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PRIMARY RESEARCH PAPER

Growth response of the picoplanktic *Picocystis salinarum* and the microplanktic *Limnospira (Arthrospira) fusiformis* strains from Lake Nakuru (Kenya) to rapidly changing environmental conditions

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Abstract The East African soda lakes are known worldwide for their huge populations of lesser flamingos. Their phytoplankton community is often dominated by the cyanobacterium *Limnospira fusiformis*, the main food of lesser flamingos. In the early 2010s, the population of the cyanobacterium collapsed and the picoplanktic green alga *Picocystis salinarum* became dominant in Lake Nakuru. Consequently, lesser flamingos had to migrate to other lakes in search of food. To establish the reasons for the success of *P. salinarum*, photosynthesis measurements have been performed on monoalgal cultures of both species. The examined environmental variables (temperature, light intensity) were not responsible for the dominance of *P. salinarum* either alone or in their any combination. Moreover, photosynthetic activity of the cyanobacterium was higher by an order of magnitude during all light and temperature treatments. Co-cultivation of *L. fusiformis* and *P. salinarum* in a chemostat revealed that a possible reason for the *Limnospira* replacement can be a rapid and remarkable increase of conductivity, as *P. salinarum* showed higher level of tolerance to this rapid change. Shortly

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after returning to the initial conductivity levels, the population of *L. fusiformis* recovered quickly.

Keywords *Limnospira fusiformis* · *Picocystis salinarum* · Lake Nakuru · Ecophysiology · Chemostat · Competition experiment · Photosynthetic characteristics

Introduction

Inland saline lakes occur worldwide with a total volume almost equaling that of freshwater lakes (Shiklomanov, 1990; Williams, 1993). Alkaline saline lakes of East Africa are characterized by an ionic dominance of sodium, carbonate, and bicarbonate (Jirsa et al., 2013). The core soda lakes in the Kenyan part of the African Rift Valley are lakes Nakuru, Bogoria, Magadi, and Elmentaita. These lakes provide extreme habitats with high pH (9–11), conductivity (20–120 mS cm^{-1}), water temperature (20–40°C), and high grazing pressure on the primary producers (Vareschi, 1982; Ballot et al., 2004; Oduor & Schagerl, 2007a; Schagerl & Burian, 2016). The Kenyan alkaline saline lakes are endorheic and are recharged mainly by rainfall, seasonal surface streams, and (mostly hot) springs (Oduor & Schagerl, 2007a; Renaut et al., 2017). As a result of their highly stochastic environmental dynamics, temporal fluctuations in the ionic components result in unexpected shifts in phytoplankton species composition (Vareschi, 1982; Melack, 1988; Oduor & Schagerl, 2007a; Krienitz & Kotut, 2010; Schagerl, 2016).

The East African alkaline saline lakes are worldwide famous for supporting huge populations of lesser flamingos (*Phoeniconaias minor* (Saint Hilaire, 1798)); the most famous being Lake Nakuru (Vareschi, 1978). These lakes are among the most productive ecosystems in the world owing to their high primary productivity provided by phytoplankton (Melack, 1981; Oduor & Schagerl, 2007b; Schagerl et al., 2015). Most of the time, phytoplankton is dominated by a spirally twisted, filamentous cyanobacterium, microplanktic (20–200 µm size class) *Limnospira fusiformis* (Voronichin) Nowicka-Krawczyk and Mühlsteinová & Hauer (syn. *Arthrospira fusiformis* (Voronichin) Komárek & Lund) (Cyanobacteria, Oscillatoriales) (Fig. 1a; Vareschi, 1978; Dadheech et al., 2010; Krienitz & Kotut, 2010; Kaggwa et al., 2013a; Schagerl et al., 2015; Krienitz, 2018). The key to the survival, success, and dominance of *L. fusiformis* is its fast growth and high photosynthetic rate (Talling et al., 1973; Melack & Kilham, 1974; Oduor & Schagerl, 2007b; Pálmai et al., 2013). Its size and spirally twisted form make it suitable for being sieved effectively by the special bill lamellae of lesser flamingos, hence *L. fusiformis* serves as the main food source for these birds. A strong relationship between the quantity of phytoplankton (dominated by *L. fusiformis*) and the number of the birds has been described (Jenkin, 1957; Vareschi, 1978; Vareschi & Vareschi, 1984; Krienitz & Kotut, 2010; Kaggwa et al., 2013b; Mgimwa et al., 2021). In the absence of their main food source, lesser flamingos survive by grazing on diatoms, other cyanobacteria, and algae of suitable size or migrate to other lakes (Tuite, 2000;

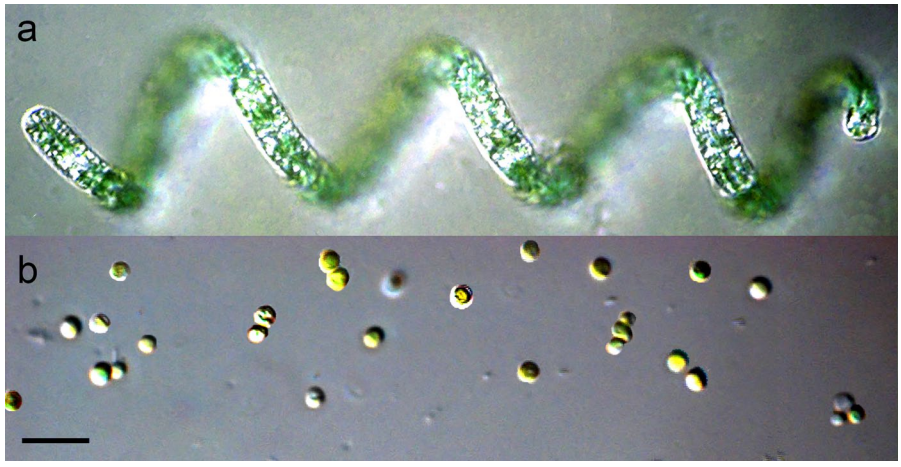

Fig. 1 **a** and **b** Light micrographs of **a** *Limnospira fusiformis* and **b** *Picocystis salinarum* (own photos) strains, isolated from Lake Nakuru. Scale bar: 10 µm

Krienitz et al., 2016). Tuite (2000) described two distinct types of lesser flamingos' distributions: the "clumped" distribution pattern, in which the majority of the total lesser flamingo population is concentrated at one or two lakes and the "dispersed" distribution pattern, in which the population is spread across all available habitats. These patterns are strongly related to the availability of *L. fusiformis.* Presence or absence of lesser flamingo clumps is strongly related to ecosystem services listed under the subsection Cultural services by the Millennium Ecosystem Assessment (2003, 2005) provided by African saline lakes on various ways (Naselli-Flores & Padisák, 2023a). They are considered as kind of firebird, the symbol of immortality by locals, moreover generate mass tourism thus establishing workplaces and contributing to national income of these regions (Krienitz, 2018).

