Algal communities of Kenyan soda lakes with a special focus on *Arthrospira fusiformis*

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Abstract: Soda lakes are simple in biodiversity, but due to their highly stochastic environmental dynamics unexpected shifts in species composition do occur. We studied key drivers for structuring phytoplankton communities and identified variables significantly influencing changes of *Arthrospira fusiformis* abundance in the Kenyan soda lakes, Nakuru and Bogoria. In both lakes, *Arthrospira fusiformis* dominated algal biomass, but in Nakuru, crashes of this taxon were recorded. The three variables sodium, pH and dry mass significantly contributed to the phytoplankton taxa pattern. *Arthrospira* was absent at highest turbidity and salinity levels, being outcompeted by the small, single–celled chlorophyte *Picocystis salinarium*. Picoplankton was in general connected to higher pH values and tended to occur anti–cyclic to *Arthrospira*. Overall, the abundance of *A. fusiformis* was influenced by the boundaries of habitat suitability, light penetration, grazers and cyanophages attacks.

Keywords: Biological, environmental, phytoplankton, saline–alkaline, salinity, *Spirulina,* cyanophage, virus

Introduction

Arthrospira fusiformis (Voronichin) Komárek et Lund (formerly called *Spirulina plantensis* Voronichin) is a filamentous cyanobacterium which occurs worldwide with a preference in tropical soda lakes (Table 1) and is capable of adaptation to a varied range of habitats, from freshwater–alkaline conditions to saline–alkaline and even hypersaline environments (Ciferri 1983; Dadheech et al. 2010). In the soda lakes of East Africa, *Arthrospira fusiformis* (hereinafter referred to as *Arthrospira*) forms an exceptionally high algal crop due to its high photosynthetic capacity turning these lakes to one of the world's most productive ecosystems (Talling et al. 1973; Melack & Kilham 1974; Oduor & Schagerl 2007a). It is the main food for the Lesser Flamingos, *Phoeniconaias minor* Geoffroy, that flock these lakes in millions (Vareschi 1978; Krienitz & Kotut 2010).

The endorheic soda lakes are prone to hydrological influences since they are often located in semi–arid regions, and their levels can fluctuate considerably in response to seasonal changes and annual differences in rainfall (Melack 1981). The dependence on phytoplankton as driving force of productivity is even greater in these extreme habitats compared to freshwater systems since they have minimal macrophyte growth and low allochthonous organic carbon input due to limited surface run–off and river–inflows (Burian et al. 2014). The dense phytoplankton, high amounts of dissolved organic matter (Jirsa et al. 2012) and increased particle loading significantly reduce the contribution of micro–phytobenthic community to overall productivity due to the resulting poor light climate in the water column (Oduor & Schagerl 2007b).

Several studies have been conducted on the algal communities prevailing in African saline lakes (e.g. Krienitz et al. 2003; Ballot et al. 2005; Schagerl & Oduor 2008; Krienitz & Kotut 2010; Kaggwa et al. 2012), where temporal trends have often indicated periodic dominance and absence of certain taxa especially at extreme salinity. Apart from the predominant *Arthrospira*, also other cyanobacteria occur in these lakes. The most important are *Anabaenopsis arnoldii* Aptekarj, *Anabaenopsis abijatae* Kebede et Willen, *Synechococcus minutus* Voronichin, *Haloleptolyng-*

bya alcalis Dadheech, Mahmoud, Kotut et Krienitz, *Chroococcus* sp., *Synechocystis* sp. and *Cyanospira* sp.. Additional phytoplankton groups include Chlorophyta, Cryptophyta and Bacillariophyceae (Schagerl & Oduor 2008; Dadheech et al. 2012; Krienitz et al. 2013). Recently, Luo et al. (2013) detected hidden diversity of eukaryotic plankton in L. Nakuru during a phase of low salinity (9.7), some sequences were related to marine organisms. It seems that the generally low diversity in these systems obtained by means of traditional methods such as light–microcopy underestimates true species number.

To date, only a few comprehensive studies have linked phytoplankton to consumers in African saline lakes. In their study on the ecology of L. Nakuru, Vareschi & Jacobs (1985) observed that most primary consumer organisms feed on the dominant primary producer, *Arthrospira*; the authors also stated that Lesser Flamingos are the main primary consumers of *Arthrospira*. Other primary consumers included the calanoid copepod *Lovenula africana* Daday, the three rotifer species *Brachionus dimidiatus* Bryce, *Brachionus plicatilis* Müller and *Hexarthra jenkinae* De Beauchamps and a few insect taxa including the larvae of two chironomid species dominating the benthic fauna of the lake. For Lake Bogoria, Harper et al. (2003) recorded a single chironomid species *Paratendipes* sp.; we observed two more taxa (unpublished data). The soda tilapia fish *Alcolapia alcalicus grahami* Boulenger, also feeds on *Arthrospira* in L. Nakuru. *Arthrospira* therefore can be treated as a key species driving a majority of secondary production in these soda lakes.

Melack (1979) related temporal variations in phytoplankton composition to changes of environmental conditions, but community shifts linked to environmental variations have not been understood very well so far (Schagerl & Oduor 2008). This enigma might be either attributed to long sampling intervals or brief sampling periods which are bound to miss out stochastically occurring short–term events in these highly dynamic systems. Over time, non–periodic biomass crashes of *Arthrospira* (Table 2) have been observed. *Arthrospira* is then replaced by other genera such as, *Anabaenopsis*, *Cyanospira*, Cryptomonads and *Picocystis salinarium* Lewin. A number of causal factors have been suggested as being responsible for this phenomenon including, changes in salinity, nutrient limitation, variation in the hydrology, heavy grazing pressure and even viral attacks (Vareschi 1982; Schagerl & Oduor 2008; Krienitz & Kotut 2010; Krienitz et al. 2013; Peduzzi et al. 2014); most of these factors however remain speculative to date.

