salinity (2016 → 2018) was associated with a significant increase in the number of phototrophic morphotypes in the brine, while between periods of high and medium salinity (2014 → 2015), as well as periods of low and extremely low salinity (2020 → 2021), this difference seems to be insignificant. On the contrary, the number of morphotypes in SBFs didn't change significantly during the study period (Fig. 7 b).

4. Discussion

4.1. Solar activity → hydrology

The relationship of solar activity to the oscillations of terrestrial water bodies around the world has long been discussed in the scientific literature [4,30–35]. There is still no clear and unified concept regarding the mechanism of this interconnection, but in general, there is a consensus that solar activity affects terrestrial hydrology through its influence on the Earth's magnetosphere and atmosphere.

The relationship of solar activity with the amount of precipitation, leading to a rise in the water level, has been shown repeatedly; a periodicity corresponding not only to the Schwabe-Wolf cycles but also to the Hale cycles (22 years) was noted [31,34,35]. Probably, this phenomenon can be used to analyze and predict the long-term patterns of the hydrological regime of the southeastern Siberian lakes. For the small lake Khilganta, the relationship between long-term fluctuations of water level and salinity and the amount of annual precipitation was revealed during the alternation of wet and dry phases during 1995–2013 [11,12,36]. The correlation between water level fluctuations and precipitation has been directly demonstrated for the large Torey lakes, where intra-century precipitation cycles lasting 25–30 years predominate [37]. But the authors didn't discuss any correlation with solar activity.

Unlike southeastern Siberian lakes, no direct correlation between the surface area of Lake Tanatar VI and the amount of annual precipitation was obvious. But we found a strong correlation with solar activity (the number of sunspots) during the 24th and the beginning of the current 25th Schwabe-Wolf cycle. We observed a direct correlation without any delayed effect. Since the Tanatar lakes

Fig. 6. The total salinity range recorded in the soda lake Tanatar VI during the study period from 2011 to 2022 (*grey line*), and the salinity ranges in which various cyanobacteria and other key phototrophs were detected. *Solid lines* – detection in brine (and in SBFs if available), *dashed lines* – detection only in SBFs (but absent in brine at these salinities). *Violet lines* – algae, *green lines* – filamentous non-heterocystous cyanobacteria, *blue lines* – unicellular cyanobacteria, *orange lines* – heterocystous cyanobacteria, *red lines* – anoxygenic phototrophic bacteria. (For interpretation of the references to color in this figure legend, the reader is referred to the Web version of this article.)

are fed mainly through groundwater [2,19], we can assume the influence of solar activity through the impact on the groundwater level. The relationship between groundwater dynamics and moisture phases was shown for the Baraba Lowland, located to the north of the Kulunda steppe [38], which confirms our assumption. Certainly, some more complex mechanism is possible that affects the level of the Tanatar lakes, and this issue requires special study.

4.2. *Solar activity → hydrology → salinity → community structure*

In the context of this work, it is important to stress that changes in solar activity are correlated with significant changes in the physicochemical parameters of the habitat of microorganisms. These changes are not abrupt (catastrophic), but slow (long-term) and oscillatory. We have studied only one crucial factor: the total salinity (pH values varied within narrow limits, and total alkalinity was directly related to total sodium carbonate-based salinity). Salinity is known to influence the composition of microbial communities in the salt and soda lakes of southern Siberia [39–42], as well as other lakes in the world. But these data were obtained on samples from different lakes and/or different years. Our previously published data on the soda lake Bitter-1 [13,14] demonstrated the effect of salinity changing from year to year. Using the data on phototrophs from the lake Tanatar VI, the present work shows that in fact, solar

