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Temporal phytoplankton dynamics and environmental variables in four Ethiopian soda lakes

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Abstract

We investigated the spatio-temporal dynamics of phytoplankton composition, chlorophyll-a as a proxy for algal biomass, and abundance in relation to environmental parameters in four Ethiopian soda lakes: Arenguade, Beseka, Chittu, and Shala. Triplicate water samples were collected from each lake from January to December 2020, four times in different seasons. Lake Chittu had the highest chlorophyll-a concentration, followed by Lake Arenguade, Beseka and Shala. Chlorophyll-a concentrations generally increased during the post rainy and dry season. The results of LR models are high for lakes Arengude, Beseka and Chittu. Lakes Shala and Beseka had the highest number of phytoplankton taxa, with both taxa composition and abundance dominated by Bacillariophyceae. Cyanoprokaryota, particularly *Limnospira fusiformis*, predominated in the abundance of Lakes Arenguade and Chittu. Water temperature, Secchi depth, turbidity, electrical conductivity, soluble reactive phosphorus, nitrate and silica significantly influenced the phytoplankton community structure. Long-term trend analysis revealed changes in phytoplankton biomass and lake taxonomic composition. The alteration in phytoplankton biomass and species composition of the lakes could be attributed to three factors: (1) frequent high-velocity explosions conducted for seismological studies in the past. This impact caused a dramatic increase in lake level in the case of Lake Beseka leading to a drop in nutrient concentration; (2) climate change and (3) salt content. Overall, our findings suggest that phytoplankton composition, biomass, and abundance varied according to seasonal fluctuations, emphasizing the possible effects of anthropogenic and natural causes on their community structure.

Keywords Ethiopian soda lakes, Abundance, Biomass, Environmental parameters, Chlorphyll-a

Introduction

Soda lakes are highly alkaline aquatic environments where carbonate is a dominant dissolved anion due to evaporative concentration (Schagerl 2022). They are found worldwide but, abundant in the Eastern Rift Valley, stretching from the Red Sea through Ethiopia and Kenya to Tanzania (Oduor and Schagerl 2007; Schagerl and Renaut 2016). Even if they are often considered as 'extreme' aquatic environments, they are amongst the most productive natural ecosystems and are remarkable natural assets with considerable economic and non-economic values (Valiente Parra et al. 2022). The lakes vary dramatically in terms of hydrology and ecology because of fluctuations both in water level and environmental conditions (Trauth et al. 2010). Due to seasonal changes, saline lakes naturally fluctuate in size, depth, and salinity. These changes have direct effects on the biota that populate the lakes (Harper et al. 2016).

Soda lakes in Ethiopia support a variety of animals including birds, crocodiles, and fish. These lakes have been facing different threats due to anthropogenic and natural activities. Lake Arenguade has undergone

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considerable change in lake chemistry and dramatic decline in phytoplankton biomass and productivity (Girma et al. 2012). Reduction in water level of Lake Abijata might be due to soda ash extraction and upstream diversion that causes high salinization, change in the biota and fish stock collapse (Legesse et al. 2004; Ayenew and Legesse 2007; Wagaw et al. 2019). Expansion of Lake Beseka triggered dilution and shift in the phytoplankton community of the lake (Goerner et al. 2009; Dinka 2017).

Ethiopian Rift Valley Lakes have been in focus of research since the early 1990s (Kebede et al. 1994; Kebede and Willén 1996; Zinabu 2002). In recent years, some studies on the composition and structure of phytoplankton have been conducted in Ethiopian soda lakes, on a single lake (Girma et al. 2012; Ogato and Kifle 2014; Ogato et al. 2015; Wagaw et al. 2021). The main role of phytoplankton in aquatic ecosystems is provision of primary food in most food webs, so that life in there will be sustainable (Vajravelu et al. 2018). It is well known that phytoplankton structure is highly sensitive to environmental alterations (Kawabata et al. 1997; Salm et al. 2009). Changes in the physicochemical parameters of lake water can affect the phytoplankton community structure, and function (Litchman et al. 2010). In addition, phytoplankton structure is influenced by seasons that in turn influence the physicochemical parameters of each lake (Ndebele-Murisa 2014). In the face of climate change and increasing anthropogenic impact, data concerning trends of changes in phytoplankton abundance and physicochemical alterations can serve as important proxy indicator to prompt appropriate aquatic ecosystem and catchment management strategies.

In almost all former surveys, comparative ecological studies to examine the biological integrity of multiple lakes linked to temporal patterns of phytoplankton community structure and environmental variables is lacking. This study intends to contribute to the above mentioned knowledge gap by presenting timely data of phytoplankton abundance and physicochemical parameters. Furthermore, the findings in this study are important in understanding phytoplankton community structure which gives insight into the whole ecology for saline lakes and will be useful in maintaining these delicate ecosystems.

Materials and methods

Study area

This research was conducted in four different Ethiopian soda lakes: Arenguade, Beseka, Chittu, and Shala (Fig. 1). Lakes Chittu, Beseka (Metahara), and Shala are all located within the Main Ethiopian Rift system of the East Africa, while Lake Arenguade is located on the western escarpment of the Ethiopian rift system (Klemperer and Cash 2007). Data from the National Meteorological Agency of Ethiopia (ENMA) were used for the monthly rainfall data of the sample year 2020.

Lake Arenguade (also known as Haro Hadho) is situated 45 km south of Addis Ababa at latitude 8° 41.856′ N and longitude 38° 58.796′ E with an altitude of 1900 ma.s.l. It is a small soda lake which is part of a large group of volcanic explosion lakes known as the Bishoftu crater lakes (Schagerl and Renaut 2016). The lake has a closed basin with no obvious inlet or outlet. It receives water primarily from direct rainfall and run-off from its own small catchment (Girma et al. 2012). The lake region experiences two rainy seasons: minor (February to April) and major (June to September) (Baxter 2002). Kebede (2002)stated that Lake Arenguade is named Arenguade for the dense production of the filamentous blue-green alga *Arthrospira fusiformis* (currently described as *Limnospira fusiformis* by (Nowicka-Krawczyk et al. 2019).

Lake Beseka (Metahara) is located in the central Ethiopian Rift Valley, about 200 km southeast of Addis Ababa at 8° 51.5′ N, latitude and 39° 51.5′ E longitude. It is a volcanically dammed, shallow endorheic lake, having an average elevation of 950 m a.s.l. The lake has an average and maximum depths of 6 and 11–12 m, respectively (Tekle-Haimanot et al. 2006). The surface area of Lake Beseka has grown significantly over the last few decades, from 10.8 km^2 in 1972 to 52.1 km^2 in 2020 (Gebremichael et al. 2022). Increased ground water inflow from the western part of the watershed (Goerner et al. 2009), increased discharges in the form of hot springs (Belay 2009), lake neotectonism (Dinka 2017) and irrigation return water from the adjacent farms (Alemayehu et al. 2006) are some of the reported causes of this expansion. The general climate of the area of the lake is semi-arid with a mean annual temperature of 25 °C and a total mean annual rainfall of 534 mm (Belay 2009). There are two main seasons: the rainy season (June–August) and the dry season (9 months) (Alemayehu et al. 2006). As the Lake is situated in the central rift valley region, it is vulnerable to the occurrences of different tectonic and volcanic activities (Dinka 2012).