The purpose of this study was to address this knowledge gap by using a holistic approach which included a simultaneous data collection of over 20 environmental variables and various biological parameters covering almost all ecosystem components. In order to account for short generation times of tropical plankton organisms and stochastic population dynamics in tropical systems, a short–term sampling design with weekly intervals was applied for sixteen months in the two Kenyan soda lakes, Nakuru and Bogoria. Data on environmental and biological variables were related to the phytoplankton community composition and *Arthrospira* biomass. Shifts in community structures enabled us to make evidence derived ecological inferences on the interactions of primary producers and other ecosystem components in these lakes.

Fig 1. Map showing Kenya and sampling sites of the two studied saline–alkaline lakes, Nakuru and Bogoria.

Materials and methods

The data used for this study were collected from Lakes Nakuru and Bogoria located in Central Kenya (Fig. 1) over a period of sixteen months in weekly intervals (July 2008 to October 2009). All samples were collected 10 cm below surface. Salinity and pH were measured *in situ* using a multiprobe
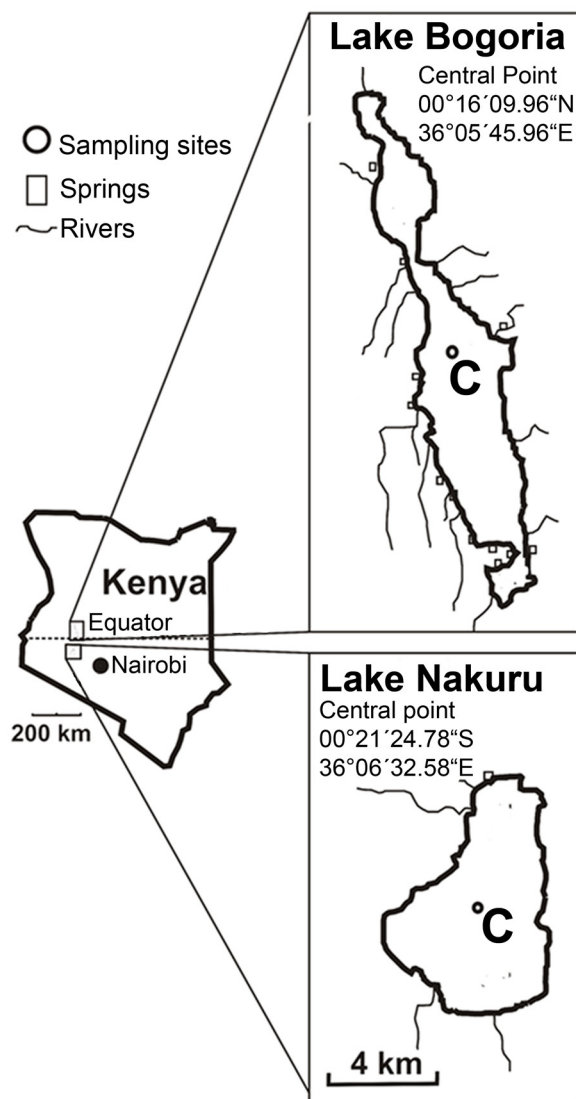
Table 1. Geographical occurrence of *Arthrospira fusiformis* in saline alkaline lakes.

Continent	Country	Lake	Reference
Africa	Kenya	Bogoria, Nakuru, Sonachi, Simbi, Oloidien, Elmenteita Magadi	Melack & Kilham 1974; Melack 1979, 1981, 1988, 1996, 2009; Vareschi 1982; Ballot et al. 2005; Schagerl & Oduor 2008; Krienitz & Kotut 2010
	Ethiopia	Abijatae, Arenguade, Chitu, Kilotes	Talling et al. 1973; Kebede 1997
	Tanzania	Natron, Eyasi, Big Momella, Magad, Manyara, Reshitani, Tulusia	Melack & Kilham 1974; Tuite 1981
	Uganda	Katwe, Masehe	Mungoma 1990
	Chad	Chad, Rombou, Djikare, Mombolo, Macu–Leyla	Iltis 1969a, b, 1971; Ciferri 1981, 1983
	Sudan	Dariba	Fott & Karim 1973
Asia	Turkey	Van	Hammer 1986
	India	Shambhar, Mansagar	Dadheech et al. 2010
Central America	Mexico	Texoco	Ciferri 1981; Dadheech et al. 2010
Europe	Serbia	salty puddles (Baranda)	Fuzinato et al. 2010

(WTW Multi 340i Wissenschaftlich Technische Werkstätten Weilheim, Germany). Light intensity was measured as photosynthetically active radiation (PAR) using a light meter (Skye Instruments, Quantum sensor, Wales, Great Britain).

Dry and ash mass. Dry mass was analysed by filtering a known volume of the raw sample on pre–weighed and pre–combusted filters (45 μm pore size; Ederol BM/C, Battenburg, Germany). Filters together with residue material were dried at 95 ± 5 °C until a constant weight was achieved. Ash mass was measured by reweighing filters after combustion in a muffle furnace for 2 h at 550 °C.

Nutrients and ions analysis. Unfiltered lake water was analyzed for total nitrogen and total phosphorus while filtered water samples were used for analysis of soluble reactive phosphorus, ammonium–N, nitrate–N and dissolved nitrogen. Standard methods of analyses (American Public Health Association 1995) were modified to cater for the high buffering capacity of the alkaline water. Total alkalinity (m–value at pH 4.3), pH and acidity (p–value at pH 8.2) were determined titrimetrically. Magnesium (Mg^{2+}), calcium (Ca^{2+}), sodium (Na^+), chloride (Cl^-), potassium (K^+) and sulphate (SO_4^{2-}) were analyzed by ion chromatography (Metrohm Compact IC 761, Metrohm IC Filtration Sample Processor 788).

Cyanophages. Samples collected with a plankton net (30 μm mesh size) were fixed with glutaraldehyde to a final concentration of 2%. *Arthrospira* filaments were prepared for transmission electron microscopy (Peduzzi et al. 2014) to identify infected cells.

