Atelomix in Ethiopian Highland Lakes: their role in phytoplankton dynamics and ecological features

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Abstract

The objectives of this review were to synthesize the community structure of phytoplankton and the role of atelomix in the phytoplankton dynamics in Ethiopian highland lakes. Changes in a lake's physical structure, light dynamics, and availability of nutrients are closely associated with phytoplankton ecology, and phytoplankton assemblages provide insight into phytoplankton responses to these environmental changes. Based on the available information, a total of 173 species of phytoplankton are grouped under seven classes, Chlorophyceae (80 taxa), Bacillariophyceae (55 taxa), Cyanophyceae (24 taxa), Dinophyceae (6 taxa), Eugleonophyceae (6 taxa), Xanthophyceae (1 taxon), and Cryptophyceae (1 taxon) were recorded in five different tropical Ethiopian highland lakes. Chlorophyceae and Bacillariophyceae dominated in terms of species composition. Partial atelomixis, seasonality, and low nutrient concentrations seem to be the main drivers in structuring phytoplankton composition and abundances in Ethiopian highland lakes, characterized by a high diversity of atelomix-dependent benthic diatoms and desmids. Thus, this review will help understand the role of atelomix and nutrient availability in the phytoplankton composition and biomass of tropical highland lakes of Ethiopia.

Keywords: Atelomix, Benthic diatoms, Desmids, Highland lakes, Nutrient

Introduction

Ethiopian highland lakes are important natural freshwater resources for various reasons like a source of water for humans, livestock, and agricultural irrigation, a source of revenue from fishing and commercial and recreational resorts (eco-tourism) (Degefu & Schagerl, 2015; Fetahi et al., 2014). Also, like Rift Valley Lakes, many tropical Ethiopian highland lakes have great ecological and scientific importance (Tessema et al., 2020; Wondie et al., 2017). However, lakes throughout the high-latitudes have been drastically altered as a result of increasing human population density, unsustainable tourism industry, shoreline and crater rim modification, water abstraction for irrigation, and changes in land cover (Degefu et al., 2014). Limnologists have developed a scientific basis for diagnosing and anticipating environmental and biological changes in tropical highland lakes in Ethiopia (Degefu et al., 2014; Fetahi et al., 2014; Tessema et al., 2020).

Phytoplankton as one component of an aquatic ecosystem play keys ecological roles in the ecosystem: (1) maintaining the balance of the ecosystem and its complex food webs (Vallina et al., 2017) as their species diversity, biomass and production determine the strength of the energy transfer (Degerman et al., 2018; Ghedini et al., 2021) and they are autotrophic organisms and usually found in aquatic ecosystems serving as the base food sources for most aquatic organisms like zooplankton, fishes and crustaceans (Manickam et al., 2020; Tharik et al., 2021), (2) they play a very vital role in controlling the carbon level in the atmosphere and generate about half the atmospheric oxygen through the process of photosynthesis (Basu & Mackey, 2018; Käse & Geuer, 2018) and (3) are very good biological indicator to understand the water quality and they also respond to other physiological indicators like pH, oxygen, salinity, temperature, light and toxic chemicals (Manickam et al., 2020). Therefore, their distribution is mostly explained as a response to a complex of environmental factors operating at various scales of different biotic and abiotic factors (Wagaw et al., 2021). The effects of seasonality and nutrient availabilities (Tessema et al., 2020), underwater light conditions and phytoplankton buoyancy characteristics (Degefu et al., 2014) wind and temperature regime (Degefu & Schagerl, 2015), food availability and trophic conditions (Fetahi et al., 2014) have all been revealed as key driving factors for heterogeneity of phytoplankton composition and biomass in Ethiopian highland lakes. These factors are highly influenced during the stratification period of the lake (Degefu & Schagerl, 2015).