An abrupt change in phytoplankton composition was observed by Krienitz & Kotut (2010): following the collapse of *L. fusiformis*' population, the picoplanktic green alga *Picocystis salinarum* R.A. Lewin (Picocystophyceae) became dominant. Although *P. salinarum* was characterized by high abundance, their small cells with a diameter of only 2–3 µm (Fig. 1b; Lewin et al., 2000) were too small to be eaten by the flamingos. According to a similar phenomenon observed in Lakes Elmenteita and Nakuru, the occurrence of *P. salinarum* is presumable since 1973–1974. As Melack (1988) described, a rapid increase in the salinity of the lakes was followed by the collapse of the population of *L. fusiformis* and the green algae dominated nanoplankton became dominant. Though the dominant species was not identified at that time it could have been the two decades later described *P. salinarum*. Interestingly, *P. salinarum* usually occurs in temperate alkaline saline waters, but is also able to form blooms under ice (Table 1). Since the identification of *P. salinarum* in the year 2000, various studies have been carried out on this eukaryote (Roesler et al., 2002; Fanjing et al., 2009; Ben Ali et al., 2017, 2021; Ben Ouada et al., 2018a, b; Delgado et al., 2021; Phillips et al., 2021; Singh et al., 2022, 2023). It has been reported to be a good food source for invertebrates (Roesler et al., 2002), tolerates heavy metal solutions quite well and has the ability to remove bisphenol forms (Ben Ali et al., 2017, 2021; Ben Ouada et al., 2018a, b). The ability to metabolize inorganic arsenic was reported for a *Picocystis* strain from Mono Lake (Glabonjat et al., 2020). *P. salinarum* was found in several hypersaline habitats and its biomass productivity and photosynthetic activity were enhanced in very high dissolved inorganic carbon concentration and salinity (salinity ≈ 150‰) and found to be suitable for bicarbonate-based carbon capturing (Singh et al., 2022, 2023).

Both *L. fusiformis* and *P. salinarum* prefer alkaline saline habitats; however, the number of documented co-occurrences is low (Table 1). The co-occurrence of *Picocystis* and *Limnospira* was first described in Lake Nakuru (Krienitz & Kotut, 2010; Krienitz et al., 2012) and later in Lake Dziani Dzaha (Cellamare et al., 2018; Bernard et al., 2019). In both studies, the huge dominance of *L. fusiformis* in the phytoplankton biomass was observed. However, in contrast to the East African soda lakes, in Lake Dziani Dzaha, the cyanobacterium was not replaced by *P. salinarum*. Hence, both species were dominant within their taxonomic and ecological groups in Lake Dziani Dzaha: *L. fusiformis* was responsible for 99.99% (8,249,182 sequences) of Cyanobacteria abundance, while *P. salinarum* accounted also for 99.99% (1,480,251 sequences) of eukaryotic phytoplankton species (Bernard et al., 2019).

To our knowledge, no study on any Kenyan strain of *P. salinarum* has been conducted so far except our previous work (Pálmai et al. 2020). Although *L. fusiformis* is a well-known species and has been the target of many ecological and biotechnological studies (Cifferi, 1983; Affan et al., 2015; Castro et al., 2015; Ronga et al., 2019; Shao et al., 2019), no laboratory experiment focusing on the co-existence of *L. fusiformis* and *P. salinarum* has been published. In the current study, we focused on the effects of three important abiotic environmental factors: temperature, light intensity, and conductivity. First, we determined the photosynthetic activity of *L. fusiformis* in a wide range of temperature and light intensity in a monoculture. Thereafter, we examined the effect of rapid conductivity changes on a mixed culture of the two species in a chemostat to reveal whether it can explain dominance shift between the two species.

Materials and methods

Strains and cultivating

Photosynthesis and co-cultivation experiments were carried out with *Limnospira fusiformis* (KR

Table 1 Occurrences of *Limnospira fusiformis* and *Picocystis salinarum* in alkaline saline lakes worldwide and the documented co-occurrences of the species marked with bold (after Schagerl et al., 2015; Krienitz et al., 2016; Tarazona Delgado et al., 2017; Pálmai et al., 2020)

Continent & Country	Lake	GPS	References
L. fusiformis			
Africa Kenya	**Bogoria**	**0.252955; 36.101129**	Ridley et al. (1955), Tuite (1981), Melack et al. (1982), Hindák (1985), Harper et al. (2003), Ballot et al. (2005), Schagerl & Oduor (2008), Krienitz & Kotut (2010), and Krienitz et al. (2016)
	Nakuru	**– 0.360927; 36.090687**	Rich (1932), Melack & Kilham (1974), Tuite (1981), Melack et al. (1982), Vareschi (1982), Ballot et al. (2005), Schagerl & Oduor (2008), Krienitz & Kotut 2010), and Krienitz et al. (2016)
	Sonachi	– 0.78262; 36.261692	Rich (1932), Ballot et al. (2005), and Krienitz et al. (2016)
	Simbi	– 0.367341; 34.629801	Melack (1979), Ballot et al. (2005), Krienitz et al. (2016)
	Oloidien	– 0.813959; 36.277494	Krienitz & Kotut (2010), Krienitz et al. (2013), Krienitz et al. (2016), and Luo et al. (2017)
	Elmenteita	– 0.444375; 36.24069	Rich (1932), Melack & Kilham (1974), Melack (1988), Ballot et al. (2005), Schagerl & Oduor (2008), and Krienitz et al. (2016)
	Magadi	**– 1.9124; 36.269837**	Tuite (1981) and Krienitz et al. (2016)
Africa Ethiopia	Abijata	7.625062; 38.611943	Talling et al. (1973)
	Arenguade	8.695547; 38.975971	Talling et al. (1973), Kebede & Ahlgren (1996), Kebede (1997), and Girma et al. (2012)
	Chitu	7.405367; 38.42133	Ogato & Kifle (2014) and Kumssa & Bekele (2014)
	Kilotes	8.804113; 39.084535	Talling et al. (1973)
Africa Tanzania	Big Momella	– 3.222658; 36.908526	Melack & Kilham (1974), Tuite (1981), Lugomela et al. (2006), Krienitz et al. (2016), and Hamisi et al. (2017)
	Magad	– 3.189168; 35.534479	Melack & Kilham (1974)
	Manyara	– 3.627707; 35.823856	Melack & Kilham (1974), Tuite (1981), Lugomela et al. (2006), Kihwele et al. (2014), and Krienitz et al. (2016)
	Reshitani	– 3.231451; 36.908277	Melack & Kilham (1974)
	Tulusia	– 3.211139; 36.906988	Tuite (1981) and Krienitz et al. (2016)
Africa Namibia	Walvis Bay Bird Paradise	– 22.964366, 14.533817	Krienitz et al. (2016)
Africa South Africa	Kamfers Dam	– 28.672288, 24.763816	Hill et al. (2013) and Krienitz et al. (2016)
Africa Uganda	**Katwe**	**– 0.128273; 29.867407**	Mungoma (1990) and Krienitz et al. (2016)
	Masehe	– 0.100676; 30.177943	Mungoma (1990)
Africa **France, Mayotte Island**	**Lake Dziani Dzaha**	**– 12.771; 45.288667**	Cellamare et al. (2018) and Bernard et al. (2019)
Africa Chad	Chad	13.102705; 14.510394	Ciferri (1983) and Sili et al. (2012)
	Rombou	14.091489; 15.216202	Iltis (1969)
	Mombolo	14.029776; 14.497099	Iltis (1971)
Africa Sudan	Dariba	12.951702; 24.256724	Fott & Karim (1973)
	Jebel Marra	12.95182; 24.259121	Fott & Karim (1973)
Africa Egypt	Lake Mariout	31.08011; 29.79562	Hamad et al. (2023)