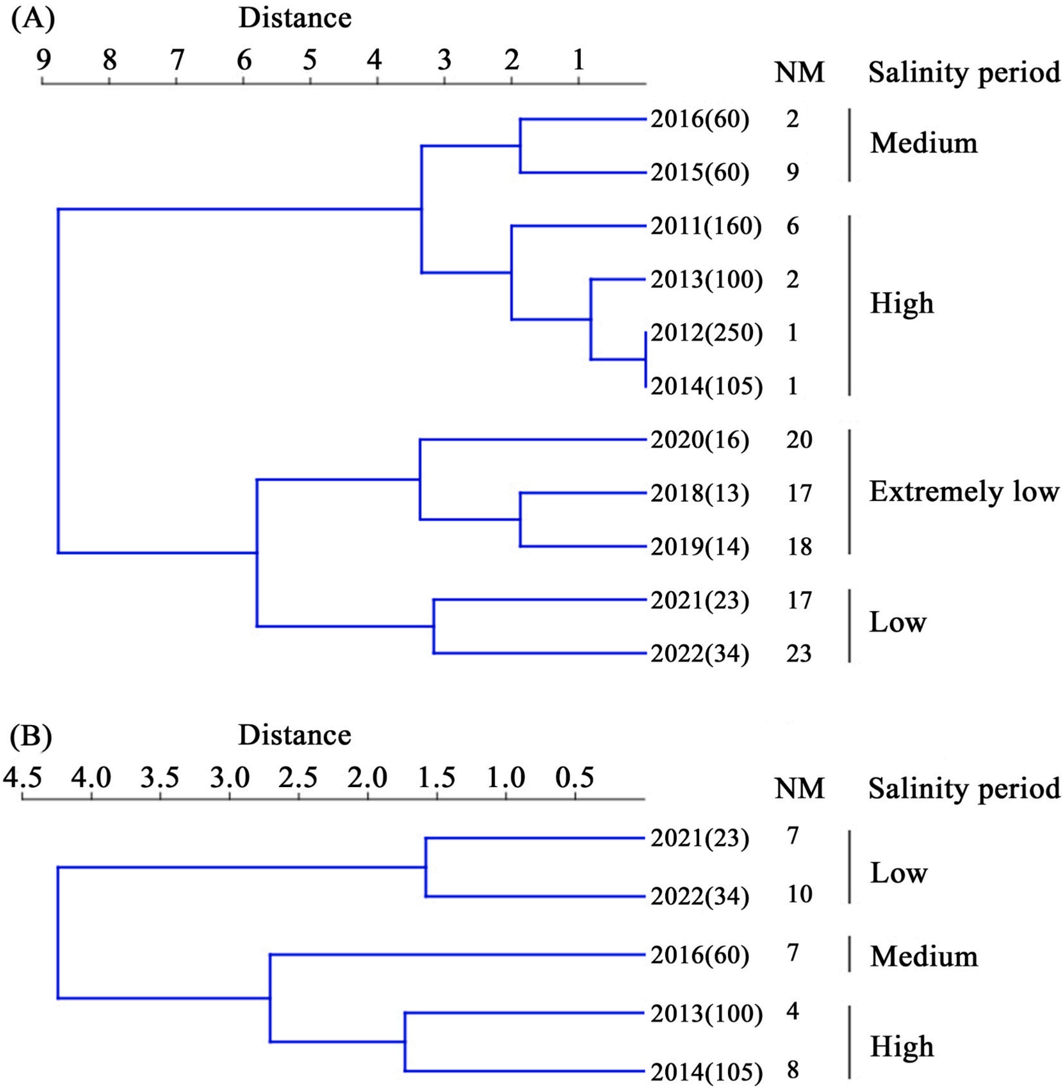

Fig. 7. Clustering of phototrophic complexes in brine (A) and SBFs (B) based on the presence/absence matrices (Tables S4 and S5) of the key phototrophic morphotypes. NM – total Number of Morphotypes found in samples.

activity cycles determine the total salinity of the lake water, which in turn determines communities and microorganisms that will develop in the same lake in a particular period of the cycle (Figs. 4 and 7).

It is also worth noting that, despite the general patterns of processes in the same region, each lake retains its individuality. Thus, the ranges of salinity changes in lakes Tanatar VI and Bitter-1 differ: 13–250 g/l and 30–400 g/l, respectively. There are both an overlapping range and individual hydrochemical features: Bitter-1 never experienced extremely low salinity, and Tanatar VI never experienced extremely high salinity. Thus, long-term observations of these lakes show that they “pulse” in different salinity ranges and pass through different stages, and the “overall long-term portrait” of phototrophic communities in these lakes varies [13,14]; and unpublished data]. Observations about different temporal variations in planktonic communities were also made when studying the long-term dynamics of the Torey lakes [10].