Limnological studies of the Ethiopian lakes have predominantly been carried out within the Rift Valley Lakes (Kebede et al., 1994; Woldesenbet & Mengistou, 2020; Wondmagegn & Mengistou, 2020). However, Ethiopian highland lakes have not received adequate attention from the limnological community (Degefu & Schagerl, 2015; Wondie et al., 2017). Similarly, to date, plankton composition and community structure in several Ethiopian highland water bodies have been studied (Degefu & Schagerl, 2015; Degefu et al., 2014; Fetahi et al., 2014; Tessema et al., 2020)(Fig. 1). However, synthesized information and a comprehensive review of these phytoplankton studies of Ethiopian highland lakes and further phytoplankton responses to partial atelomix and nutrient concentration are still lacking. In this regard, this review is the first serious effort in gathering the baseline information on phytoplankton species diversity, ecological status, and role of atelomix in highly-threatened Ethiopian highland lakes, based on the previous research articles (Fig. 1).

Limnological Features of Ethiopian Highland Lakes

The concentrations of major limnological properties in Ethiopian highland lakes are illustrated in Table 1. The average Secchi depth (water transparency), which varied, was recorded between 0.87 and 12 meters. Lake Dendi has the highest Secchi depth value (12 m), which may be related to the lake's oligotrophic trophic status and abundant phytoplankton (*Chl-a* = 0.1 g/L) (Degefu et al., 2014). While Lake Tana has the lowest value (0.87 m), it is shallow, has a low eutrophic trophic zone, and has abundant phytoplankton (*Chl-a* = 38 g/L) (Tibebe et al., 2019; Wondie et al., 2017). In Ethiopian highland lakes, where higher Secchi depth is associated with lower phytoplankton biomass, there is a direct inverse link between phytoplankton biomass (*Chl-a*) and water transparency. On the other hand, the morphological characteristics of lakes, particularly shallower depth, significantly impact on Lake Tana's lower Secchi depth. Because of the shallow depth, there is a higher rate of organic matter decomposition in the sediments, which increases the number of suspended particles in the benthic zone and may be the source of Lake Tana's high turbidity (Tibebe et al., 2019; Wondie et al., 2017). Studies have also shown that Secchi depth varies between lakes due to various factors, including phytoplankton biomass, lake morphology, catchment soil erosion, and internal lake processes, including resuspension and diffusion (Mohammed et al., 2023; Tessema et al., 2020).

Lakes in the highlands of Ethiopia had decreased mean nutrients. All Ethiopian highland lakes have modest levels of nitrate (NO_3-N), nitrite (NO_2-N), and ammonia (NH_4-N), although Lake Tana has slightly greater levels than the others (Table 1). The nitrogen content of the lake reduces as it gets deeper. The lakes' NO_3-N contents varied between 1 and 763 g/L. There are more NO_3-N atoms (763 g/L) in Lake Tana. Among the nutrient concentration in lakes, total phosphorus (TP) varied from 6.7 μg/L to 862 μg/L in Lake Dendi and Lake Tana, respectively. A phosphorus and nitrogen nutrient constraint may occur in the lake environment since Lake Dendi has low nutrient concentrations (Degefu & Schagerl, 2015; Degefu et al., 2014). However, the shallowest Lake Tana's greater nutrient levels may favor primary productivity (Tibebe et al., 2019; Wondie et al., 2017). Although the lake's higher turbidity and dissolved solid concentrations are generally limit phytoplankton growth (Kahsay et al., 2022; Mucheye et al., 2022).

The trophic condition of Ethiopian highland lakes ranged

Table 1. Physico-chemical characteristics of Ethiopian highland lakes

Parameter	Lake					
	Dendi	Wonchi	Ziqualla	Hyqe	Ardibo	Tana
Secchi (m)	12	5	1	2.75	3.28	0.87
Zeu (m)	33	14	1.7	4.95	9.87	2.61
Conductivity (µS/cm)	120	201	78	909.95	704.86	148.5
Salinity (‰)	0.1	0.1	0.24	NA	0.3	0.075
Alkalinity (meq/L)	1.5	2.32	1.5	9.88	2.14	2.98
pH	8.27	8.1	7.91	9.06	9.4	7.9
NO_2-N (µg/L)	1.0	0.3	2.4	6.49	NA	150
NO_3-N (µg/L)	18	1	15	41.6	36.53	763
NO_4-N (µg/L)	90	79	48	NA	NA	200
NH_4-N (µg/L)	90	79	48	257.17	83.9	800
SRP (µg/L)	2.9	3.4	15.7	21.81	23.84	326
TP (µg/L)	6.7	8.4	21.6	58.1	69.15	862
Chlorophyll-a (µg/L)	0.1	3.2	2.2	21.3	3.28	38
Na^+ (mg/L)	7.8	42.5	12.7	61.2	85.1	NA
K^+ (mg/L)	3.4	6.8	2	4.2	8.2	NA
Mg^{2+} (mg/L)	5.1	1.4	4.22	97.8	38.5	NA
Ca^{2+} (mg/L)	14.7	8.4	17.43	1.02	11.5	NA
F^- (mg/L)	0.3	2.7	0.4	1	0.5	NA
Cl^- (mg/L)	3.2	3.3	3.4	35.8	14.2	NA
SO_4^{2-} (mg/L)	0.9	1.09	0.15	2.8	2	NA