Lakes Chittu and Shala are located some 287 km south of Addis Ababa, within the Abijata-Shala Lakes National Park (Baxter 2002). They are found in the hydrologically closed system of the Ziway-Shala basin, lacking obvious surface outflow. Direct precipitation and a few hot springs on its shores feed Lake Chittu (Ayenew and Legesse 2007), while Lake Shala is fed by direct precipitation, several hot springs and two rivers (Adabat and Gidu) (Baumann et al. 1975). The lakes region has semi-arid to sub-humid type of climate with an average annual precipitation of 600 mm and temperature of 25 °C (Legesse and Ayenew 2006). The region has two seasons: dry (October

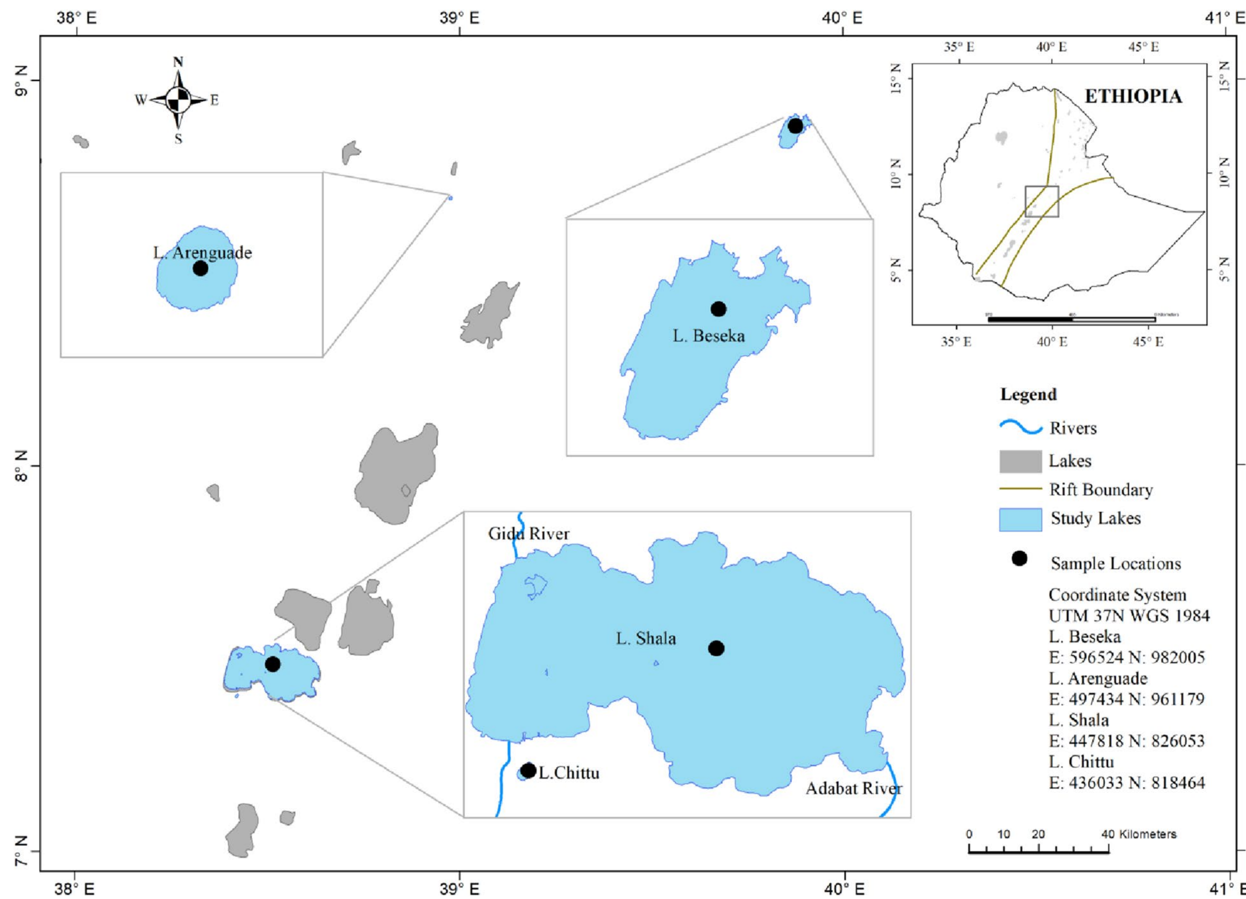

Fig. 1 Location map of the study area indicating the four lakes

to February) and wet (March to September). The wet season is characterized by a bimodal pattern of rainfall, with minor rainy period extending from March to May and major rainy period from June to September. In addition, it has a higher rate of evaporation than precipitation (Ogato and Kifle 2014). Lake Chittu is highly productive due to dominance of its monoalgal population of *A. fusiformis (L. fusiformis)* (Kebede and Willén, 1996) whereas, Lake Shala is known for its low phytoplankton productivity with the absence of *L. fusiformis*, and its predominated by diatoms and cryptomonads (Kebede et al. 1994; Ogato and Kifle 2017; Wagaw et al. 2021).

Sampling and analysis

Sampling sites are indicated in Fig. 1. Triplicate water samples were collected from the study lakes surrounding each sampling site from 50 to 100 m distances from January to December 2020, four times in different seasons (Dry-January, Pre-rainy-June, Rainy-July, Post rainy-November). Dissolved oxygen (DO), electrical conductivity (EC), pH, temperature and turbidity were measured in situ using a multi-metric probe (HQ40d) and turbidimeter (OakatonT-100 model). In situ conductivity measure was corrected to conductivity at 25 °C, using a temperature coefficient of 2.3% per °C (Talling and Talling 1965). Secchi depth (ZSD) was measured using a standard black and white Secchi disc of 20 cm diameter. Nutrients were analyzed at Addis Ababa University laboratory, following the standard methods described in APHA (1999). Samples were determined manually by non-automated methods. Part of the water samples were filtered through Whatman Glass Fibre Filter papers (GF/F) and stored in polyethylene bottles near 4 °C for nutrient analyses, which were done within 48–72 h of sample collection. Ammonium nitrogen (NH_3-N) was determined by phenate method; soluble reactive phosphorus (SRP) and total phosphorus (TP) were determined using ascorbic acid method, while total phosphorus (TP), was measured after digesting the unfiltered sample using potassium persulfate. Nitrate (NO_3-N) was determined using sodium-salicylate method and silica (SiO_2) was determined by the Molybdo-silicate method.

Plankton were collected by plankton net hauls (15 µm) and fixed with Lugol's iodine solution. Samples were analyzed by subsampling 1 mL from the 50 mL sample volume and then placing into the Sedgewick rafter counting cell (Hotzel and Croome 1999). Phytoplankton was then counted with a Nikon inverted light microscope (NIKONTS100, Germany) at a magnification of 40–400×. Diatoms were identified after acid digestion. Samples were boiled with 4 mL concentrated hydrochloric acid (HCl 97%) for 30 min. Potassium permanganate ($KMnO_4$) solutions were added until sample turns purple. After the samples became cold, distilled water was added and repeatedly rinsed to remove chemicals (Taylor et al. 2007). The phytoplankton taxa were identified using different identification keys (Komárek and Anagnostidis 2005; Van Vuuren 2006; Brierley et al. 2007; Bellinger and Sigee 2010). The phytoplankton abundance calculation was done using the equation in Hotzel and Croome (1999). For the filamentous and colonial algae, the number of cells in 20 filaments and colonies of filamentous and colonial algae was counted, and the mean cell number per filament or colony of a taxon was determined. The number of filamentous or colonial taxa multiplied by the average number of cells per filament or colony was used to determine their abundance.

Chlorophyll-a concentration was used as proxy estimator of phytoplankton biomass. Chlorophyll-a (Chl-a) concentration was analysed spectrophotometrically, using 90% cold acetone as an extraction solvent. Filterable amount of sample was filtered using Whatman Glass Filter Fibre papers (GF/F), and the filters were kept at −20 °C for at least 8 h to aid extraction of pigments. The filters were then ground with a tissue grinder, and the extract was centrifuged at 3000 rpm for 10 min after 12 h of extraction. The supernatant was measured at 665 and 750 nm using a spectrophotometer. Chl-a concentration was calculated according to (Lorenzen 1967).

Statistical analysis

Spatial and temporal variations among results of physicochemical parameters, Chl-a and phytoplankton abundance between seasons, were analyzed using Kruskal–Wallis method of variance (ANOVA) in R software (version 4.3.1) (R Core Team 2020). Box plots were plotted using ggplot2 package (Villanueva and Chen 2019). In order to visualize the relationship between environmental variables of the lakes, an ordination plot with a Principal Component Analysis (PCA) using R package FactoMineR was used. PCA with varimax rotation was applied to the 8 selected (eigenvalues > 1) environmental variables to identify the variables that have the greatest influence on phytoplankton biomass. Chl a was explained by the PC generated in the PCA in the subsequent Multiple Linear Regression Analyses (LR). Redundancy Analysis [RDA using R package vegan] was also used to examine the effect of environmental variables on the relative abundance of phytoplankton communities (Borcard et al. 2011). Detrended correspondence analysis (DCA) was performed to calculate the lengths of gradient axes and provided the greatest gradient length of 3.34 along the first axis. When the first axis length is between 3 and 4, both linear and unimodal methods can be applied (Lepš and Šmilauer 2003). So, we decided to use an RDA since the percentage of total variance described by RDA (69.4%) was higher than CCA (62.6%). Prior to analyses, Hellinger transformation (Phytoplankton species data) and environmental variables (except pH) were standardized for normality (Legendre and Gallagher 2001) and differences were considered as significant when $p < 0.05$. Based on the 999 Monte Carlo permutations, the significance of these RDA model has been evaluated. Multicollinearity between explanatory variables has been tested by the Variance Inflation Factor (VIF < 10). As a result, the following variables were added to the model: water temperature, Secchi depth + turbidity + electrical conductivity + soluble reactive phosphorus + nitrate and silica. Similarity Percentage (SIMPER) test using simper function in vegan was performed to determine which phytoplankton taxa contributed significantly to different site types and the similarity among samples at each site (Clarke 1993). The phytoplankton taxa selected from the simper test were then considered for analysis.