Table 1 (continued)

Continent & Country	Lake	GPS	References
Asia Turkey	Van	38.619062; 42.948814	Hammer (1986)
Asia India	Shambhar	26.933713; 75.089209	Dadheech et al. (2010)
	Mansagar	26.956082; 75.848905	Dadheech et al. (2010)
	Israel	River Yarkon	32.097258; 34.791249
		Kishon River	32.588693; 35.264852
Central America Mexico	Texcoco	19.465917; − 98.9699	Dadheech et al. (2010)
South America Brazil	Salina da Reserva	− 18.960278, − 56.623611	Costa et al. (2016)
	Salina do Meio	− 18.974167, − 56.6475	Costa et al. (2016)
Europe Serbia	salty puddles (Baranda)	45.080955; 20.476929	Fužinato et al. (2010)
Europe Greece	Lake Koroneia	40.686704; 23.141598	Moustaka-Gouni et al. (2007)
Picocystis salinarum			
Africa Kenya	**Bogoria**	**0.252955; 36.101129**	Krienitz et al. (2012)
	Nakuru	**− 0.360927; 36.090687**	Krienitz et al. (2012)
	Magadi	**− 1.9124; 36.269837**	Krienitz et al. (2012)
	Hot Springs Magadi	− 1.977585; 36.23848	Krienitz et al. (2012)
Africa **France, Mayotte Island**	**Lake Dziani Dzaha**	**− 12.771; 45.288667**	Cellamare et al. (2018) and Bernard et al. (2019)
Africa Tunisia	Essed valley, sewage	35.989757; 10.502778	Ben Ali et al. (2017) and Ben Ouada et al. (2018a, b)
Africa **Uganda**	**Katwe**	**− 0.128273; 29.867407**	Krienitz et al. (2012, 2016)
	Bagusa	− 0.102778, 30.173333	Krienitz et al. (2016)
Asia P.R. China	Lake Dagenoer	42.683485; 115.84986	Fanjing et al. (2009)
Asia Russia	Lake Tanatar VI	51.620276; 79.816436	Samylina et al. (2010)
	Lake Altaiskoye	53.425940, 91.584786	Makeeva & Osipova (2022)
Asia India	Lake Sambhar	26.941672, 75.086469	Krienitz et al. (2016), Krienitz (2018), and Singh et al. (2023)
North America USA	San Francisco Salt Works	37.688579; − 122.3176	Lewin et al. (2000)
North America USA	Lake Mono	38.006943; − 118.9864	Roesler et al. (2002) and Phillips et al. (2021)
North America USA	San Elijo Lagoon	33.014362; − 117.2532	Wang et al. (2014)
South America Peru	Laguna La Milagrosa	− 12.54471; − 76.72312	Tarazona Delgado et al. (2017)
Peru	Laguna La Mellicera	− 12.54287; − 76.72521	Tarazona Delgado et al. (2017)

2005/117) and *Picocystis salinarum* (KR 2010/2) strains from the collection of Leibniz-Institute of Freshwater Ecology and Inland Fisheries. Both strains were collected from Lake Nakuru, Kenya. Their taxonomic identities were confirmed by molecular phylogenetic analyses (Dadheech et al., 2010; Krienitz et al., 2012). The sequences of 16S-23S ITS and *cpc* BA IGS of the *Limnospira fusiformis* strain were stored at the National Center for Biotechnology Information (NCBI) under the accession numbers FJ001900 and FJ001933. The sequence of the small subunit (SSU) rRNA gene of the *Picocystis salinarum* strain was stored at NCBI under the accession number HM990668.

Monoalgal stock cultures of the two species were held in M_0 medium with the following ingredients: 15 g l^{-1} $NaHCO_3$, 4 g l^{-1} Na_2CO_3, 0.1 g l^{-1} NaCl, 0.08 g l^{-1} Na_2-EDTA, 0.01 g l^{-1} $FeSO_4 \times 7H_2O$, 0.2 g l^{-1} $MgSO_4 \times 7H_2O$, 0.5 g l^{-1} K_2HPO_4, 2.5 g l^{-1} $NaNO_3$, 0.04 g $l^{-1}CaCl_2$, and 1 ml l^{-1} of A_5-micronutrients, with the conductivity of 19.6 mS cm^{-1} (salinity ~ 10.5‰) and pH 9.8 (Shafik et al., 2014; Pálmai et al., 2020). The cultures were maintained at 20 ± 1°C and 65 µmol photons m^{-2} s^{-1} in 12:12 light:dark cycle in the Alga Culturing Laboratory of Research Group of Limnology (University of Pannonia, Veszprém, Hungary).