SRP, Soluble Reactive Phosphorus; TP, total phosphorus.

widely from oligotrophic to eutrophic states (Table 2). Several variables often govern this, including the concentrations of nutrients, primarily nitrogen and phosphorus, phytoplankton biomass (chlorophyll-a), and Secchi depth (Degefu et al., 2014; Mohammed et al., 2023; Tessema et al., 2020; Tibebe et al., 2019; Wondie et al., 2017). Degefu et al. (2004), stated that low nutrient concentrations limited eutrophic conditions and excessive algal growth concerning phosphate and nitrogen content. Using this figure as a benchmark, the TP concentration in Lake Tana may promote the growth of algae, which may be the reason for the lake's highest trophic level (Tibebe et al., 2019). Additionally, the polymictic structure of the lake and its shallow depth, which results in a reduced Secchi depth, are morphological characteristics that may contribute to highly eutrophic conditions; this is shown in Lake Tana (Dersseh et al., 2019; Kebedew et al., 2020). According to Carlson's trophic state classification criteria, Lake Dendi and Lake Wonchi are oligotrophic since they have the lowest TP and *Chl-a* contents and the highest Secchi depth (Degefu et al., 2014).

In the majority of lake waters, the sum of the concentrations of Cl^-, SO_4^{2-} and HCO_3^- equals the total concentrations of main cations such Ca, Mg, Na, and K. Magnesium and calcium are significant cations in Ethiopian highland lakes (Demlie et al., 2007; Degefu & Schagerl, 2015), in contrast to the rift valley lakes of Ethiopia that are dominated by waters of the Na-HCO_3^- type (Ayenew, 2005; Rango et al., 2009). Demlie et al. (2007) and Degefu & Schagerl (2015) claim that the geology of the catchment region plays a role in the predominance of magnesium and calcium in Ethiopian highland lakes. This also caused very low total salt contents, electrical conductivity, and alkalinity (Table 1). As a result, there is a strong correlation between the overall concentrations of main cations in water and the rock substrate in the watershed (Alemayehu et al., 2006; Ayenew, 2005; Demlie et al., 2007).

Role of Atelomix in Deep Tropical Ethiopian Highland Lakes

Deep tropical highland lakes are considered ecosystems experiencing low climatic variability, and therefore are

Table 2. Phytoplankton biomass (*Chl-a*) and TSI of Ethiopian highland lakes based on the Carlson's TSI

Trophic state indices	Lake					
	Dendi	Wonchi	Ziqualla	Hayq	Ardibo	Tana
Chl-a (μg/L)	0.1	3.04	2.2	4.03	3.28	38
TSI (TP)	31.56	34.75	48.46	56.94	65.25	88.405
TSI (*Chl-a*)	11.31	41.95	38.20	51.46	41.5	58.23
TSI (Sec)	24.19	36.81	50.01	41.95	65.23	62.66
Mean TSI	22.37	37.84	45.56	43.16	57.33	69.77
Trophic state	Oligotrophic	Oligotrophic	Mesotrophic	Mesotrophic	Eutrophic	Eutrophic