Results

Description of environmental variables

Meteorological data showed a typical seasonal air temperature dynamic, with an increasing trend in the period of dry (November–January) and decreasing trend in wet (June–August) seasons for all lakes which has been clearly described in our previous study (Melese and Debella 2023). The annual rainfall ranged between 0 and 347 mm with a maximum precipitation in June–August (rainy season) and minimum rainfall in November- January (post rainy & dry) (Fig. 2A). Overall, 67.2% variance in the environmental variables is explained by the first and second PCA axis (Fig. 2B). The first axis explained 42.4% and correlated positively with DO and temperature but negatively with EC and salinity, differentiating Lake Beseka from other lakes. The second axis explains 24.8% of the variation in environmental variables and is strongly associated with turbidity, ammonia and TP.

The values for spatial physicochemical parameters of water samples during the study period were visualized using boxplots in Fig. 3. As a Additional file 1, temporal results for water quality measurements were provided (Additional file 1: Table S1A–D). The concentration of dissolved oxygen and Secchi depth were higher in Lake Shala; whereas, water temperature was higher in Lake

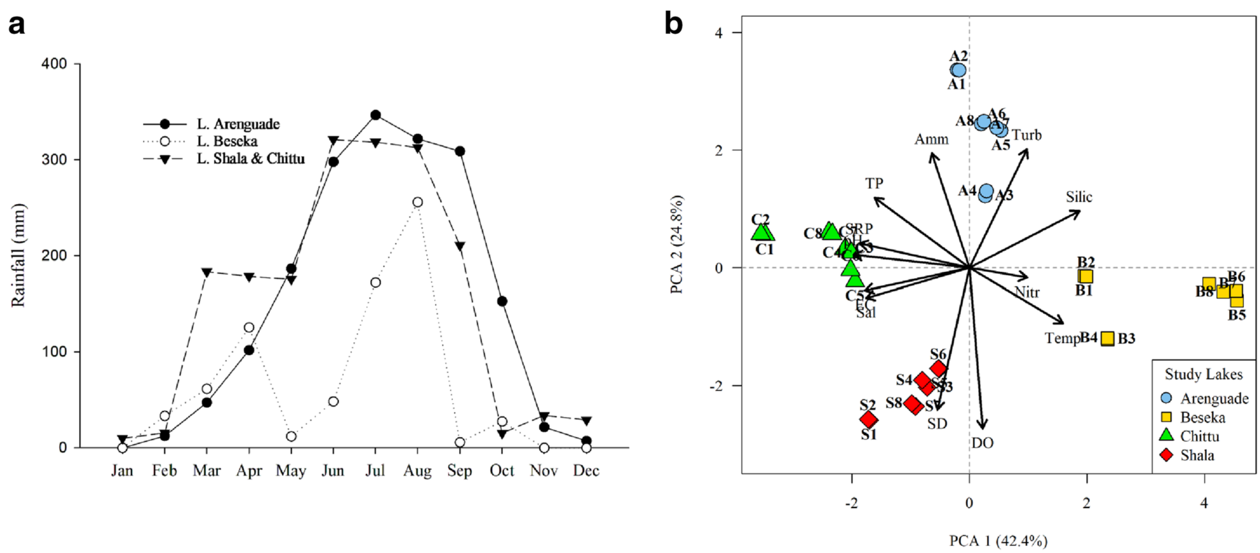

Fig. 2 Monthly rainfall data of the three lakes during the study year 2020 (**A**), Principal Component Analysis (PCA) biplots showing the relationship between environmental variables and lake types during the study periods (**B**). pH, Temperature (Temp), Dissolve oxygen (DO), Electrical conductivity (EC), Turbidity (Turb), Secchi depth (SD), Salinity (Sal), Soluble reactive phosphorus (SRP), Nitrate (Nitr), Ammonia (Amm), silica (Sil) and Total phosphorus (TP)

Beseka (Fig. 3a, b, f). Lake Chittu had higher pH, conductivity and salinity (Fig. 3c, d, g) and turbidity was higher in Lake Arenguade (Fig. 3e). Dissolved oxygen concentration was in the range of 3.12–8.47 mg L^{-1}. Water temperature fluctuated between 21.6 and 27.5 °C with the minimum record in Lake Arenguade, while pH was in the range of 7.9–10.7, indicating alkaline condition. Turbidity and Secchi depth ranged between 10.8 and 44.5 NTU and 0.23 to 0.62 m, respectively. Electrical conductivity (EC) and salinity ranged between 2.52 and 70.24 mS cm^{-1} and 1.42–45.6 g L^{-1}, both showing minimum values in Lake Beseka.

Major algal nutrients such as nitrogen forms (NO_3-N and NH_3), SRP, TP and SiO_2 are presented in Fig. 4. The concentration of ammonia was higher in Lake Arenguade (Fig. 4a). Lake Chittu had higher soluble reactive phosphorus and total phosphorus (Fig. 4c, d). Nitrate and ammonia concentrations ranged between 9.14–164.4 μg l^{-1} and 44.86–224.4 μg l^{-1} respectively. Recorded soluble reactive phosphorus and total phosphorus values from all lakes ranged between 0.25–2.37 mg L^{-1} and 0.75–3.21 mg L^{-1} both showing lower concentration in Lake Beseka. Silica values fluctuated between 1.4 to 96.17 mg L^{-1}.

Phytoplankton species composition and abundance

A total of 56 phytoplankton taxa belonging to six families of phytoplankton, namely, Cyanoprokaryota, Bacillariophyceae, Chlorophyceae, Cryptophyceae, Dinophyceae and Euglenophyceae were recorded from all four lakes (Additional file 1: Table S2). Least number of taxa (15) was observed in L. Chittu, followed by L. Arenguade, which had 20 taxa, whereas L. Beseka and L. Shala had 26, and 39 taxa identified, respectively (Table 1). A single cryptophyte species was observed in L. Chittu but not in the other three lakes.

Phytoplankton biomass expressed as Chl-a in Lakes Arenguade and Chittu was higher than in Lakes Beseka and Shala (Fig. 5). It ranged from 85.5 to 160.0 μg L^{-1} for L. Arenguade, 1.1 to 11.6 μg L^{-1} for Lake Beseka, 103.4 to 174.6 μg L^{-1} for L. Chittu and 5.4 to 35.6 μg L^{-1} for L. Shala. Generally, the spatial phytoplankton biomass ranged between 1.1 and 174.6 μg L^{-1} from all lakes. Temporal phytoplankton biomass showed higher values during the rainy and post rainy seasons in Lakes Chittu and Shala respectively. In Lake Beseka, phytoplankton biomass was high during the dry season (January 2020) and as low as 1 μg L^{-1} after the rainy season (November) (Fig. 6). Seasonal variations in phytoplankton biomass showed significant variation ($p < 0.05$) in all lakes but phytoplankton abundance shows no significant variation between seasons.