Photosynthesis experiments

The photosynthetic characteristics of *L. fusiformis* were examined during exponential growth phase of monoalgal culture in M_0 medium. We compared our results on the photosynthetic characteristic of *L. fusiformis* with previously published findings on *P. salinarum* (Pálmai et al., 2020). We investigated the photosynthetic activity of the species in 63 combinations of temperature and light intensity within the variable ranges of the two species' natural habitats. We used the protocol in a photosynthetron system that was previously described by Üveges et al. (2012), Pálmai et al. (2013, 2020), and Lengyel et al. (2015). Measurements were carried out between 10 and 40°C with 5°C increments. The measuring temperature was provided by a Neslab RTE-211 circulating water bath. Tungsram F74 daylight tubes provided the following nine light intensities: 0; 15; 55; 130; 250; 360, 680; and 1480 and 1900 µmol m^{-2} s^{-1}. Biomass-specific photosynthetic activity was determined by oxygen yield measurements: the culture was homogenized in a 15-L vessel and then divided into Karlsruhe flasks (~ 250 ml). The first measuring was carried out at 10°C. We started the process with a 1-h pre-incubation in the dark. As the photosynthetic activity of the species was followed by measuring dissolved oxygen (DO) concentration (IntelliCAL LDO101 sensor, Hach Lange), DO was measured at the beginning of the experiment (t = 0 h), then after 1 h (t = 1 h), and after 2 h (t = 2 h) (Pálmai et al. 2020). Respiration, net-, and gross photosynthesis were calculated using the formula of Wetzel & Likens (2000). Subsequently, photosynthetic activity–light intensity (P–I) curves were fitted and the photosynthetic parameters (P^B_{max}: biomass-specific maximum photosynthetic production, I_k: onset of saturation, α: light utilization parameter, β: photoinhibition parameter, R^B: biomass-specific respiration) calculated according to Webb et al. (1974) in the absence and to Platt et al. (1980) in the presence of photoinhibition, using GraFit 7.0 software (Leatherbarrow, 2009).

Co-cultivation experiment

Growth and co-cultivation of the two species were examined in a continuous culture in a chemostat developed by Shafik et al. (2001). The culturing vessel, with the approximate volume of 1 L, was placed into an aquarium filled up with distilled water, at constant temperature of 29 ± 1°C provided by a Thermo Scientific AC150-A25 circulating bath. The light intensity on the outer surface of the culturing vessel was 200 µmol m^{-2} s^{-1} (which decreased rapidly after entering the culturing vessel because of the high cell density) with a 12:12 light:dark cycle provided by daylight tubes of Tungsram (F74). The values of temperature and light intensity were selected based on previous field observations (Vareschi, 1982; Krienitz & Kotut, 2010; Jirsa et al., 2013) and our photosynthesis measurements (Fig. 2a, b, c, d; Table 2; Pálmai et al., 2020) to provide preferable conditions for both species' growth. The aquarium was illuminated from one side and the walls of the other three parts of the aquarium were covered by mirrors to provide homogeneous illumination. The mixed culture was aerated with sterilized air (obtained by passing air through a Millipore membrane filter with 0.2 µm pore size) from the bottom of the cultivating vessels to avoid the effect of the different sinking rates of the species. That is, the air supply was not only

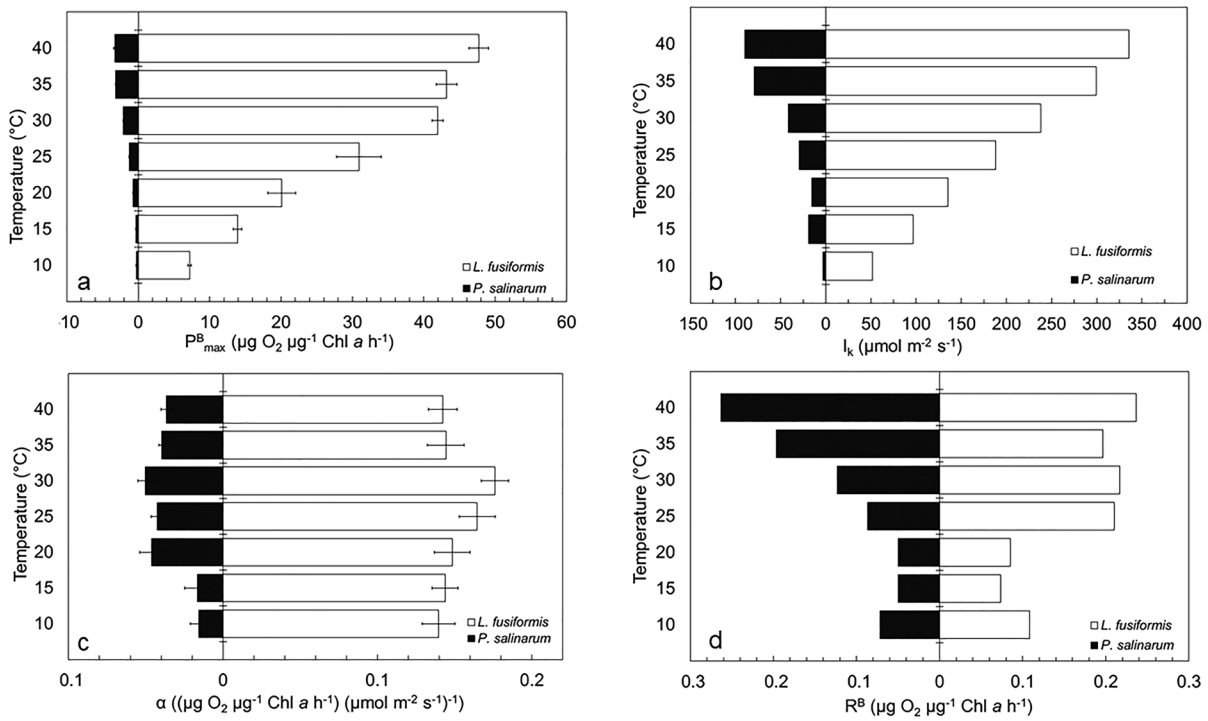

Fig. 2 Photosynthetic parameters of *Limnospira fusiformis* (KR 2005/117) (empty bars) and *Picocystis salinarum* (KR 2010/2) (black bars) strains isolated from Lake Nakuru in M_0 medium at different temperatures, and the error bars represent the standard deviations. Data of *Picocystis salinarum* were obtained from Pálmai et al. (2020), **a** Biomass-specific maximal gross photosynthetic activity (P^B_{max}), **b** Onset of saturation (I_k), **c** Light utilization (α), and **d** Biomass-specific respiration (R^B). P^B_{max} value of *L. fusiformis* at 45°C on **a** is calculated from the fitted curve on the measuring data in the 10–40°C range

responsible for the supply of CO_2 but also for the continuous mixing of the culture. Culturing medium was continuously added by a Masterflex L/S Variable-Speed Drive at a flow rate of 285 ± 18 ml d^{-1}. We applied chemostat system to avoid any kind of nutrient limitation, but as we studied a mixture of two species with very different growth rates, steady state (when the dilution rate is equal to the species growth rate) was not reached for both species in all phases.