TSI, Trophic State Index; TSI (TP), TSI referred to total phosphorus; TSI (*Chl-a*), TSI referred to chlorophyll-a; TSI (SD), TSI referred to Secchi depth.
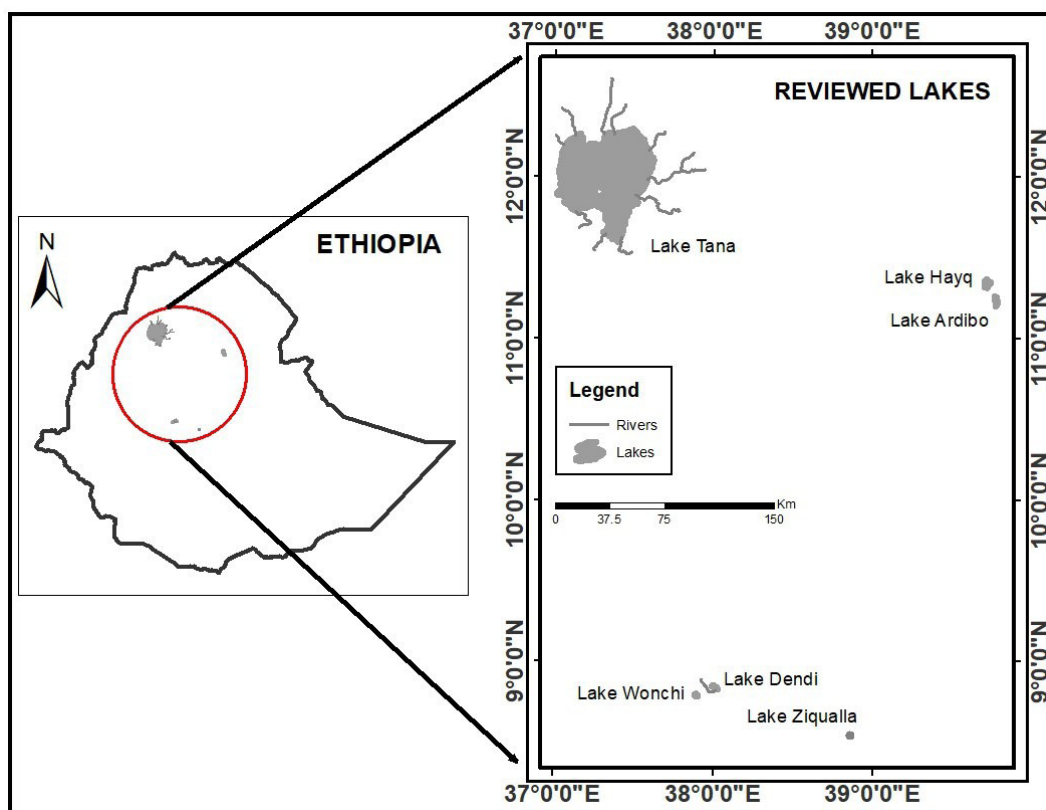

Fig. 1. Location of reviewed lakes.

ecosystems supporting uniform phytoplankton community which can persist for years (Melack, 1979). However, studies suggested that seasonal changes in water temperature and density, driven by climate, are equally important in tropical regions as in temperate ones (Degefu et al., 2014; Fetahi et al., 2014; Tessema et al., 2020) a phenomenon called atelomix. These changes determine mixing periods with the input of light and energy that control the balance between phytoplankton growth and loss (Barbosa & Padisák, 2002; Souza et al., 2008). Even though the night-time mixing due to nocturnal cooling can destroy a diel thermocline, the deeper seasonal thermocline/chemocline remained stable (Baxter & Golobitsh, 1970; Talling & Lemoalle, 1998), restricting the mixing to within the epilimnion. This dynamics pattern is termed as a partial atelomixis (Barbosa & Padisák, 2002; Souza et al., 2008) and was already found to be a driving force of phytoplankton assemblage in tropical and

subtropical water bodies (Lewis, 1986). Since the thermocline is developed during the summer and contributes to epilimnetic mixing, it has been considered a partial atelomixis (Barbosa & Padisák, 2002).