Multiple linear regression analysis of Chl-a on varimax rotated PC's

Relationship between Chl-a scores and selected PC's obtained from PCA using environmental variables determined by LR analysis to identify the best predictors of phytoplankton biomass. PCA extracted two significant PC's that accounted for 77.1% of the total variation

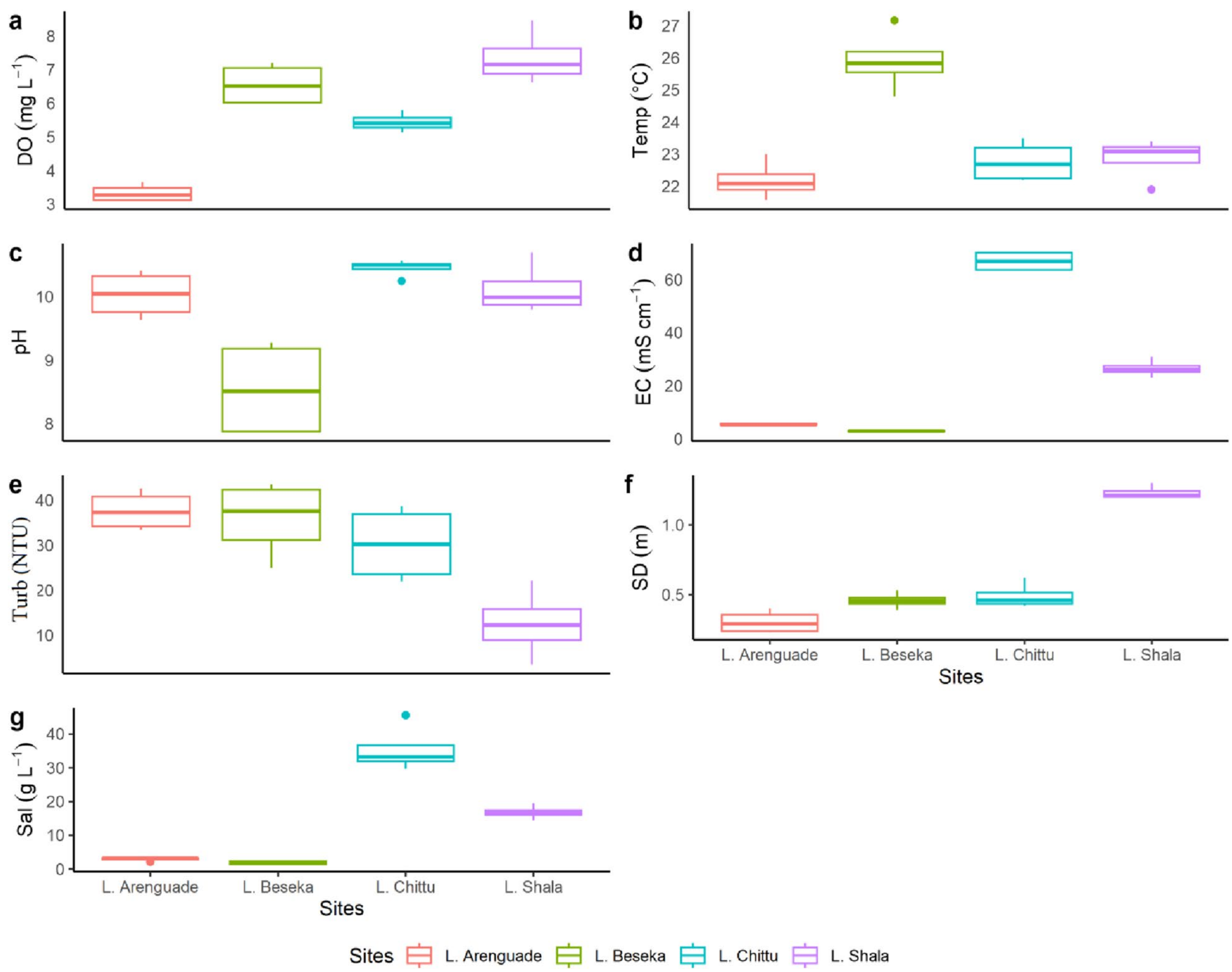

Fig. 3 Boxplots depicting the median results in solid lines of environmental variables (**a**–**g**); in the four Ethiopian soda lakes (present study). Dissolve oxygen (DO), Temperature (Temp), pH, Turbidity (Turb), Secchi depth (SD), Electrical Conductivity (EC) and Salinity (Sal)

(Additional file 1: Table S3). High loadings of ammonia, silica, (negative secchi depth) in PC1 and temperature, turbidity, (negative conductivity) were found in PC2 for L. Arenguade. The LR produced a significant model that described 27.4% of the changes in Chl a caused by PC1 and PC2. PCA for L. Beseka also extracted two PC's that explained 71.3% of the total variation. Temperature, ammonia, (negative conductivity) and nitrate, (negative SRP) were variables with the highest factor loadings in PC1 and PC2 respectively. LR generated a significant model that describes 28.7% of the Chl a variation due to PC1 & PC2. For L. Chittu, PCA extracted two PC's which explained 79.7% of the total variation. Conductivity, ammonia, (negative turbidity) in PC1 and silica, SRP, (negative temperature) in PC2 were variables with the highest factor loadings. LR generated a significant model that describes 20.3% of the Chl a variation due to PC1 & PC2. However, PCA for L. Shala, extracted three PC's that explained 90.2% of the total variation. Secchi depth, nitrate (negative conductivity) in PC1 and temperature, (negative turbidity) in PC2 were variables with the highest factor loadings. SRP was the only variable with high factor loading from PC3. LR produced a significant model that describes only 9.8% of the Chl a variation due to PC1 & PC2 (Additional file 1: Table S3).

Percentage contribution to the total taxa composition and abundance in the lakes are presented in Fig. 7. Bacillariophytes dominated both the taxa composition and abundance of lakes Beseka (58%, 89%) and Shala (64%, 92%), whereas Cyanoprokaryotes dominated the abundance in lakes Arenguade (72%) and Chittu (80%). The maximum total phytoplankton abundance was recorded in L. Arenguade, followed by L. Chittu and Beseka while L. Shala had the lowest. The highest peaks in phytoplankton abundance were observed in November in Lakes Arenguade, Chittu and Shala, and January in Beseka. In