Zooplankton. Surface water samples were taken 10 cm below surface with a 10 l Schindler sampler. Rotifers were concentrated with a 50 μm sieve, fixed with formalin (5% final concentration) and counted following the Utermöhl (1958) protocol. Presence of crustacean zooplankton was checked regularly with a plankton net (200 μm), but densities were constantly below 0.1 ind.l⁻¹ and quantitatively not important. For ciliates, 250 ml of lake water was fixed with Bouin's so-

lution (5%), stained using the Quantitative Protargol Staining Technique (QPS) by Montagnes & Lynn (1993) and counted with a compound microscope (1000×). For this study we used the biomass of *Arthrospira* ingesting taxa based on feeding experiments with dominant rotifers and ciliates of African soda lakes (Burian et al. 2012).

Phytoplankton community composition and biomass. Phytoplankton community composition was determined using lake water samples fixed with formalin. The taxa were identified with the aid of established identification keys (Komárek 2003; Komárek et al. 2003; Shubert 2003; Kociolek & Spaulding 2003). To determine the biovolume of the various community taxa, the identified cells for each taxa were enumerated and measured using an inverted microscope (Nikon Diaphot, Nikon, Tokyo) at 100× and 200× magnification (for *Arthrospira* and *Anabaenopsis*) and 400× for other taxa according to Utermöhl (1958). Biovolumes were estimated using geometric formulae of the shapes similar to the respective phytoplankton cells (Hillebrand et al. 1999). At least thirty cells for each taxon identified were measured to give the average size and biovolume. For conversion of cell volume into biomass, a conversion factor of 1 was used (Wetzel & Likens 1991).

Statistical analysis. For investigating species–environment relationships, non–metric methods were applied. Prior to analysis, species abundance was 4th root transformed to down–weight dominant taxa. Non–metric multidimensional–scaling (NMDS) was based on Bray–Curtis similarities and resulted in a 2–dimensional solution of 0.16 minimum stress and a 3–dimensional solution of 0.11 minimum stress (Kruskal stress value; 1000 iterations). Taxa responsible for pruning groups according to their site similarities were obtained with LINKTREE (minimum group size = 5, minimum split size = 10; minimum split r = 0.65).

The community pattern along artificial axes obtained by NMDS was post–hoc related to environmental variables; the non–parametric routine BIOENV was applied to find significant contributions environmental variables explaining the

species pattern (1000 permutations, p < 0.001; Rho = 0.512; resemblance matrix based on Euclidian distances). Environmental variables were normalized prior to calculations and – if necessary – log transformed to achieve normal distribution. All statistics mentioned above were performed with the statistical package Primer V6.1.15 (CLARKE & GORLEY 2006).

To determine variables significantly influencing *A. fusiformis* abundance, a linear regression with stepwise selection of environmental variables was performed based on the Lake Nakuru data set (Table 4; for this lake, the complete data set including cyanophages was available). Prior to analyses, variables were standardized to zero–means–unit variance. The problem of multicollinearity was minimized by considering only significant variables with variance inflation factors ≤ 1.2; Durbin–Watson–statistics (= 1.57) indicated only very low autocorrelation; heteroscedasticity was checked visually by a scatter plot of predicted values against predicted residuals (residuals were normally distributed). Statistics was performed with PASW Statistics 18 (SPSS – IBM Corp.); graphs were plotted with Sigmaplot 12.2 (Systat Software Inc.).

RESULTS

High amounts of nutrient concentrations were measured in both lakes with the exception of nitrate–N (Table 3). pH ranged from 9–10 for both lakes while salinity concentrations varied widely in L. Nakuru (16–62) and were more constant in L. Bogoria (37–48). Sodium concentrations were exceptionally high and coupled with elevated alkalinity levels typical of the saline–alkaline nature of these lakes. Exceptional high chlorophyll–*a* amounts (46–1351 µg.l⁻¹, L. Nakuru; 92–1059 µg.l⁻¹, L. Bogoria) and low light penetration were also recorded (coefficient of attenuation in L. Nakuru 4–18; in L. Bogoria 2–13). The abundances of rotifers (*Brachionus plicatilis* Mueller, *Brachionus dimidiatus* Bryce and *Hexathra jenkinae* De Beauchamps) and large ciliates (> 60 µm) in L. Nakuru were 2–3 times higher than in L. Bogoria.

Four main phytoplankton groups were present including, cyanobacteria, cryptomonads, green algae and diatoms. In L. Nakuru, a total of 23 taxa were observed during the study period which amongst others included *Arthrospira fusiformis, Anabaenopsis abijatae, A. elenkinii, A. arnoldi, Haloleptolyngbya alcalis, Raphidiopsis curvata* FRITSCH et RICH, *Synechococcus* sp., *Synechocystis* cf. *salina* WISLOUCH, *Cryptomonas* spp., *Chlorococcus* sp., *Nitzschia* sp., *Navicula* sp., *Monoraphidium minutum* NÄGELI, and *Euglena* spp.. For L. Bogoria, 18 taxa were observed with increased abundances of *Arthrospira fusiformis, Anabaenopsis abijatae*, *Picocystis salinarum*, *Chlorococcus* sp., *Cryptomonas* spp., *Monorphidium minutum*, *Nitzschia* sp. and *Synechocystis* sp.. In both lakes, *Arthrospira* dominated the overall biomass. Contribution of *Arthrospira* to the phytoplankton community in L. Nakuru ranged from 0 to 98 % of the total phytoplank-

Table 2. *Arthrospira* biomass crashes in alkaline–saline lakes.