Roles and relevance of partial atelomixis, water column stratification, and relative nutrient concentration are commonly reported affecting phytoplankton dynamics in Ethiopian highland lakes (Degefu & Schagerl, 2015; Fetahi et al., 2014; Tessema et al., 2020). For instance, although the mean difference between the minimum and maximum daily air temperature provides a driving force for the pattern of stratification (Degefu & Schagerl, 2015), the dominance of relatively heavy, non-buoyant, and non-motile planktonic desmids and diatoms in Lake Hayq (Fetahi et al., 2014; Tessema et al., 2020), Lake Ardibo (Mohammed et al., 2023) and Lake Wonchi (Degefu & Schagerl, 2015) was explained through partial atelomixis. This phenomenon possibly drives the selection of algal groups, favoring the maintenance of heavy desmids and also the suspension of benthic diatoms throughout the layer (Degefu & Schagerl, 2015; Fetahi et al., 2014; Tessema et al., 2020). Also, stratification patterns of the water column may take precedence and favor relatively heavy and non-motile planktonic and benthic species to stay within the epilimnion extending over several meters (Degefu & Schagerl, 2015; Fetahi et al., 2014). Partial atelomixis and its ecological significance in structuring phytoplankton communities were also emphasized by Souza et al. (2008), mostly in favor of the planktonic desmids and diatoms in deep tropical high-mountain lakes. According to Degefu & Schagerl (2015) and Mohammed et al. (2023), the dominance of desmids and diatoms in deep Ethiopian highland lakes is explained through the special stratification and mixing regime in the water column, which favors the fast-sinking species to remain within the euphotic zone.

Similar observations were also reported in several water bodies with consistent daily mixing and relevant climates, like Lake Zirahuén, Mexico (Tavera & Martínez-Almeida, 2005), Dom Helvécio and Carioca Lakes, Brazil (Barbosa et al., 2012, 2018; Souza et al., 2008); Lake Cuicocha, Ecuador (Gunkel & Beulker, 2009) and Feitsui Reservoir, Taiwan (Wu & Kow, 2010). All these studies found that partial atelomixis keeps heavy algal desmids and non-motile diatoms in suspension and avoids ultimate sedimentation to the dark layers (hypolimnion). Padisák et al. (2009) and Sui et al. (2016) also described the remarkable ability of desmids and benthic diatoms to tolerate mixing and capacity for buoyancy regulation.

Phytoplankton Diversity of Ethiopian Highland Lakes

The list of phytoplankton in Ethiopian tropical highland lakes is summarized in Table 3. In six different Ethiopian highland lakes namely, Lake Wonchi, Dendi, Ziqualla, Hayq, Ardibo and Tana, a total of 173 species of phytoplankton is documented, which consists of 80 species of Chlorophyceae, Bacillariophyceae (55 taxa), Cyanophyceae (24 taxa), Dinophyceae (6 taxa), Eugleonophyceae (6 taxa), Xanthophyceae (1 taxon), and Cryptophyceae (1 taxon). The phytoplankton taxonomic category of Ethiopian highland lakes although common in temperate lakes (Degefu & Schagerl, 2015; Degefu et al., 2014; Fetahi et al., 2014; Tessema et al., 2020).

The number of phytoplankton taxa varied among the lakes and ranged from 85 in Lake Tana (Wondie et al., 2017) to 14 phytoplankton species in Lake Dendi (Degefu et al., 2014). A total of 65 and 57 phytoplankton species recorded from topographically tropical highland closed lakes, Lake Hayq (Fetahi et al., 2014; Tessema et al., 2020) and Lake Ardibo (Mohammed et al., 2023), respectively. These are followed by Lake Wonchi (53), Ziqualla (18) and Dendi (14) (Degefu & Schagerl, 2015; Degefu et al., 2014) (Table 3).

In Lake Tana, 15 blue-greens, 37 diatoms, 28 greens, and 5 other minor groups have been recorded (Wondie et al., 2017). According to Wondie & Mengistou (2006), diatom, blue-green and green algae dominated Lake Tana and accounted for over 90% of the total phytoplankton biovolume. Degefu & Schagerl (2015) also reported the dominance of green algae (Chlorophyta and Streptophyta) that contributed 82% (33 taxa) of the total phytoplankton biomass, followed by Bacillariophyceae (Diatoms) (12%, 11 taxa) and Dinophyceae (3%, 2 taxa), whereas Cyanobacteria and others taxa were of minor importance in Lake Wonchi. Degefu et al. (2014) also made their study of phytoplankton in two different highland lakes and recorded an algae community of 14 taxa in Lake Dendi and Ziqualla (18 taxa). According to Degefu et al. (2014), the phytoplankton community in Lake Dendi was dominated by coccal green algae, desmids, and dinoflagellates, whereas chlorococcales, in particular, *Botryococcus braunii* and benthic diatoms in were dominant in Lake Ziqualla.