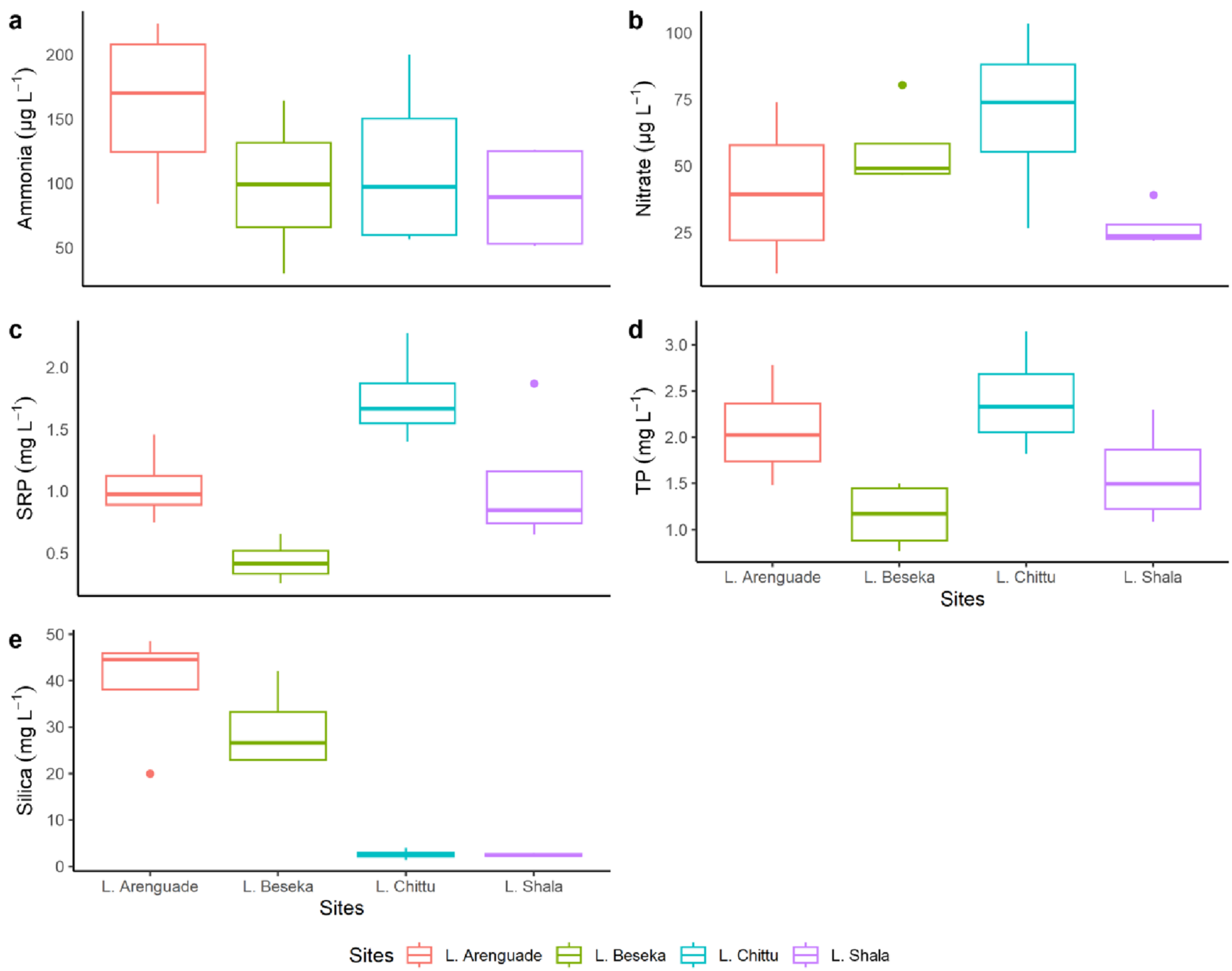

Fig. 4 Boxplots depicting the median results in solid lines of algal nutrients (**a**–**e**); in the four Ethiopian soda lakes, during the present study period. Ammonia (Amm), Nitrate (Nitr), soluble reactive phosphorus (SRP), total phosphorus (TP) and Silica (Sil)

Additional file 1: Table S4, a table showing the temporal trends of phytoplankton groups in each lake is provided. As shown in the table, in Lakes Arenguade and Chittu, the density of cyanoprokaryotes was found to be high in January and November respectively. Bacillariaphytes density has shown higher values during the post rainy season in Lakes Beseka and Shala.

Relationships between phytoplankton communities and environmental factors

The relation of the phytoplankton abundance to environmental factors has been tested by the Redundancy analysis (RDA). Abundance data have been associated with thirteen environmental variables and seven significant ($P < 0.05$) environmental variables were identified in to RDA model, using VIF and forward selection method. RDA explained 69.36% of the total variance of the species distribution related to environmental variables for axis one accounting for 52.81% and axis two accounting for 16.55%. Secchi depth, turbidity, electrical conductivity, soluble reactive phosphorus, nitrate and silica are environmental variables that have significant relationships with phytoplankton as shown in Fig. 8. *Euglena* sp., *Phacus* sp. and *Raphidiopsis africana* occurrence coincided with increase in turbidity, whereas abundance *of Limnospira fusiformis, Cryptomonas marssonii, Anabaenopsis abijatae* and *Monoraphidium minutum* was associated with SRP concentration (Fig. 8).

The abundances of most diatoms were positively correlated with nitrite concentrations. *Desmodesmus communis, Dolichospermum flos-aquae, Coelastrum astroidem, Pediastrum duplex* and *Oosystis* sp. were positively affected by water temperature and negatively affected by conductivity. The majority of the abundances of diatoms showed a positive correlation with lakes Shala and Beseka, whereas *Aulacoseira granulata* tended to be

Table 1 Checklist of identified phytoplankton taxa in the four Lakes Arenguade, Beseka, Chittu and Shala during the current study period

L. Arenguade	L. Beseka	L. Chittu	L. Shala	
Bacillariophyceae	Bacillariophyceae	Bacillariophyceae	Bacillariophyceae	*Cosmarium depresum*
Achnanthidium minutissimum	*Achnanthidium minutissimum*	*Achnanthidium minutissimum*	*Achnanthidium minutissimum*	*Monoraphidium minutum*
Amphora sp.	*Amphora aequalis*	*Amphora pediculus*	*Amphora veneta*	*Oosystis* sp.
Aulacoseira distans	*Amphora pediculus*	*Cyclotella* sp.	*Amphora pediculus*	*Scenedesmus* sp.
Aulacoseira granulata	*Aulacoseira distans*	*Cymbella affinis*	*Aulacoseira distans*	Cyanoprokaryota
Cyclotella sp.	*Aulacoseira granulata*	*Diatoma* sp.	*Aulacoseira granulata*	*Anabaena* sp.
Cymbella affinis	*Cyclotella* sp.	*Epithemia gibba*	*Ceratoneis arcus*	*Limnospira fusiformis*
Navicula sp.	*Cyclotella meneghiniana*	*Navicula* sp.	*Cyclotella* sp.	*Microcystis aeruginosa*
Nitzschia sp.	*Cymbella affinis*	*Nitzschia* sp.	*Cymbella affinis*	*Raphidiopsis africana*
Pinnularia sp.	*Diatoma* sp.	*Rhopalodia gibberula*	*Diatoma* sp.	Dinophyceae
Rhopalodia gracilis	*Fragilaria* sp.	Chlorophyceae	*Epithemia frickei*	*Peridinium cinctum*
Surirella engleri	*Navicula* sp.	*Cosmarium depresum*	*Epithemia turgida*	Euglenophyceae
Chlorophyceae	*Nitzschia* sp.	*Monoraphidium minutum*	*Fragilaria* sp.	*Euglena* sp.
Coelastrum astroidem	*Rhopalodia gibberula*	Cryptophyceae	*Frustulia rhomboides Gom-*	*Phacus* sp.
Cosmarium sp.	*Rhopalodia gracilis*	*Cryptomonas marssonii*	*phonema affine*	
Monoraphidium minutum	Chlorophyceae	Cyanoprokaryota	*Gomphonema minutum*	
Cyanoprokaryota	*Closterium acutum*	*Anabaenopsis abijatae*	*Gomphonema* sp.	
Chroococcus minutus	*Coelastrum astroideum*	*Limnospira fusiformis*	*Gyrosigma obtusatum*	
Limnospira fusiformis	*Desmodesmus communis*	*Spirulina major*	*Navicula* sp.	
Raphidiopsis africana	*Oosystis* sp.		*Nitzschia dissipata*	
Dinophyceae	*Pediastrum duplex*		*Nitzschia* sp.	
Glenodinium sp.	*Scenedesmus bicaudatus*		*Pinnularia* sp.	
Euglenophyceae	*Scenedesmus ellipticus*		*Rhopalodia gibberula*	
Euglena sp.	Cyanoprokaryota		*Rhopalodia gracilis*	
Phacus sp.	*Dolichospermum flos-aquae*		*Stephanodiscus* sp.	
	Raphidiopsis africana		*Surirella engleri* Chlorophy-	
	Dinophyceae		ceae	
	Peridinium sp.		*Chlorella* sp.	
	Euglenophyceae		*Closterium actum*	
	Euglena sp.		*Coelastrum astroidem*	

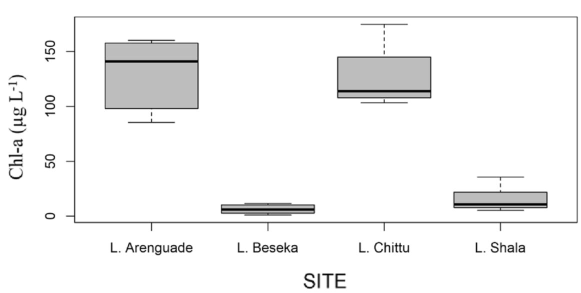

Fig. 5 Spatial variations in phytoplankton biomass (Chl-a) during the study period

high in Lake Beseka. In L. Chittu, *Limnospira fusiformis* was more abundant, whereas *Raphidiopsis africana* was abundant in L. Arenguade.

Discussion

This comparative study of phytoplankton patterns in four Ethiopian soda lakes provided further insights into their ecology and highlighted the need for careful management of these fragile ecosystems. High turbidity and reduced secchi transparency in Lake Arenguade can be caused by high algal density and shallow depth of the lake (Padisak and Naselli-Flores 2021). Lake Shala's higher dissolved oxygen concentration and Secchi depth, and lower turbidity compared to the other lakes, could be attributed to: atmospheric mixing with surface water by convective currents due to the lake's atelomictic nature (Akagha et al. 2020; Padisak and Naselli-Flores 2021); and warm surface temperatures (Sahoo et al. 2017). These findings are consistent with observations made by Ogato and Kifle (2017) and Wagaw et al. (2021).