In the co-cultivation experiment, we applied the mixture of the above described monoalgal cultures. The initial biomass concentration ratio in the mixed culture was 90:10 *L. fusiformis:P. salinarum* µg chlorophyll *a* l^{-1} in a cultivating chamber with a volume of 1 L. The initial chlorophyll *a* concentration of *L. fusiformis* was 2000 µg l^{-1} and for *P. salinarum*, it was 220 µg l^{-1}. We applied 90:10 ratio in order to represent the naturally high dominance of *L. fusiformis* in the phytoplankton. Samples were taken three times a week to estimate population sizes by counting individual numbers according to Utermöhl (1958). For microscopic analyses, 10 ml subsample was preserved in Lugol's solution and 1 ml of HCl (1N) was added to the samples to avoid the decomposition of the cells in the alkaline environment. Settling units were counted in a 3 ml counting chamber after at least 12 h of settling, as a settling unit on filament was considered in the case of *L. fusiformis* and one cell in the case of *P. salinarum.*

To examine the effect of the rapidly changing environment on the co-existence of the two species, a 90-day experiment was run. We modified the conductivity of the initial M_0 medium by increasing the concentration of $NaHCO_3$ to 60 g l^{-1} and the concentration of Na_2CO_3 to 16 g l^{-1}. The conductivity of the initial medium was at a similar level to that reported by Krienitz & Kotut (2010) to be the minimum, while the conductivity of the medium with increased level of carbonates was higher than the median conductivity of Lake Nakuru reported by the same authors. The

Table 2 Photosynthetic parameters of *Limnospira fusiformis* (KR 2005/117) isolated from Lake Nakuru measured at different temperatures in M_0 media

Photosynthetic parameters	10°C	15°C	20°C	25°C	30°C	35°C	40°C
Limnospira fusiformis							
P^B_{max}	7.22	13.91	20.1	30.91	41.96	43.19	47.7
I_k	52	97	135	188	238	299	335
α	0.14	0.14	0.15	0.17	0.18	0.14	0.14
β	0.0029	0.0056	0.0099	0.0064	–	–	–
R^B	0.11	0.07	0.09	0.21	0.22	0.2	0.24
P^B_{max}/R^B	66.64	189.71	236.44	147.19	193.64	219.63	201.54
Picocystis salinarum							
P^B_{max}	0.29	0.31	0.71	1.26	2.09	3.16	3.3
I_k	3	19	15	29	42	79	90
α	0.1	0.017	0.046	0.04	0.05	0.04	0.04
β	1×10^{-4}	3.15×10^{-5}	9.31×10^{-5}	2×10^{-4}	2×10^{-4}	2×10^{-4}	5×10^{-4}
R^B	0.07	0.05	0.05	0.09	0.12	0.2	0.26
P^B_{max}/R^B	4.08	6.26	14.26	14.50	16.96	16.04	12.51

Values of *Picocystis salinarum* were calculated from the raw data of Pálmai et al., (2020). P^B_{max}: biomass-specific maximal gross photosynthetic production (μg O_2 μg^{-1}Chl *a* h^{-1}), I_k: onset of saturation (μmol m^{-2} s^{-1}), α: light utilization parameter ((μg O_2 μg^{-1}Chl *a* h^{-1}) (μmol m^{-2} s^{-1})$^{-1}$), β: photoinhibition parameter ((μg O_2 μg^{-1}Chl *a* h^{-1}) (μmol m^{-2} s^{-1})$^{-1}$), and R^B: biomass-specific respiration (μg O_2 μg^{-1}Chl *a* h^{-1})

experiment consisted of three phases: in phase I, the mixed culture was grown in M_0 medium for 30 days, where the conductivity was 19.66 ± 0.15 mS cm^{-1} (salinity ~ 10.5‰) and the pH was 9.84 ± 0.05. In phase II, the conductivity of the medium was increased to 52.53 ± 1.47 mS cm^{-1} (salinity ~ 31.1‰) and the pH decreased to 9.5 ± 0.05; the mixed culture was grown in this modified medium for another 30 days. For the last 30 days, in phase III, the conductivity was returned to the initial level (20.41 ± 0.81 mS cm^{-1}; salinity ~ 11.0‰) along with an increase of pH (9.84 ± 0.06). During the 90-day experiment, we monitored the changes in the conductivity and the pH of the medium at each sampling time. Conductivity of the medium was measured by an HQ40d Hach Lange multimeter equipped with an Intellical CDC401 sensor and the pH with an Intellical PHC201 sensor.

Results

Photosynthesis measurements

We recorded increasing photosynthetic activity of *L. fusiformis* between 10 and 40°C. The highest biomass-specific maximal gross photosynthetic activity (P^B_{max} = 47.7 μg O_2 μg^{-1} Chl *a* h^{-1}) of *L. fusiformis* was obtained at 40°C (Fig. 2a; Table 2). Similarly, temperature positively influenced the onset of saturation (I_k) of the species. *L. fusiformis* had high optimum light intensity at all measuring temperatures and its highest I_k was 335 μmol m^{-2} s^{-1} at 40°C (Fig. 2b; Table 2). Good light utilization (α) was observed along the applied temperature gradient: α values of the species varied between 0.14 and 0.176 (μg O_2 μg^{-1} Chl *a* h^{-1}) (μmol m^{-2} s^{-1})$^{-1}$ (Fig. 2c; Table 2). Photoinhibition occurred at the temperature range of 10–25°C. The biomass-specific respiration (R^B) values of the species were about the same level in the 10–20°C temperature range. However, with a further increase of the temperature we found a remarkable increase in the R^B values at the 25–40°C temperature range (Fig. 2d; Table 2). The small R^B values coupled with very high level of P^B_{max} resulted in very high P^B_{max}/R^B values (Table 2).