Date of crash	Lake	Reference
1971	Elmenteita	MELACK & KILHAM 1974
1973	Nakuru	VARESCHI et al. 1981
1973 (Mar– Sep)	Bogoria	MELACK 1976
1973,1974	Elmenteita	MELACK 1988
1974	Nakuru	VARESCHI 1982
1974, 1976	Elmenteita	TUITE 1981
1974 (Jan–Mar)	Nakuru	TUITE 2000
2001 (Jun)	Nakuru	BALLOT et al. 2004
2001 (Oct)	Bogoria	HARPER et al. 2003
2002 (Sep)	Elmenteita	BALLOT et al. 2004
2004	Elmenteita	SCHAGERL & ODUOR 2008
2004 (Jul to Oct)	Bogoria	SCHAGERL & ODUOR 2008
2006	Bogoria	KRIENITZ & KOTUT 2010
2008 (Dec)–2009 (Apr) & 2009 (Sep–Oct)	Nakuru	KAGGWA et al. 2012
2011	Elmentaita	KRIENITZ et al. 2013
2012	Nakuru	KRIENITZ et al. 2013

ton biovolume with an average of 39.1±47.1 (SD) mm³ L⁻¹. There were pronounced shifts in community composition in L. Nakuru with two significant drops of *Arthrospira* between December 2008 and March 2009 and September to October 2009. In contrast, the phytoplankton community composition was more homogenous in L. Bogoria and largely (80 %) dominated by *Arthrospira* with an average total biovolume of 68.3±29.0 mm³.l⁻¹.

NMDS analysis of phytoplankton species revealed that the taxa shaping the phytoplankton communities in both lakes were mainly *Arthrospira fusiformis*, *Anabaenopsis* spp., *Picocystis salinarum*, *Haloleptolyngbya alcalis*, diatoms and picoplankton, which was not identifiable to a lower taxonomic level by means of light–microscopy (Fig. 2). Phytoplankton composition was much more diverse in L. Nakuru compared to L. Bogoria, which was predominated by *Arthrospira* throughout the sampling period (Fig. 2). NMDS also clearly revealed that either mainly *Arthrospira* is present in high number or this taxon is replaced by a more diverse community. Environmental variables were post–hoc related to NMDS axes (Fig. 2): *Arthrospira* occurred at intermediate sodium and salinity levels and was outcompeted at increased ion concentrations by small picoplankton including *Picocystis salinarium*. At low salinity and elevated silicate concentrations, dia-

Table 3. Environmental and biological variables (mean ± s.d.) of L. Nakuru and L. Bogoria related post hoc to the phytoplankton community pattern using the non–parametric routine BIOENV method of analysis (variables considered = ●; variables in **bold** significantly explained the species–environment relationship).

BIOENV	Variable	Nakuru	Bogoria
●	**pH**	**10.1 ± 0.2**	**10.0 ± 0.2**
●	**Dry mass (g.l⁻¹)**	**0.2 ± 0.3**	**0.2 ± 0.04**
●	**Na (mg.l⁻¹)**	**17383.8 ± 9823.1**	**25446.1 ± 1657.1**
●	Salinity (‰)	29.3 ± 13.4	43.1 ± 3.5
●	Temperature (°C)	25.1 ± 1.9	28.6 ± 1.5
●	Coefficient of attenuation	9.5 ± 3	7.9 ± 2.1
●	Si (mg.l⁻¹)	99.6 ± 26.3	50 ± 18.6
●	Wind Speed (km.h⁻¹)	4.2 ± 1.8	6.6 ± 1.7
●	Ciliates (mg C.l⁻¹)	1.8 ± 2.3	0.7 ± 1.4
●	Nitrate–N (g.l⁻¹)	16.1 ± 9.5	11.3 ± 3.4
●	Rotifers (mg C.l⁻¹)	2.1 ± 3.4	0.6 ± 1.6
	Ash free dry mass (g.l⁻¹)	0.1 ± 0.1	0.2 ± 0.02
	Ash mass (g.l⁻¹)	0.1 ± 0.2	0.1 ± 0.03
	Soluble reactive phosphorus (µg.l⁻¹)	905.2 ± 1085.3	3052.6 ± 679.8
	Total phosphorus (µg.l⁻¹)	3371.1 ± 1876.1	6011.1 ± 1522
	Ammonium–N (mg.l⁻¹)	123.8 ± 129.1	12 ± 32.1
	Dissolved Nitrogen (mg.l⁻¹)	24.8 ± 13.3	3.5 ± 0.4
	Total Nitrogen (mg.l⁻¹)	24 ± 11.8	4.7 ± 1.1
	Total alkalinity (meq.l⁻¹)	588.1 ± 322.8	992 ± 106.8
	Total Organic Carbon (mg.l⁻¹)	443.2 ± 308.1	59 ± 13.2
	K (mg.l⁻¹)	504.5 ± 239.7	411.6 ± 25.6
	Chlorophyll–*a* (mg.l⁻¹)	371.8 ± 252.4	284.4 ± 139.8
	Heterotrophs (mg C.l⁻¹)	4 ± 1.7	1.8 ± 0.7
	Cyanophages (% infected cells)	1.0 ± 3.6	1.1 ± 3.6

toms and *Anabaenopsis* prevailed.

The pattern of sampling dates/sites based on species occurrences was also supported by groups pruned by LINKTREE routine (Figs 3 and 4). Blooms of *Arthrospira fusiformis* (E and F) were clearly separated from other groups, F was additionally characterized by increased levels of small flagellates. Samples without *A. fusiformis* (A) coincided with highest salinity levels, high attenuation and increased dry mass during the dry period of L. Nakuru. Also *Picocystis salinarium* thrived at elevated ion concentrations (groups C and D). Table 3 summarizes the environmental and biological variables that were used in analyzing the species–environment relationship. Out of the 11 variables considered by the BIOENV routine, only three significantly contributed to the species pattern, i.e. sodium,

pH and dry mass ($p < 0.001$).