The high number of phytoplankton taxa in lakes Shala and Beseka might be associated with less extreme conditions (Diego et al. 2015). For example, Lake Beseka is undergoing consistent changes in its chemical composition which shows decline in pH, alkalinity, salinity and electrical conductivity due to lake expansion causing dilution (Melese and Debella 2023) that may be beneficial for phytoplankton diversity. It is known that circumneutral pH favors high phytoplankton diversity than extreme pH ranges on both sides (Fang et al. 2018). Different phytoplankton species exhibit varying tolerances to pH extremes (Fang et al. 2018). Some species have evolved mechanisms to cope with acidic or alkaline environments, but these adaptations may come at a cost in terms of growth efficiency or competitive ability (Kebede 1997).

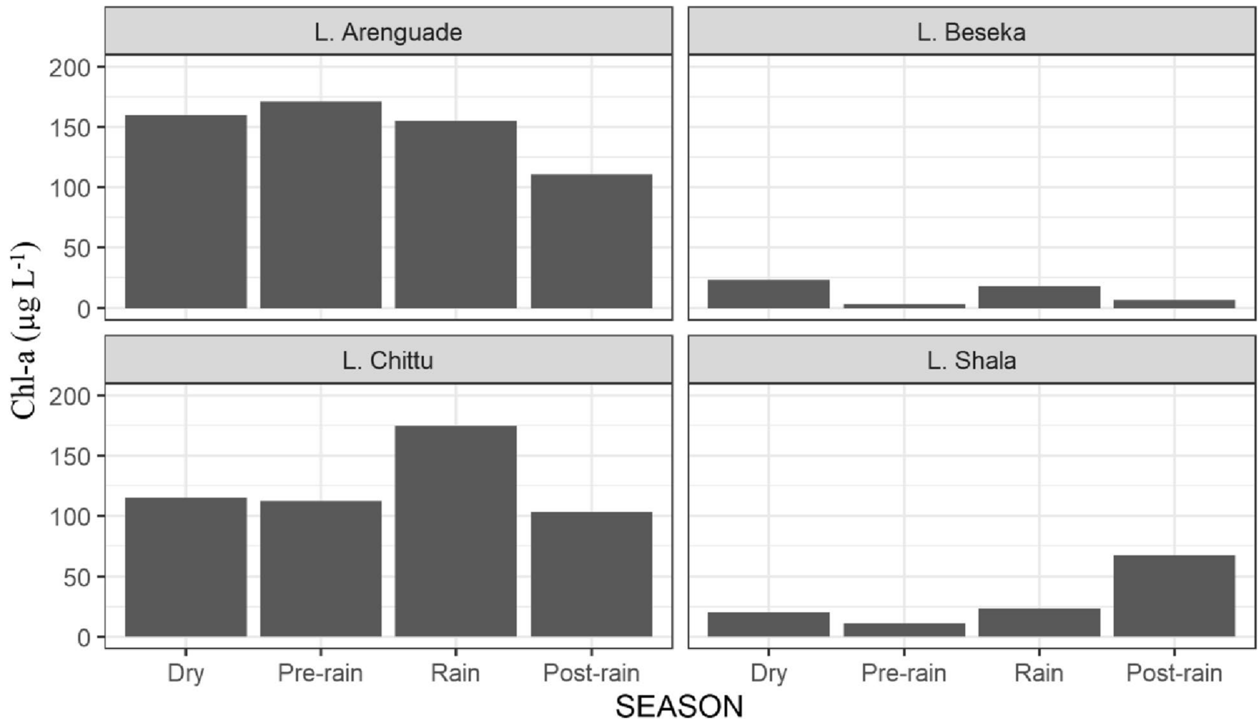

Fig. 6 Seasonal variations in phytoplankton biomass (Chl-a) during the study period

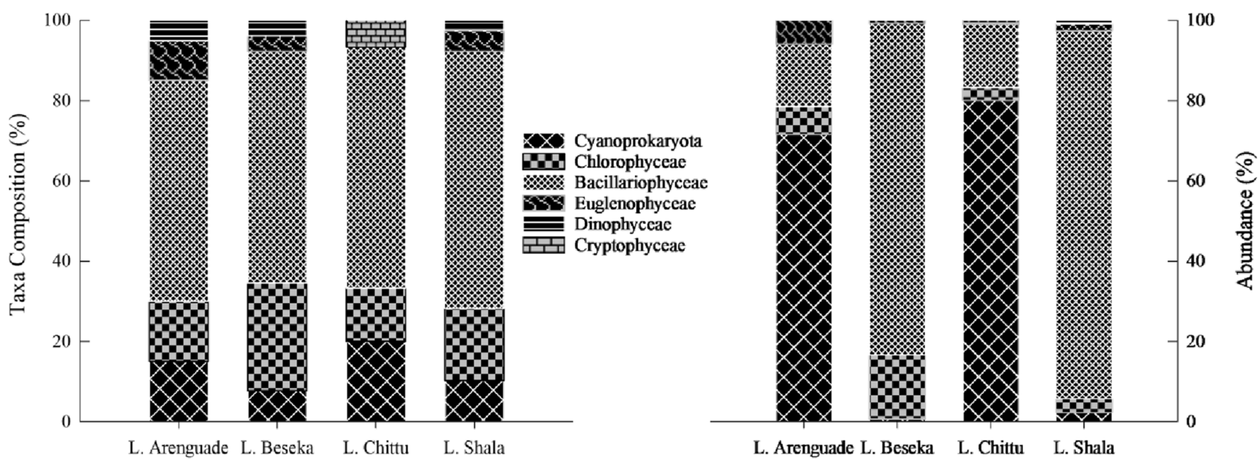

Fig. 7 Percentage contribution to the total number of phytoplankton species and abundance of phytoplankton groups in the four study lakes during the present study

The presence of a higher concentration of Chl-a in L. Chittu, followed by L. Arenguade, could be attributed to their shallow depth, which could result in regeneration and resuspension of nutrients from the bottom sediments, resulting in an increased abundance of cyanobacteria, particularly *L. fusiformis*, which is a major contributor to phytoplankton biomass and primary productivity (Okoth et al. 2009; DeLong et al. 2014; Mhlanga et al. 2017). The high Cattle population and bird droppings dumped on lake shores also predicted to contribute to increased source of nutrients in these lakes (Melese and Debella 2023). The result of this study is aligned with the report by Ogato and Kifle (2014) in L. Chittu and Girma et al. (2012) in L. Arenguade. (Okoth et al. 2009) similarly, high Chl-a concentrations reported in shallow (up to 1 m depth) alkaline-saline Lake Nakuru, Kenya.