We recorded the lowest, but still considerable photosynthetic activity for *L. fusiformis* in the light intensity range 15–130 μmol m^{-2} s^{-1}. At the lowest two light intensities only a slight effect of

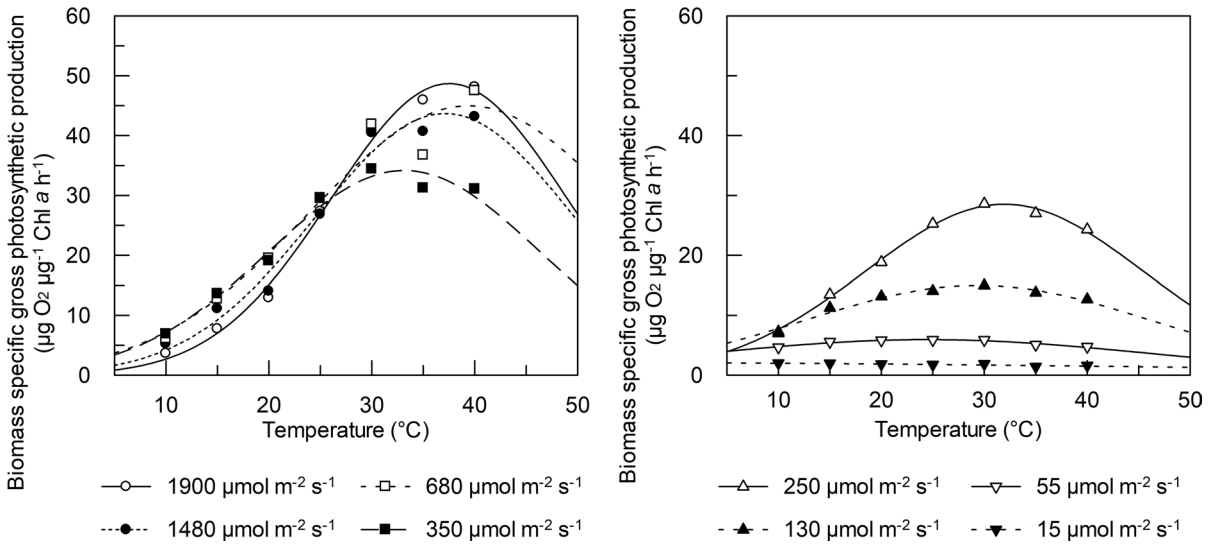

Fig. 3 Temperature dependence of biomass-specific gross photosynthetic production of *Limnospira fusiformis* (KR 2005/117) from Lake Nakuru was obtained from laboratory experiment performed at different light intensities

temperature was observed. At the light intensity range of 130–250 µmol m^{-2} s^{-1}, the highest photosynthetic activity of the species was recorded at about 30°C (Fig. 3). The rapid increase in photosynthesis with the increasing light intensity confirms the good light utilization of the species. Alongside an increase in photosynthetic activity at higher light intensity range, a slight increase in temperature optima was observed. At high light intensities, photosynthetic activity of the species increased with the increasing temperature, with the highest photosynthetic activity being recorded at the highest temperature.

Co-cultivation experiment

We examined the effect of rapid shifts in conductivity on the growth of mixed culture of *L. fusiformis* and *P. salinarum* in two culturing media characterized by different conductivity values, obtained by altering $NaHCO_3$ and Na_2CO_3 concentrations.

In phase I, an increase in the biomass of both species (Fig. 4) was observed in the initial medium. This increase in biomass was continuous and in a straight line for *L. fusiformis* until a shift to the high conductivity medium. This is in contrast to *P. salinarum*, which almost reached a steady state by the end of phase I.

Following the shift in medium, the biomass of both species began to decrease. In phase II, the biomass of *L. fusiformis* decreased during the entire high conductivity phase. In case of *P. salinarum*, a remarkable decrease in biomass was recorded; however, the green alga was able to adapt to the changes in the conductivity and from the middle of phase II (~2 weeks after the medium change) its biomass began to grow. At the end of phase II, *P. salinarum* had reached a steady state again. On return to the initial medium in phase III, the biomass of both species began to increase following an initial stationary state. In phase III, *L. fusiformis* remained at an exponential growth phase all the way to the end of the experiment. In contrast, *P. salinarum* reached steady state again. The growth of the two species did not reach the level of the initial section in phase I.

Discussion

The East African alkaline saline lakes are highly productive ecosystems (Melack, 1979, 1981; Oduor & Schagerl, 2007b; Schagerl et al., 2015). The very high primary production is often caused by a single phytoplankton species, *Limnospira fusiformis*, serving as essential food source for the lesser flamingos (Jenkin, 1957; Vareschi, 1978; Krienitz & Kotut,