Tessema et al. (2020) also reported 44 species of phytoplankton in highland Lake Hayq of which 17 species were Chlorophyceae, Bacillariophyceae (16 species), Cyanophyceae (5 species), Euglenophyceae (2 species), Dinophyceae (5 species),

Table 3. List of phytoplankton documented in Ethiopian highland lakes

Taxon	Lakes						Remarks*
	Wonchi	Dendi	Ziqualla	Hayq	Ardibo	Tana	
Chlorophyceae							
Acutodesmus acuminatus		+					*
Ankistrodesmus angustus						+	
Ankistrodesmus falcatus				+			
Ankistrodesmus gracilis	+						
Ankistrodesmus sp.						+	
Ankyra sp.	+						
Arthrodesmus sp.				+			
Botryococcus braunii			+				
Chlamydomonas sp.						+	
Chlorella fusca	+	+	+				
Chlorella vulgaris	+						
Chlorella sp.					+	+	
Chodatella cingula				+			
Chodatella subsalsa				+			
Closterium acutum						+	
Closterium praelongum	+		+				
Closterium venus			+				
Closterium sp.					+	+	
Coelastrum astroideum				+			
Coelastrum cambricum					+		
Coelastrum sp.	+			+			
Cosmarium contractum	+	+			+	+	*
Cosmarium punctulatum	+						*
Cosmarium tenue	+						*
Cosmarium sp.				+	+		*
Crucigenia sp.					+		
Desmidium swartzii						+	
Dictyosphaerium sp.	+	+					
Elakatothrix sp.	+				+		
Euastrum evolutum	+						*
Eudorina sp.	+					+	
Golenkinia radiate					+		
Haematococcus sp.						+	
Kirchneriella sp.	+			+	+		
Lagerheimia longiseta	+						
Micractinium sp.					+		*
Micrasterias radians	+						*
Monoraphidium sp.	+					+	
Oedogonium sp.					+	+	
Oocystis eremosphaeria						+	
Oocystis lacustris					+	+	
Oocystis parva						+	

Table 3. Continued

Taxon	Lakes						Remarks*
	Wonchi	Dendi	Ziqualla	Hayq	Ardibo	Tana	
Oocystis sp.	+			+		+	
Ooplanctella planoconvexa		+					
Pandorina sp.					+		
Pediastrum simplex	+			+	+	+	
Pediastrum sturmii				+			
Pediastrum boryanum	+			+		+	
Pediastrum duplex	+	+		+	+	+	
Planktosphaeria sp.	+				+		
Radiococcus polycoccus		+					
Scenedesmus armatus	+		+				
Scenedesmus bijugatus					+		
Scenedesmus incrassatulus						+	
Scenedesmus quadricauda	+			+			
Scenedesmus cingulum				+			
Scenedesmus obesum				+			
Scenedesmus uplandicum				+			
Scenedesmus sp.				+			
Schroederia setigera						+	
Schroederia sp.					+		
Staurastrum bullardii				+			
Staurastrum convergens						+	
Staurastrum gracile						+	
Staurastrum longebrachiatum						+	
Staurastrum triangularis var. *triangularis*						+	
Selanstrum sp.						+	
Spirogyra sp.					+		
Staurastrum bullardii					+		
Staurodesmus curvatus var. *latus*						+	
Staurodesmus pingue	+						*
Staurodesmus leave	+						*
Staurodesmus quadrangulare	+			+			*
Staurodesmus sp.	+						*
Synura uvella				+	+		
Tetraedron minimum	+			+	+		
Volvox sp.				+	+		
Xanthidium antilopaeum	+						*
Xanthidium octocorne	+						*
Zygnema sp.	+						*
Bacillariophyceae							
Achnanthes taeniata					+		
Aulacoseira distans						+	
Aulacoseira granulate						+	
Aulacoseria sp.			+	+	+		