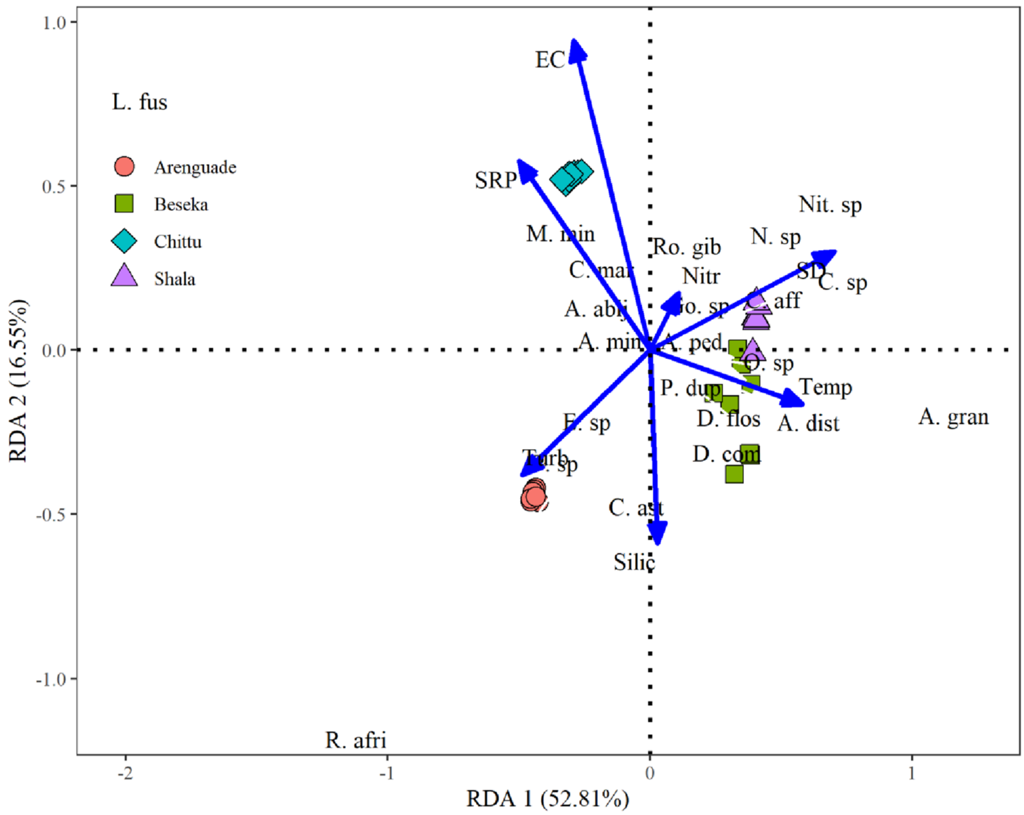

Fig. 8 Redundancy Analysis (RDA) triplots, showing relationship between significant environmental variables and phytoplankton communities in four lakes during the study periods. Water temperature (Temp Electrical conductivity (EC), Turbidity (Turb), Secchi depth (SD), soluble reactive phosphorus (SRP), Nitrate (Nitr) and Silica (Sil). *Limnospira fusiformis* (L. fus), *Raphidiopsis Africana* (R. afri), *Anabaenopsis abijatae* (A. abij), *Dolichospermum flos-aquae* (D. flos), *Monoraphidium minutum (M.* min), *Oosystis* sp. (O. sp), *Coelastrum astroidem* (C. ast), *Achnanthidium minutissimum* (A. min), *Cryptomonas marssonii* (C. mar), *Cyclotella* sp. (C. sp), *Cymbella affinis* (C. aff), *Aulacoseira granulate* (A.gran), *Desmodesmus communis* (D. com), *Aulacoseira distans* (A. dist), *Navicula* sp. (N. sp), *Euglena* sp. (E. sp), *Phacus* sp. (P.sp), *and Nitzschia* sp (Nit. Sp), *Amphora pediculus* (A. ped), *Rhopalodia gibberula* (Ro.gib), *Gomphonema* sp. (Go. Sp), *Pediastrum duplex* (P. dup)

Generally, Chl-a concentrations have increased during the post rainy and dry season, which may be due to high light intensity and rising temperatures in January, that tended to stimulate photosynthetic activities and increased phytoplankton population density as a possible result of high nutrient concentrations due to high evaporation rates (Amin 2006; Carvalho et al. 2016; Sahoo et al. 2016; Awortwi et al. 2018). Similarly, higher temperatures in Kenya's Rift Valley alkaline saline lakes have stimulated the biomass of phytoplankton (Schagerl and Oduor 2008). Additionally, during the dry period, blooms of cyanobacteria were observed in the saline lakes of the Nhecolndia region of Brazil, contributing considerably to the biomass of phytoplankton (Costa et al. 2016).

The temporal Chl-a changes observed in these lakes was consistent with certain environmental factors. The results of LR models are high for lakes Arengude, Beseka and Chittu. In the catchments of Lakes Arenguade and Chittu, huge cattle and bird populations can contribute to increased nutrient concentrations in the lakes by flushing excrement into the lakes (Melese and Debella 2023). Lake Beseka is not a stabilized lake, as the lake's surface area and level have increased and human encroachment on its watershed has increased. These anthropogenic activities still control the environmental activities of lakes and generally influence phytoplankton biomass.

The abundance of lakes Beseka and Shala were dominated by high percentage composition of Bacillariophytes. This might be attributed to their tolerance to a wide range of environments and lower size range of edibility by the top grazers or filter feeders (Stenger-Kovács et al. 2014; Padisak and Naselli-Flores 2021). Again, high nitrate concentrations in L. Beseka may have favored diatom population expansion, as these species are good phosphorus competitors but weak nitrogen competitors (Donald et al. 2013).

The result of this study is in consistent with the study by Kebede and Willén (1996), Delelegne (2006), Zinabu et al. (2002) and Wagaw et al. (2021) but not with Ogato and Kifle (2017), reported dominance of cryptomonads in Lake Shala. The dominance of diatoms has been reported by different previous researchers in different alkaline-saline lakes in Ethiopia, such as Lake Abijata (Kumssa and Bekele 2014).

Cyanoprokaryotes dominated the abundance of lakes Arenguade and Chittu, which might be attributed to their dominance in nutrient rich systems, especially, elevated phosphorus concentrations (Attayde and Hansson 1999). Among cyanoprokaryotes, *Limnospira* species largely dominated the abundance of both lakes. These species have a special physiological adaptations to high pH, salinity, and nutrient concentrations (Costa et al. 2016). The fact that these lakes are preferred habitats for a large number of Lesser Flamingos, feeding on *L. fusiformis* (Spirulina) has been known since the 1980s. Similarly, dominance of Cyanobacteria has been reported for tropical soda lakes (Schagerl and Oduor 2008; Ballot et al. 2009; Ndebele-Murisa et al. 2010; Mhlanga et al. 2017; Koskei et al. 2019), soda lakes of the Kulunda steppe, China (Wen et al. 2005) and also saline lakes of the Nhecolndia region of Brazil (Costa et al. 2016). The higher peak values of phytoplankton abundance observed in lakes Arenguade, Chittu and Shala during the post-rainy season could be attributed to stable nutrient concentration after runoff introduced high nutrient levels into the lakes. Nutrient concentration in a water body is the main factor affecting the growth of phytoplankton (He et al. 2022). The high relative abundance of Bacillariophytes during the post-rainy season could be attributed to more stable hydrographic factors (e.g., temperature), increased nutrition availability due to runoff from the catchments during the rainy season (Vajravelu et al. 2018; Zhang et al. 2019), and a substantial increase in transparency (Simiyu et al. 2022). The dominance of cyanoprokaryotes and chlorophytes in cell densities during rainy periods could be attributed to high precipitation recorded during the rainy season (June–August 2020), resulted in high terrestrial run off from the catchment in to the lake which can stimulate growth of phytoplankton populations (Rao et al. 2018). This observation is in line with the findings of Ogato and Kifle (2017) for L. Shala.

Different responses to the main physicochemical drivers have been observed for the abundance of plankton and biomass dynamics. RDA models indicated that the main drivers of phytoplankton abundance has been significantly influenced by water temperature, dissolved oxygen, chlophyll-a, Secchi depth, turbidity, electrical conductivity, soluble reactive phosphorus, nitrate and silica during the present study. Water temperature has a direct effect on phytoplankton by affecting their physiology and metabolism (Li et al. 2021). An increase in water temperature increases phytoplankton nutrient uptake, increasing phytoplankton growth rates (Thomas and Litchman 2016). In this study, water temperature was the key driving factor, affecting abundance of *D. communis, D. flos-aquae, C. astroidem* and *Oosystis* sp., positively and conductivity affected them negatively. This could be attributable to adaptation of Chlorophytes to relatively higher temperatures and their restriction to low conductivity (Frau et al. 2021). This is in comparable with other studies in Kenyan Rift Valley Lakes, where conductivity has a negative impact on abundance of chlorophytes (Schagerl and Oduor 2008). *Euglena* sp., *Phacus* sp. and *R. africana* occurrence coincided with increase in turbidity since they are especially common in decomposing organic matter-rich systems (Koskei et al. 2019). *L. fusiformis*, *C. marssonii*, and *M. minutum* abundance was related to both Chl-a and Soluble Reactive Phosphorus (SRP) concentration. This might be due to the fact that high Cyanoprokaryotes contribution to the phytoplankton biomass and an increase in the supply of SRPmay also be supporting the abundance of phytoplankton (Ndebele-Murisa et al. 2010; Trombetta et al. 2019). The majority of abundances of diatoms showed positive correlations with lakes Shala and Beseka, whereas *A. granulate* tended to be high in L. Beseka, which indicated the diatoms dependency on mixing to get nutrients from bottom sediments (Yang et al. 2016). In L. Chittu, *L. fusiformis* was more abundant, whereas *R. africana* was abundant in L. Arenguade. The extreme dominance in the abundance of *L. fusiformis* in L. Chittu might be due to their ability to regulate their buoyancy, tolerance level to wide salinity concentration and its ability to cope with very low light intensity (Okechukwu 2009; Schagerl et al. 2015; Bernard et al. 2019).