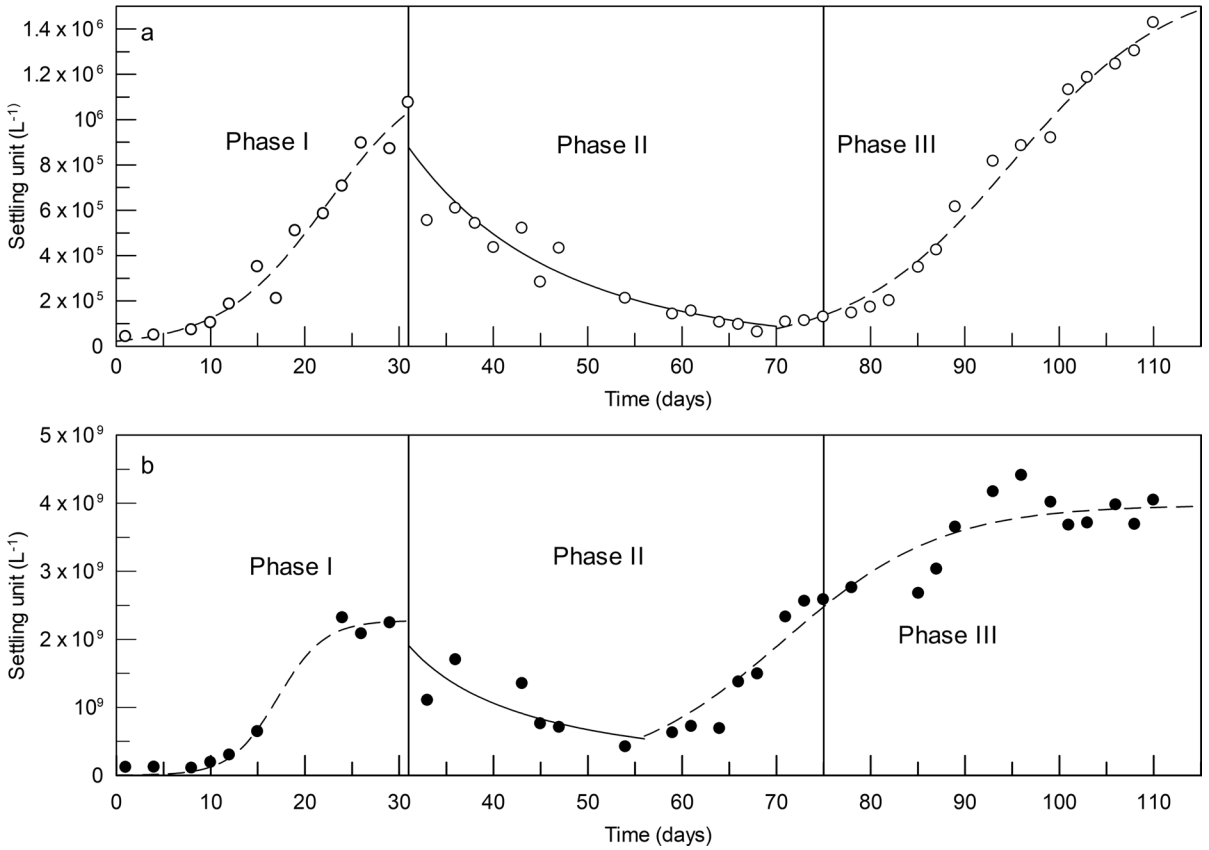

Fig. 4 Growth curves of *Limnospira fusiformis* (**a**, empty circles) and *Picocystis salinarum* (**b**, black circles) in continuous culture in phase I (dashed line in M_0 medium, pH 9.84 ± 0.05, conductivity = 19.66 ± 0.15 mS cm^{-1}, salinity ~ 10.5‰), phase II (solid line, in modified medium, pH 9.5 ± 0.05, conductivity = 52.53 ± 1.47 mS cm^{-1}, salinity ~ 31.1‰), and phase III (dashed line in M_0 medium, pH 9.84 ± 0.06, conductivity = 20.41 ± 0.81 mS cm^{-1}, salinity ~ 11.0‰). Dots represent the counted settling units per liter; vertical lines indicate the change of the medium on day 31 and 75

2010; Krienitz, 2018). In these extreme habitats, phytoplankton composition is affected by several environmental variables including a number of abiotic factors such as nutrient availability, temperature, light intensity, conductivity, and also by biotic factors, like inter- and intraspecific competition and viral infections (Vareschi, 1979, 1982; Vareschi & Vareschi, 1984; Jirsa et al., 2013; Peduzzi et al., 2014; Krienitz et al., 2016; Schagerl & Burian, 2016).

Limnospira fusiformis is considered to prefer higher temperatures: the positive correlation between temperature and photosynthetic activity of the species is well known and has been confirmed by previous studies as well as by our recent results (Vonshak, 1997; Pálmai et al., 2013; Table 2). In previous studies, *P. salinarum* was found to have a photosynthetic activity lower by an order of magnitude or even more compared to *L. fusiformis* which is in line with our results (Roesler et al., 2002; Pálmai et al., 2020). The photosynthetic activity of the green alga showed a strong temperature dependence with photoinhibition occurring over a wide range of temperatures (Pálmai et al., 2020), while in case of *L. fusiformis*, we found photoinhibition only at lower temperatures (Table 2). This huge difference between the P^B_{max} of the two species was also recorded in our previous study in Cl^--dominated medium (Pálmai et al. 2013). Similar levels of biomass-specific respiration of *P. salinarum* and *L. fusiformis* were recorded along a wide range of temperature, but the cyanobacterium had high P^B_{max} and these huge differences resulted in an extremely high P^B_{max}/R^B ratio. This observation has also been described for other cyanobacteria species

(Van Liere & Mur, 1980; Vonshak, 1997). In contrast, *P. salinarum* had a moderate ratio along the temperature gradient with P^{B}_{max}/R^{B} values similar to those recorded by Humphrey (1975) for several algal species.

Light availability in the East African region is quite good; however, the high turbidity caused by both wind and bioturbation by a huge population of birds and shading by high phytoplankton crop results in a high light attenuation within the water column (Vareschi, 1982; Oduor & Schagerl, 2007b). These light conditions coupled with high temperature create suitable habitat for both species. According to our results *L. fusiformis* can utilize higher light intensity, at least for shorter periods of time without photoinhibition even at high temperature but also performs well under lower illumination (Vonshak, 1997; Pálmai et al., 2013; Table 2). In contrast, the turbid and light limited water column offers favorable conditions for both *P. salinarum* and *L. fusiformis*, as they have good light utilization (Kebede & Ahlgren, 1996; Roesler et al., 2002; Fanjing et al. 2009; Pálmai et al., 2020; Table 2). The pigment composition of the two species as described by Bernard et al. (2019) also supports our findings on the difference in the light tolerance ranges. Although, photoinhibition in *P. salinarum* was recorded over a wide range of temperature (Pálmai et al., 2020) in its natural environment, the species can avoid the negative effect of high light intensity of the surface layer by occupying the deeper parts of the water column characterized by lower light availability (this sometimes means only 20–30 cm below the surface), hence avoiding the surface layer (Vareschi, 1982; Oduor & Schagerl, 2007b).

Since both photosynthetic activity and growth of *P. salinarum* are far below the values of *L. fusiformis*' (Kebede & Ahlgren, 1996; Roesler et al., 2002; Fanjing et al., 2009; Pálmai et al., 2013, 2020; Table 2), we assumed that another abiotic environmental factor or changes in this factor could be the reason for the dominance change between the two species in the Kenyan soda lakes. Krienitz & Kotut (2010), Schagerl et al. (2015) and Krienitz (2018) attributed the dominance of *P. salinarum* in the soda lakes of East Africa to the rapid changes in salinity.

Although there are no previous experiments on the growth of the Kenyan strains in mixed cultures, some studies have revealed that the two species remarkably differ in salt tolerance. Increasing sodium salt (Na_2SO_4, NaCl, $NaHCO_3$) concentrations has a negative effect on the growth of *L. fusiformis* and also alters the morphology of the cyanobacterium (Kebede, 1997). Kebede (1997) recorded a negative correlation between the concentration of three sodium salts and the growth rate of *L. fusiformis*, with the highest growth occurring at a salinity of 13.2‰. A salinity range of 10–25‰ was found to be optimal for the growth of *L. fusiformis* in different media (Chen, 2011), which was also confirmed by our observations. The negative effect of high salinity (high NaCl concentration) was also recorded for *P. salinarum*; however, the eukaryote species has a higher salinity tolerance range than *L. fusiformis* (Kebede & Ahlgren, 1996; Kebede, 1997; Roesler et al., 2002; Fanjing et al., 2009; Schagerl & Burian, 2016; Pálmai et al., 2020; Singh et al., 2023).