To get insight into key–variables significantly influencing *Arthrospira* abundance, a multiple linear regression was performed. Out of 11 variables potentially influencing species abundance like nutrients, irradiance supply or wind speed, grazers or virus infections, three contributed significantly to the model (Fig. 5). Nutrients were of minor importance (high amounts were continuously available), but light penetration (here defined inversely as coefficient of attenuation) turned out as a key variable. Biological variables that contributed significantly to the model were zooplankton grazers of *Arthrospira* (rotifers and all ciliates larger than 60 µm) and cyanophages; these variables were positively related to *Arthrospira*.
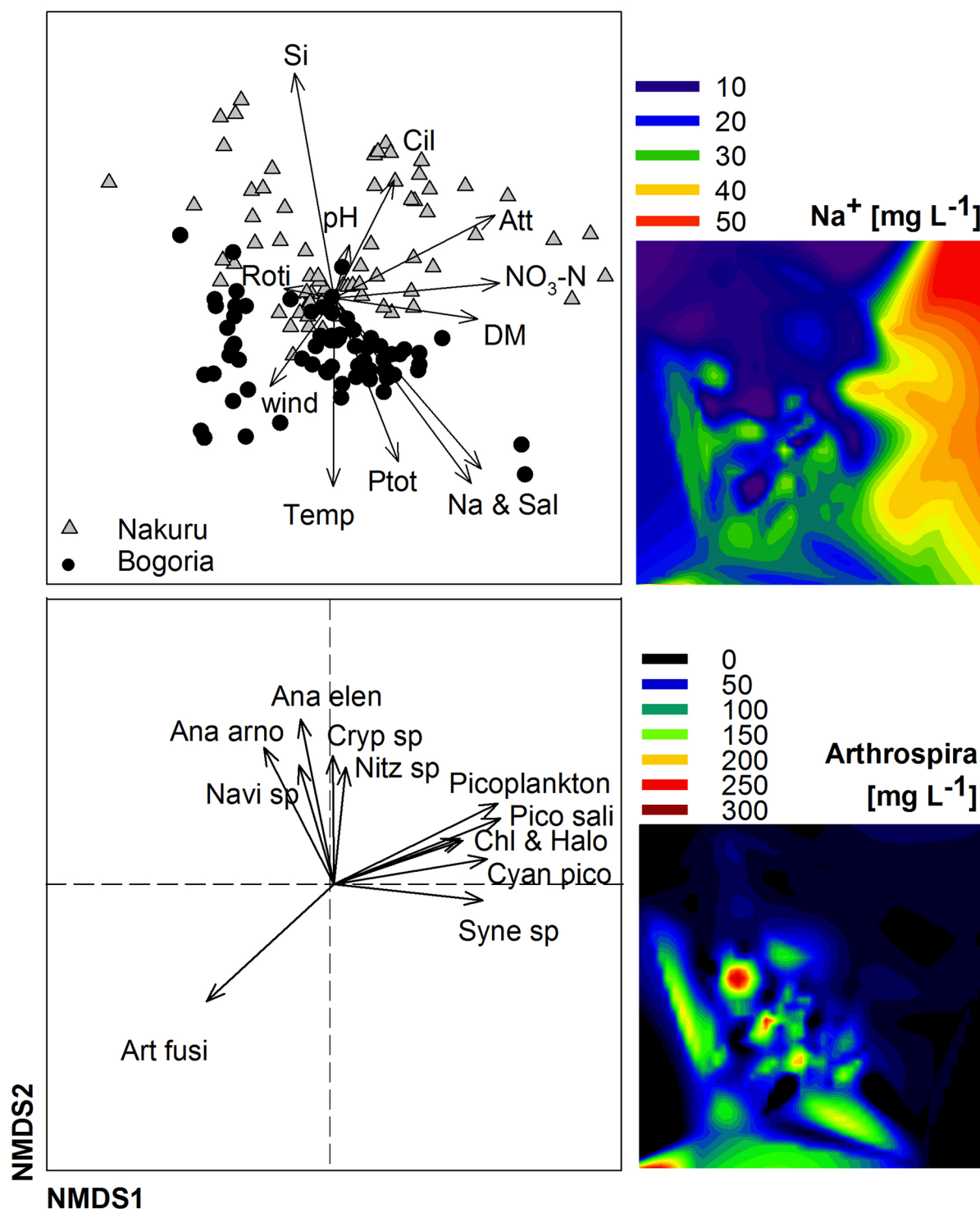
Fig. 2. MSD–plot based on species data. Top left: sites and *post–hoc* related environmental variables with correlations > 0.5 on NMDS axes. Bottom left: Taxa with high explanation value (r > 0.5) of the NMDS model. Top right: Sodium is one out of three parameters significantly explaining the community pattern; sites correspond to NMDS plot. Bottom right: *Arthrospira* biomass distribution along the sites, which correspond to the NMDS plot.

DISCUSSION

Soda lakes are commonly located in arid (25–200 mm annual precipitation) and semiarid (200–500 mm) regions (HAMMER 1986; SCHAGERL & ODUOR 2008). Similar to saline lakes found elsewhere in the world, they re-

spond quickly and significantly to even small climatic changes because of their discrete nature (WILLIAMS 1981; (PADISÁK 1998). GARCIA et al. (1997) observed that as soda lakes become shallower and the surface–to–volume ratio increases, they become more physically controlled. Changes in the water budget greatly

Table 4. Summary statistics of the linear regression model.