Salinity limits found for all studied morphotypes indicate an inevitable radical change in biodiversity, which can occur in shallow water bodies with such a wide range of salinity, as illustrated in Figs. 6 and 7. This may result in the fact that the microbial communities of the same lake observed in different phases of the intra-century climatic cycle will differ more than the microbial communities of similar lakes located on different continents [43]. It is reasonable to assume that the patterns we have identified can be extrapolated to other taxonomic and functional groups of microorganisms. Although it should be noted that the salinity limits identified in this study can’t be considered the true boundaries of the global distribution of detected morphotypes since our analysis was limited to one lake with the studied discrete salinity values.

These results fit within the framework of The Concept of Multiplicity of Ecosystem Alternative Stable States (CMEASS), according to which communities, ecosystems, and populations can exist in more than one stable state, which differs in biodiversity and functioning [44].

4.3. Community structure → functioning

The microbial diversity of salt lakes is directly translated into the functional potential of the communities. It has been previously shown that salinity is an important factor determining the rates of biogeochemical elementary cycles of carbon, nitrogen, and sulfur [11,13,18,45,46]. Important processes carried out by phototrophic microorganisms are the primary production of organic matter and the fixation of atmospheric nitrogen under aerobic conditions (for prokaryotes). According to previously published data [13,18,45], the salinity limit of about 100 g/L may be the boundary separating high and low rates of total photosynthesis and nitrogen fixation (NF) by phototrophic communities in saline alkaline lakes. In the case of lake Tanatar VI, this salinity value corresponds to the boundary between periods of medium and high salinity, which doesn't coincide with the boundary at which a significant change in diversity occurred (60 g/L, Fig. 6). This emphasizes that the salt limits that determine the intensity of microbial processes may differ from the ecophysiological salt limits of individual microorganisms. It was previously shown for soda lakes of the Kulunda steppe that communities with non-heterocystous cyanobacteria that developed in the range of 55–100 g/L demonstrate a NF rate comparable to communities with heterocystous cyanobacteria that occurred in a lower range of 25–60 g/L [18]. Thus, there was a change in the structure of the community but not in its overall functioning (regarding NF), which is important for the ecosystem as a whole.

It is worth noting that the main mechanism of salinity limitation in certain functional groups of prokaryotes lays in different energy yields of catabolism, which determine their ability to synthesize osmoprotectants [47,48]. Therefore, in saline lakes with neutral pH, the boundaries may differ due to other ecophysiological limits of halophilic microorganisms compared to natronophilic ones because of the important difference in the osmotic properties between the sodium chloride and sodium carbonate brines [15,16].

Nevertheless, salinity is an important factor that directly controls the overall activity of microbial communities in salt lakes. Due to the indirect influence of long-term periods of solar activity on cyclic salinity fluctuations, it can be concluded that during each solar Schwabe-Wolf cycle, the supply of certain products of microbial activity (for example, organic matter, bound nitrogen, and methane cycling) to the ecosystem may change. Such influence of solar activity on the periodicity of lake productivity in the Holocene (12 Ka – Present) has been directly shown for southernmost South America [49] and during the late Early Cretaceous (123–120 Ma) for south-eastern Mongolia [50].

5. Limitations of this study

The empirical results reported herein should be considered in light of some limitations related to the retrospective and observational nature of the study. In particular, such limitations include the non-use of molecular methods for identifying microorganisms and the lack of quantitative estimates of the occurrence of phototrophic microorganisms, as well as the question of the reproducibility of the data obtained.

Algological monitoring studies have traditionally used morphological approaches. Phototrophic microorganisms and microalgae are quite large in size and have a diverse and easily recognizable cell morphology, which allows annual monitoring without the use of molecular methods. However, molecular methods, in particular DNA metabarcoding, are now becoming more common. Today, the ability to distinguish cryptospecies is the most important advantage of metabarcoding over morphological identification when studying cyanobacteria and microalgae [51,52], although recent publications show that both approaches give generally congruent results in different ecosystems [13,51,53,54]. To emphasize that our study didn't assess the presence of cryptospecies, we used the term "morphotypes" instead of "species." In summary, we believe that we assessed the biodiversity of the studied organisms quite fully, and this limitation didn't fundamentally affect the conclusions drawn.