Previous studies have confirmed that the populations of *L. fusiformis* collapse from time to time. The population collapse has been associated with a high turbidity and/or salinity periods of the lake (Melack, 1988; Schagerl et al., 2015). Empirical studies (Krienitz & Kotut, 2010; Schagerl et al., 2015; Krienitz, 2018) found a close relation between *L. fusiformis* biomass and salinity. Krienitz et al. (2012) observed that *P. salinarum* became dominant in Lake Nakuru following a drastic decrease in water level, accompanied by rapid and drastic changes in salinity, which was confirmed by in our current experimental study under laboratory conditions.

Beside the abiotic factors, two main biotic factors also affect the population size of *L. fusiformis*: intensive grazing pressure and virus infections that may result in a collapse of the cyanobacteria population and indirectly that of the entire food web as well (Peduzzi et al., 2014). Vareschi (1978) estimated the food requirements for an adult flamingo to be 70 g d^{-1} of dry mass. This means that there could be a strong pressure on *L. fusiformis* population even under favorable environmental conditions if a clumped distribution (Tuite, 2000) pattern of the flamingos occurs. A drastic change in the lake level of the observed cases was followed by a crash in the resident population of *L. fusiformis*. A lack of tolerance for this kind of change coupled with a high grazing pressure and viral infections can easily lead to the temporary disappearance of *L. fusiformis*. Following the collapse of the cyanobacterium, the lesser flamingos migrate to other lakes resulting in a dispersed

distribution pattern (Tuite, 2000) and a reduction in grazing pressure, which allows the recovery of *L. fusiformis* population. According to Vareschi (1979) and Vareschi & Vareschi (1984) grazing by fish or zooplankton is not considered as main threat to *L. fusiformis* population. *Tilapia graham* Boulenger, 1912 shifted to filtering the cyanobacterium in Lake Nakuru, but it is implausible that it could significantly reduce the biomass of *L. fusiformis* (Vareschi, 1979). Zooplankton has a higher indirect impact on the phytoplankton due to its nutrient recycling activity compared to its direct grazing effect. The absence of this nutrient recycling can result in a nutrient limitation but it was usually observed in parallel with or after the decrease of *L. fusiformis* (Vareschi, 1978; Vareschi & Jacobs, 1984; Melack, 1988).

Due to the generally good nutrient supply in the East African lakes and based on our observations that the Kenyan strains' light requirements only partially overlap (see I_k values in Table 2), resource competition for nutrients or light between the two species can be excluded. Even though, in previous cultivation studies usually higher I_k values have been recorded under laboratory conditions, compared to field measurements (Kebede & Ahlgren, 1996; Oduor & Schagerl, 2007b; Schagerl & Burian, 2016), the remarkable differences between the I_k values of the examined to species (Table 2) indicate considerable differences in their light preference. However, sometimes nitrogen limitation occurs in these habitats (Oduor & Schagerl, 2007a, 2007b), but this limitation affects the growth of both species negatively (Delgado et al., 2021; Schagerl et al., 2022) since they are not N_2 fixers under natural (aerobic) conditions. The latter may explain the "silent" and chiefly subdominant co-occurrence of the diazotrophic *Anabaenopsis* in these lakes (Krienitz et al., 2016). The co-occurrence implies that *P. salinarum* and *L. fusiformis* can exist in the same habitat and dominate the phytoplankton together; however, the green alga is not able to overgrow *L. fusiformis* under stable environmental conditions. Whereas, the biomass of *L. fusiformis* in the soda lakes of East Africa is usually measured in tens to hundreds of mg l^{-1}, the highest biomass of *P. salinarum* in Lake Nakuru ranges from 7.1 to 7.4 mg l^{-1} (Vareschi, 1982; Krienitz et al., 2012, 2016). These data suggest that *P. salinarum* benefits more from the environmental changes, hence becoming an active competitor for *L. fusiformis*.

In a wider context, the African lakes where *L. fusiformis* and/or *P. salinarum* may occur or co-occur are typical examples of extreme environments, in many cases constrained by multiple stressors; salinity being one of the most important ones (Padisák & Naselli-Flores, 2021). In these extreme environments, species are not selected by their "best capacities" (see difference in maximum production rates of *L. fusiformis* and *P. salinarum*) but by their physiological tolerance to the prevailing "extreme." As to salinity tolerance, there are a number of mechanisms, mostly physiological, making it possible to exist in inland saline habitats where the salt content may well exceed that of the seawater (Stenger-Kovács et al., 2023). Under such circumstances, it is not the species' trait affiliations (Padisák & Naselli-Flores 2021; Naselli-Flores & Padisák, 2023b) but their physiological and evolutionary adaptations that may lead to "success." At present and with the lack of exact physiological studies, we do not know the biochemical instruments that enable the small, less productive green alga *P. salinarum* to outcompete *L. fusiformis*.

Nevertheless, according to our experiments, the periodic collapse of *L. fusiformis* might, therefore, be strongly associated with the combination of rapid environmental changes (Vareschi, 1982; Melack, 1988; Kebede, 1997; Schagerl et al., 2015; Oduor & Kotut, 2016) and biotic factors, such as cyanophage attacks, grazing, or interspecific competition (Peduzzi et al., 2014; Schagerl et al., 2015). Even though *L. fusiformis* covers a high range of salinity, it is sensitive to rapid changes in the physical environment that predicts the possibility of systematic collapses of the cyanobacterium population in future as a result of the rapid changes in water level in between the dry and flood periods in the East African alkaline saline lakes (Oduor & Kotut, 2016; Bett et al., 2019), especially under the increasing frequency of extreme events driven by the ongoing climate change (Jentsch et al., 2007; Coumou & Rahmstorf, 2012; Reichstein et al., 2013; Costa et al, 2023). Such an incident was experienced in the early 2010's when *L. fusiformis* was replaced verifiably by *P. salinarum* (Krienitz & Kotut, 2010; Oduor & Kotut, 2016). After taking into account all the factors cited above as being responsible for the dominance changes, our experiments demonstrated that the rapid salinity changes are most likely the driver of this process.

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Author contributions KK and LK studied phytoplankton communities in soda lakes and came up with the idea of testing the behavior of competing major players under controlled experimental laboratory conditions; they collected field samples, isolated the species, and established pure cultures. TP, BSz, EL, and JP conceived and designed the experiments. TP, BSz, and EL kept up the cultures, performed the experiments, and made photos. TP, BSz, and EL analyzed the data. TP wrote the first draft and all other authors improved the manuscript. All authors have read the submitted version of the manuscript and approved its submission.

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Data availability All data generated or analyzed during this study are included in this published article.

Declarations

Conflict of interest All Authors declare that they have no competing interest.

Ethical approval Not Applicable.

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