| explaining variable	non–standardised coefficient	Std– error	Beta	T	p	VIF
Attenuation	−.604	.090	−.603	−6.726	.000	1,117
logConsumer	.504	.090	.506	5.617	.000	1,125
logPhage	.207	.086	.208	2.395	.020	1,047
ANOVA–model	sum of squares	df	mean square	p	F	
regression	36.059	3	12.020	.000	25.282	
non–standardised residuals	29.951	63	.475			
total	66.010	66				
standardised residuals	min	Max	mean	Std–dev	n	
predicted value	−2.464	1.947	.000	1.000	67	
residuals	−2.394	2.173	.000	.977	67	
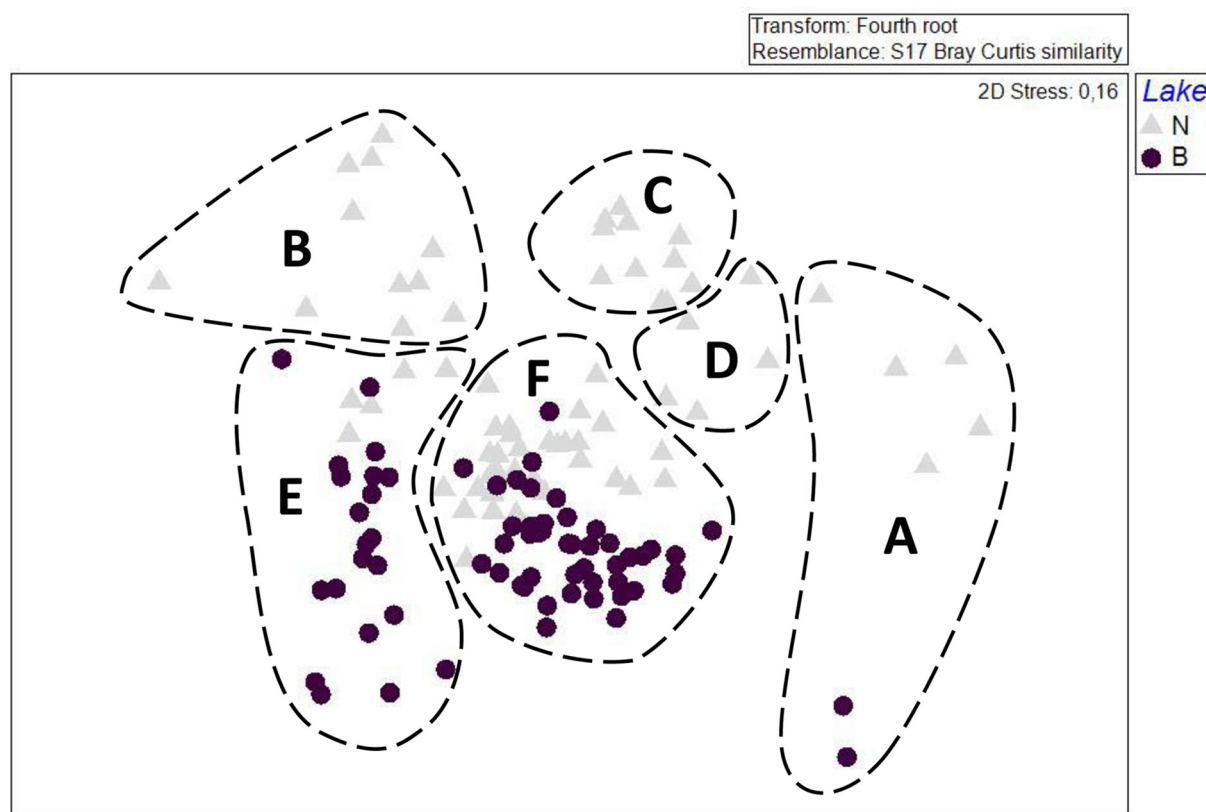
Fig. 3. NMDS–plot of algae taxa. Inclusions indicate groups pruned by the LINKTREE routine based on species data.

affect such endorheic systems which at times may be extreme, resulting in drastic algal biomass crashes (see Table 2) and big changes in community composition (SCHAGERL & ODUOR 2008, this study).

The discrete separation of the two lakes (Figs. 2, 3) based on taxa abundances reflects community responses on the very special environment offered in each of the lakes. L. Bogoria for example has been reported to be more stable compared to other endorheic lakes in Kenya, because of its higher depth (max. about 10 m), steep shores and large water volume (HARPER et al. 2003), preventing it from drying up. In contrary, L. Nakuru is like a pan; it is much shallower (average depth about 1 m) and highly prone to changes in water levels. L. Nakuru even dries up completely from time to time. This difference may account for the frequent phytoplankton community shifts and *Arthrospira* crashes observed in L. Nakuru. The influence of basin morphometry on the stability of the water column has also been observed in other saline lakes, such as L.
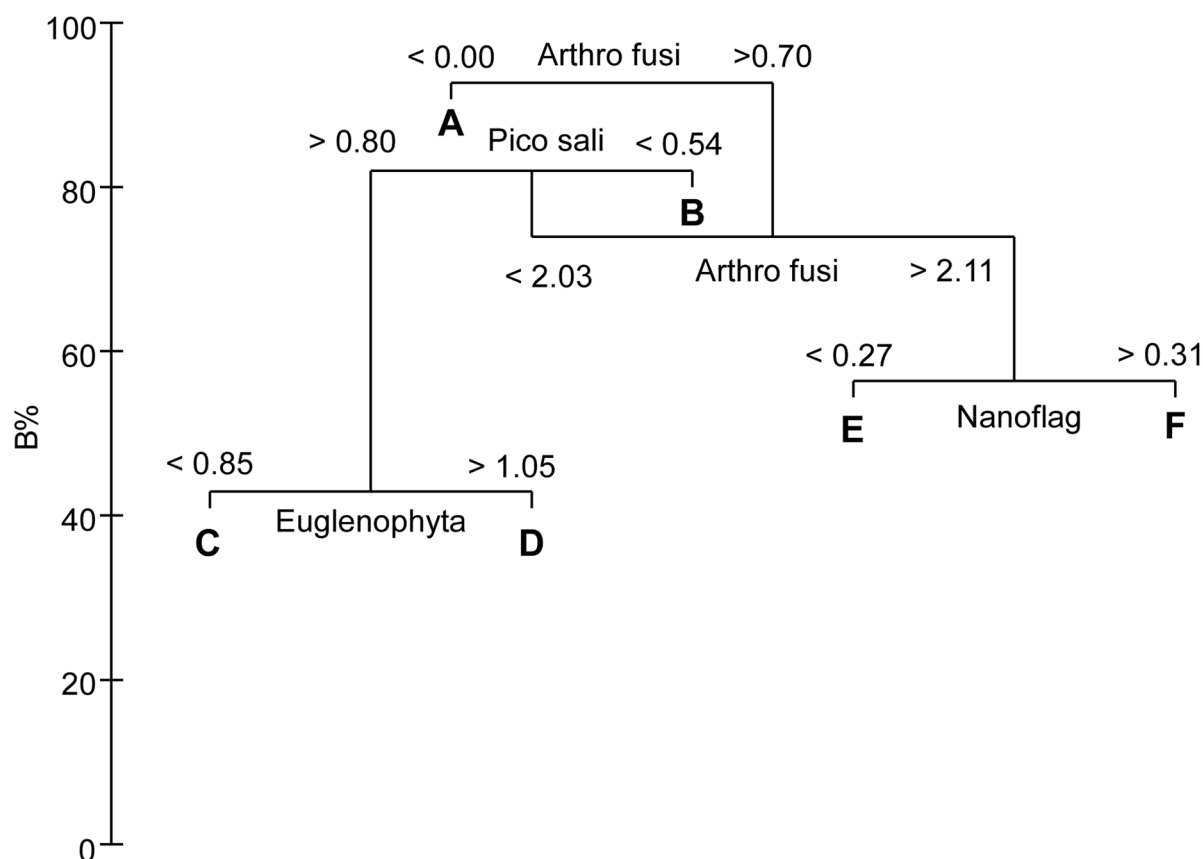
Fig. 4. LINKTREE dendrogram showing significant taxa for pruning groups; labeling corresponds to the NMDS plot (numbers = 4th root transformed taxa biomass).