Quantitative estimates of the representation of various phototrophic microorganisms could be more valuable than the qualitative analysis we used. But such estimates are very sensitive to following precise sampling and processing procedures each year to get statistically significant results. Since the collection and processing of samples were carried out using a simplified method, we focused on qualitative criteria (the presence or absence of particular morphotypes) in this retrospective analysis. The detection of vegetative (not dormant) cells or specimens of a particular microorganism under certain conditions normally indicates ecophysiological adaptations to survival in these conditions; therefore, the patterns of succession of phototrophic communities identified in this study can be considered quite correct.

Finally, the question of the reproducibility of the presented results and patterns in the future, that is, during the next cycles of solar activity, is open. Since we only have a 12-year direct observation period, we are unable to evaluate our data in relation to the longer intra-century cycles that were determined for this area. More research is needed to solve this issue, ideally accounting for all the restrictions covered in the current work as well as the possibility that longer intra-century cycles [3–5,31,34,35,37,55] could have a more significant impact.

6. Conclusion and future perspectives

Here, we analyzed only one soda lake, changing from a hyper- to hyposaline state within a 12-year cycle. The observed changes included the reservoir itself, its margin ("littoral") zone, and partially surrounding soils, which are periodically flooded. The objects of our analysis were phototrophic microorganisms (prokaryotic and some eukaryotic), since they are characterized by a very diverse and recognizable morphology. The changes that have taken place in the lake in just 12 years have been truly impressive. But they weren't catastrophic; on the contrary, it was a stage of more or less regular cyclicity, which, based on the climatic data for the region, constantly takes place with the salt lakes in this area. As the root cause that led to the observed serious changes, we assume solar activity, which determines the alternation of dry and wet phases in southwestern Siberia. Thus, our data indicate the dynamic stability of the ecosystem of Lake Tanatar VI. By dynamic stability, we mean the alternation of different alternative (structural and/or functional) stable states of an ecosystem, naturally repeated over time.

The south Siberian salt lakes are characterized by a broad range of ecological conditions: different ion compositions (chloride, sulfate, soda, etc.), pH (from neutral to alkaline), and total salinity (from hypo- to hypersaline). Many of them are of economic importance (from fishing to collecting *Artemia* eggs, as well as mining salts). In many cases, the stable functioning of lake ecosystems in this region critically depends on the functioning of indigenous microbial communities. But microbiological studies of different types of lakes are uneven. Although observations indicate that microbial communities reflect the climatic and ecological changes in this region, we still don’t have a clear understanding of the natural limits inherent in many functional groups of microorganisms and can’t predict which climate changes may become critical for the stable existence of lake ecosystems. Moreover, there is still no clear understanding of the dynamic stability of lake ecosystems and microbial communities in this region. Such an understanding will make it possible to distinguish between normal states of lakes and “catastrophic” changes that go beyond the scope of dynamic stability. Individual taxa of microorganisms or entire microbial communities can be used as environmental indicators for these purposes. Therefore, future investigations aimed at specifically studying these issues will be relevant from both a fundamental and practical point of view.

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Data availability statement

Data included in article/supp. material/referenced in article.

Declaration of AI-Assisted technologies in the editing process

During the preparation of this work the corresponding author used Quillbot for language editing. After using this tool, the corresponding author reviewed the content and takes full responsibility for the content of the publication.

CRediT authorship contribution statement

Olga S. Samylina: Writing – review & editing, Writing – original draft, Visualization, Supervision, Methodology, Investigation, Funding acquisition, Formal analysis, Data curation, Conceptualization. **Anastasia I. Kosyakova:** Investigation, Formal analysis. **Artem A. Krylov:** Writing – original draft, Methodology, Formal analysis. **Dimitry Yu Sorokin:** Writing – original draft, Supervision, Funding acquisition. **Nikolay V. Pimenov:** Project administration, Funding acquisition.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.heliyon.2024.e26120.

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