Trends in phytoplankton biomass and composition changes in the studied lakes

According to Wood and Talling (1988), the phytoplankton species that represented L. Arenguade were *L. fusiformis* (dominant), *Glenodinium* sp., and *Chroococcus minutus*. A report by Girma et al. (2012), concluded that *Anabaenopsis elenkinii* and *L. fusiformis* codominated, while *Chroococcus minutus* constituted to the lakes phytoplankton. In general, Chl-a concentrations in L. Arenguade showed a decreasing trend when compared to the 1960s (Table 2). This could be due to changes in the lake's physico-chemical characteristics (Melese and Debella 2023), which might be to the result of frequent high-velocity explosions, conducted for seismological studies causing changes in the phytoplankton community structure (Girma et al. 2012). Agricultural runoff and sewage disposal are major pollutants in Lake Beseka (Umer et al. 2020).

Cyanoprokaryotes, particularly *L. fusiformis,* predominated Lake Beseka in the 1960s. *Oscillatoria* sp.

Table 2 Phytoplankton biomass measured as Chl-a concentration over the last few decades in study lakes

Lakes	Chl-a (μg L^{-1})	Sampling years	References
L. Arenguade	400–5000	1964–66	Wood and Talling (1988)
L. Arenguade	292	March–October 1993	Jebessa (1994)
L. Arenguade	422	1989–1993	Zinabu and Taylor (1997)
L. Arenguade	160	2008–2009	Girma et al. (2012)
L. Arenguade	**130**	**2020**	**This study**
L. Beseka	29	1989–1993	Zinabu and Taylor (1997)
L. Beseka	26.7	March–May 1991	Kebede et al. (1994)
L. Beseka	9.4	2004–2005	Delelegne (2006)
L. Beseka	**6.33**	**2020**	**This study**
L. Chittu	2600	Aug. 1966	Wood and Talling (1988)
L. Chittu	224	1989–1993	Zinabu and Taylor (1997)
L. Chittu	145.5	March–May 1991	(Kebede et al. 1994)
L. Chittu	72–234	Feb. 2012–Jan. 2013	(Ogato et al. 2015)
L. Chittu	**126.4**	**2020**	**This study**
L. Shala	5	Oct. 1966	Wood and Talling (1988)
L. Shala	7.1	1989–1993	Zinabu and Taylor (1997)
L. Shala	16.6	Feb. 2012–Jan. 2013	(Ogato and Kifle 2017)
L. Shala	15.8	March–May 1991	(Kebede et al. 1994)
L. Shala	17.1	Jan.–Dec. 2018	(Wagaw et al. 2021)
L. Shala	**15.2**	**2020**	**This study**

and *Anabaenopsis arnoldii* were also reported in the phytoplankton of Lake Beseka (Wood and Talling 1988). The previous dominant phytoplankton species *L. fusiformis,* has been completely eradicated, and the phytoplankton population has shifted from cyanobacteria to diatoms. As compared to the 1970s, the change in Chl-a concentrations showed a decreasing trend (Table 2) and the number of phytoplankton taxa increased. This change in phytoplankton biomass and species composition of the lake may be associated with a drastic increase in lake volume, changing the lake's physico-chemical parameters. Melese and Debella (2023), pointed out a significant drop in the lake's pH, conductivity, alkalinity, and salinity in their prior study. This could result in dilution, which could have an impact on the Lake's phytoplankton community. Increased dilution resulted in a decrease in nutrient content and an increase in phytoplankton taxa (Angom 2011). Previous research on Lake Kilole by Lemma (2003) also revealed changes in the phytoplankton community, including the replacement of *L. fusiformis*, which was previously dominating, with other species caused by the dilution of the lake water after the diversion of River Mojo into the lake. Furthermore, changes in phytoplankton composition, which was previously dominated by *L. fusiformis*, have been observed from other East African Rift Valley Lakes, with another cyanobacterium species codominating the lake's phytoplankton (Ballot et al. 2004; Schagerl and Oduor 2008; Krienitz and Kotut 2010; Schagerl et al. 2015).

Limnospira fusiformis was the only species represented in L. Chittu in 1960s. More recently, other studies reported that *Aomoeoneis spaerophora, Cyclotella, Navicula, Nitzschia, Rhopalodia and Synedra. C. marssonii* and *C. obovata* exist in Lake Chitu (Ogato et al. 2015). Wagaw et al. (2021) clearly demonstrated long-term trends of change in phytoplankton community structures due to increasing degradation of the water chemistry caused by salt content. Long-term phytoplankton biomass and species composition analysis revealed changes in phytoplankton composition and community structure.

Conclusion

This is the first study to document the spatio-temporal variability in phytoplankton biomass and community structure in four separate Ethiopian soda lakes in relation to environmental variables. Taxonomic composition, biomass and abundances of phytoplankton groups vary greatly between lakes. A significant seasonal change has been observed in the biomass of phytoplankton on all lakes where concentrations were high during the dry season. Compared to other study lakes, lakes Shala and Beseka had the most diverse phytoplankton taxonomic representation as a result of less extreme environmental conditions and a dilution impact, generated by expansion of Lake Beseka. The LR model showed the relationships between physicochemical variables and phytoplankton biomass and showed that environmental factors have an influence on Chl-a concentration. The abundance of phytoplankton in lakes Beseka and Shala were dominated by Bacillariophytes (diatoms), whereas Cyanoprokaryotes dominated the abundance of lakes Arenguade and Chittu. Bacillariophytes formed dominant groups during the pre-rainy season whereas Cyanoprokaryotes and Chlorophytes are dominant during the rainy season. The RDA results show that environmental variables have driven phytoplankton abundance dynamics. Water temperature, Secchi depth, turbidity, electrical conductivity, soluble reactive phosphorus, nitrate, and silica significantly influenced the phytoplankton community structure. Changes in the composition and structure of the phytoplankton community have been observed in the long term analysis of biomass and species composition. Though this study was limited to four lakes and four months of sampling, in the face of climate change, drought and erratic rainfall, we presume that data from this study and our previous publication, will contribute to the missing gap of comparative studies of Lake Limnology in Eastern Africa.

Supplementary Information

The online version contains supplementary material available at https://doi.org/10.1186/s40068-023-00329-0.

Additional file 1: Table S1. Seasonal variation of environmental characteristics of the four Ethiopian soda lakes (mean ± sd) during the present study period. **Table S2.** List of phytoplankton species with their taxonomic groups identified from four Ethiopian soda lakes (Arenguade Beseka, Chittu & Shala) during the study period. **Table S3.** Results of principal component analysis with eight environmental variables (factor loadings ˃0.750 are bold). Regressions of chl-a on the principal components contain only the significant ($P < 0.05$) coefficient**. Table S4.** Seasonal variations in mean phytoplankton abundance (Cells/mL) in the studied lakes during the current sampling period.

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Author contributions
The authors confirm contribution to the paper as follows: study conception and design: HM and HJD; data collection: HM; analysis and interpretation of results: Hana Melese; draft manuscript preparation: HM; advising, revision and manuscript edition: HJD. All authors reviewed the results and approved the final version of the manuscript.

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Availability of data and materials
Not applicable.

Declarations

Ethical approval and consent to participate
All authors have read, understood, and have complied as applicable with the statement on "Ethical responsibilities of Authors" as found in the Instructions for Authors and are aware that with minor exceptions, no changes can be made to authorship once the paper is submitted.

Consent for publication
All authors want to publish the research paper entitled "Comparative Analysis on the Temporal Phytoplankton Dynamics in Relation to Environmental Variables in Four Ethiopian Soda Lakes (Arenguade, Beseka, Chittu and Shala)" in Environmental Monitoring and Assessment journal.

Competing interests
The authors have no relevant financial or non-financial interests to disclose.

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