Sonachi (MacIntyre & Melack 1982). In their study, MacIntyre & Melack (1982) cited basin morphometry to be one of the key factors contributing to the maintenance of meromixis in this lake as the short fetch reduced the impact of wind mixing by limiting the size of the waves. L. Sonachi is a small volcanic crater lake that is sheltered from wind by crater walls 30–115 m above its surface.

Phytoplankton composition in natural lakes in the temperate climates is influenced mainly by the annual cycles of solar radiation, which is reflected by temperature, thermal stratification and mixing and nutrient supply; internal factors like competition and grazing are important mainly during summer (Reynolds 1986; Wetzel 2001; Sommer et al. 2012). Conversely in the tropics, the key driving force appears to be the dry and wet seasons, which influence the chemical dynamics of the water column and ultimately their biota (Sondergaard et al. 1990; Ndebele–Murisa et al. 2010). Schagerl & Oduor (2008) found out that the variation in phytoplankton groups was associated with hydrological stability rather than water chemistry, which only explained 44% of the variance in taxa composition. We found a phytoplankton community mainly composed of cyanobacteria, which was due to the high salinity levels that prevailed in our study (mesosaline, salinity 16–62). *Arthrospira* crashes in L. Nakuru (December

2008, March 2009 and September to October 2009) created a niche–vacuum that was rapidly colonized by other phytoplankton taxa which were otherwise suppressed at high *Arthrospira* levels. The increased phytoplankton diversity in L. Nakuru is therefore, only revealed during the absence of *Arthrospira* and the overall species richness is substantially bolstered by the large variability of salinity.

The role of nutrients in structuring community was small, suggesting sufficient nutrient supply in these lakes, thus confirming earlier findings (Oduor & Schagerl 2007a). We also did not find a control of algae by grazers, which is often observed as a structuring factor of phytoplankton communities (Salmaso & Padisák 2007; Stoyneva et al. 2007). Microzooplankton in tropical soda lakes have the potential to shape phytoplankton communities (Vareschi & Vareschi 1984) though when *Arthrospira* dominates, the influence of zooplankton is very limited because of low consumer densities and a very high phytoplankton biomass (Vareschi 1982). We however cannot rule out a substantial impact of grazers at times with low *Arthrospira* densities, especially if these are combined with zooplankton blooms (Burian et al. 2014).

Salinity per se has often been regarded as the major player in structuring communities especially in saline lakes (Williams 1998; Tweed 2011). In labora-
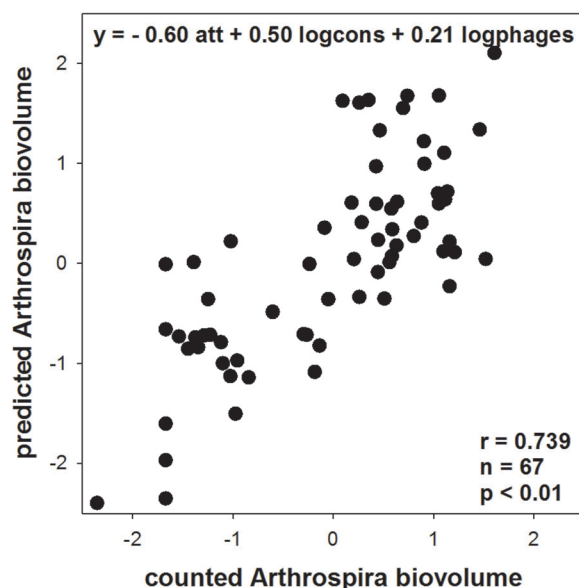
Fig. 5. Results of the linear regression model with stepwise selection. *Arthrospira* abundance was explained by irradiance supply, consumers of *Arthrospira* and cyanophages infection.

tory experiments on salinity tolerance of *Arthrospira,* VARESCHI (1982) found much wider ranges than salinity variations commonly observed in East–African soda lakes. VARESCHI et al. (1981) however reported that changes of algal composition and density in Lakes Elmenteita and Bogoria resulted from severe salinity shifts which exceeded the physiological tolerance of *Arthrospira fusiformis.* In the current study, *Arthrospira* disappeared at very high salinities (beyond 50) which exceeded its physiological tolerance for optimal growth (20–70; FAO 2008), thereby being outperformed by the chlorophyte *Picocystis salinarum.* The latter taxon has been observed by KRIENITZ et al. (2012) to occasionally replace *Arthrospira.* The occurrence of this small sized chlorophyte is of profound significance to the food chain in African soda lakes as it is non–ingestible for the Lesser Flamingo (KRIENITZ & KOTUT 2010), and thus may trigger movement of the birds between lakes.

Alkaliphiles have the ability to adapt to high (9 – 12) pH conditions and extensive studies have been performed with species that exist in soda lakes (LOPEZ–ARCHILLA et al. 2004). The high pH levels in African soda lakes originate from the carbonate rock–beds in the catchment area. It is further enhanced by exceptionally high primary productivity (TALLING et al. 1973; MELACK 1981; ODUOR & SCHAGERL 2007a) resulting into the hyper–eutrophic nature of these systems. L. Nakuru and Bogoria are highly alkaline with a dominance of Na^+ in cations and HCO_3^- and CO_3^{2-} in anions (JIRSA et al. 2012). Both pH and sodium significantly influenced the plankton community structure.

Arthrospira is morphologically adapted to withstand the harsh and often unstable conditions. This has been proven also in laboratory experiments for

some environmental factors such as irradiance (WU et al. 2005; HELBING et al. 2006), temperature (GAO et al. 2008; VONSHAK & NOVOPLANSKY 2008) salinity (KEBEDE 1997) and alkaliphilic conditions (VONSHAK & TOMASELLI 2000). In our survey, its growth seemed however to be restricted to pH levels < 10.3. *Arthrospira* was outcompeted at higher pH by picoplankton such as *Synechococcus* and *Synechocystis,* which have the advantage of a faster molecular diffusion; this is very crucial for preventing intracellular salt accumulation and faster generation times (REYNOLDS 2006).

Dry mass is a surrogate for light attenuation and water turbulence caused by strong winds resulting in re–suspension of bottom sediments. Inorganic turbidity tends to be higher in lake basins with larger fetch distances and shallower depths (WETZEL 2001) as it was observed for L. Nakuru. The large bird population of L. Nakuru further contributes to sediment re–suspension as waterfowl disturb the sediments during feeding. Commonly, inorganic suspended particles are associated with mineral precipitation in soda lakes. These fine particles contribute to scattering of solar radiation which is also called 'whitings' (WETZEL 2001). Some of the phytoplankton taxa observed in this study are known to have features that enable them to maintain their position in turbid waters and maximize light harvesting. *Arthrospira* for example, contains gas vesicles which facilitate vertical movement to the light–supplied surface layer (ODUOR & SCHAGERL 2007a). In the studied systems, high light attenuation is not only caused by re–suspended solids but also by self–shading of phytoplankton. The observed inverse relationship between light attenuation and *Arthrospira* biomass in the current study was indicative of light limitations that prevail especially during *Arthrospira* biomass peaks. SCHAGERL & ODUOR (2008) also observed that variation of *Arthrospira* biomass was related to light attention.

It has already been shown by BURIAN et al. (2012) that most of the time zooplankton grazers on *Arthrospira* are too few to affect *Arthrospira* biomass, which is in accordance to our findings (we did not find a negative correlation, which would point to such a top–down control). The positive relationship rather indicated that the consumer density was controlled by *Arthrospira* abundance (bottom–up control) emphasizing the fundamental role played by *Arthrospira* in ecosystem functioning of these lakes as also noted by other authors (VARESCHI 1982; BALLOT et al. 2004). This observation differs from the common top–down control of phytoplankton by zooplankton grazers (e.g. in L. Tanganyika, STOYNEVA et al. 2007). Other explanations of this positive correlation are linked to fish predation on zooplankton: at high *Arthrospira* densities, fish will feed mainly on the cyanobacteria, as zooplankton and *Arthrospira* overlap in size. At low *Arthrospira* abundance, fish are forced to find other food such as zooplankton. To date, these explanations however remain speculative and definitely show the urgent need

for additional studies focusing on the food web.

The control of *Arthrospira* by cyanophage (viruses) infections in African soda lakes has been proved by PEDUZZI et al. (2014). The positive relationship between *Arthrospira* and cyanophages indicated however that *Arthrospira* biomass is not controlled by the phages most of the time. They rather occur in a more mutualistic relationship, which already has been observed by other authors (SUTTLE & CHAN 1994; WANG & CHEN 2004; MÜHLING et al. 2005). Despite cyanophages having no overall negative effect on *Arthrospira* in this study, their ability to cause breakdowns of phytoplankton communities in these lakes must not be overlooked. In natural waters viruses are known to cause phage–induced mortality (REYNOLDS 2006) though their effect varies considerably (WEISSE 2003).

Shifts in phytoplankton community composition have been associated to the response of the different taxa to environmental stress expressed as changes in physical and chemical variables (VARESCHI 1982; ODUOR & SCHAGERL 2007; SCHAGERL & ODUOR 2008; KRIENITZ & KOTUT 2010). The short–sampling intervals of the current study allowed a comprehensive assessment of the phytoplankton community composition. Phytoplankton have mostly short generation times (REYNOLDS 2006), especially at high temperatures and a high temporal resolution was therefore essential to accurately capture population dynamics in our systems. It is most likely that species interactions can easily be obscured and therefore a significant insight into plankton ecology may be lost when longer sampling intervals are applied (SCHAGERL & ODUOR 2008; KRIENITZ & KOTUT 2010).

Summarizing up, our findings indicate that phytoplankton community stability is strongly connected to the stability of the physical habitat. This was revealed by the responses of the phytoplankton community to environmental oscillations that prevailed in the lakes. Even though *Arthrospira* suffers break–downs in L. Nakuru, it appears that the system always has an 'ecological memory' from which the taxon can be recruited at the onset of favourable conditions. This can be obtained by the frequent re–suspension of resting stages. The 'ecological memory' of water bodies might be controlled by mesoclimatic cycles (PADISÁK 1992; 1998) and influenced by anthropogenic effects like eutrophication (PADISÁK et al. 2010).

Taking into account the findings from this study together with other research so far conducted on African soda lakes, their community response to environmental changes has frequently been highlighted. We hypothesise that over extended periods (for instance, a decade), factors controlling the phytoplankton community composition and especially *Arthrospira* biomass will be altered depending on inter–decadal changes in climatic conditions. This will result into entirely new populations of phytoplankton species emerging and contributing further to phytoplankton diversity in these lakes but also may alter the *Arthrospira*–driven ecosystem functioning. Therefore, it is essential to implement an on–going ecological monitoring to ensure an effective management, assess climate–related changes and obtain further scientific knowledge on stochasticity of these systems.

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