Table 3. Continued

Taxon	Lakes						Remarks*
	Wonchi	Dendi	Ziqualla	Hayq	Ardibo	Tana	
Achnanthes sp.				+			
Amphora coffeaeformis						+	*
Amphora strigose				+			*
Amphora ovalis					+		*
Amphora sp.	+						*
Asterionella sp.					+		
Cocconeis sp.	+			+	+		*
Craticula sp.			+				
Cyclotella comensis				+	+		*
Cyclotella radiosa						+	*
Cyclotella regtangulare				+			*
Cyclotella sp.	+	+					*
Cymbella aspera				+			*
Cymbella cf Helvetica				+			*
Cymbella minuta						+	*
Cymbella ventricosa							*
Cymbella sp.	+		+		+		*
Diatoma vulgaris						+	*
Diatoma sp.	+						*
Epithemia adnate				+			
Epithemia argus					+		
Epithemia sorex					+		
Fragilaria sp.	+			+	+		*
Gomphonema acuminatum					+		
Gomphonema gracile						+	
Gomphonema cf. grovei						+	
Gomphonema sp.			+	+			
Gyrosigma sp.				+			
Halamphora coffeaeformis				+			
Meloseira sp.				+	+	+	
Nitzschia filiformis						+	
Nitzschia palea						+	
Nitzschia sp.	+	+	+	+			
Navicula cryptocephala						+	
Navicula antonil					+		
Navicula elegantula					+		
Navicula tripunctata					+		
Navicula sedotuscula					+		
Navicula dissipata					+		
Navicula sp.	+			+			*
Pinnularia sp.	+		+			+	*
Pleurosigma sp.					+		
Rhoicosphenia abbreviata			+			+	

Table 3. Continued

Taxon	Lakes						Remarks*
	Wonchi	Dendi	Ziqualla	Hayq	Ardibo	Tana	
Rhopalodia gibba						+	
Rhopalodia sp.				+	+		
Surirella robusta				+	+		
Surirella angusta				+			
Surirella subsalsa				+			
Synedra ulna				+	+	+	
Synedra sp.	+			+			
Tabellaria sp.	+	+			+		*
Cyanobacteria							
Anabaena ambigua					+		
Anabaena sp.	+			+		+	
Aphanothece minutissima					+		
Aphanocapsa sp.					+		
Calothrix sp.					+		
Chrococcus turgidus						+	
Chroococcus limneticus	+		+				
Chroococcus minor					+		
Coelosphaerium pallidinum					+		
Cyanodictyon endophyticum					+		
Gloeocapsa sp.					+		
Leptolyngbya sp.	+						
Lyngbya sp.					+		
Merismopedia sp.				+	+		
Microcystis aeruginosa		+	+	+	+	+	
Microcystis flos-aquae				+	+	+	
Nostoc sp.					+		
Oscillatoria sp.			+	+	+	+	
Phormidium sp.	+						
Planktolyngbya limnetica						+	
Pseudoanabaena sp.						+	
Scytonema sp.			+				
Spirulina sp.				+			
Synechococcus sp.						+	
Xanthophyceae							
Xanthonema sp.		+	+				
Dinophyta							
Gymnodinium fuscum					+		
Gymnodinium sp.				+			
Peridinium cinctum	+	+	+			+	
Peridinium gatunense						+	
Peridinium volzii						+	
Peridinium sp.	+			+	+		
Cryptophyta							

Table 3. Continued

Taxon	Lakes						Remarks*
	Wonchi	Dendi	Ziqualla	Hayq	Ardibo	Tana	
Cryptomonas sp.	+			+	+	+	
Euglenophyceae							
Euglena cf. *viridis*						+	
Euglena gracilis				+			
Euglena sp.		+		+	+		
Phacus acuminatus						+	
Phacus sp.				+	+		
Trachelomonas aspera					+		
Total no. of taxa	50	14	18	57	65	57	

*Remarks - heavy and non-motile atelomixis-dependent desmids and diatoms.

and Cryptophyceae (5 species). According to Fetahi et al. (2014) and Tessema et al. (2020), Chlorophyceae were identified as the dominant algal group and followed by diatoms. In their study, although the diatoms and chlorophytes dominated in Lake Hayq, community shifts were distinctly pronounced during March and June. The first community shift was due to a quick change from diatoms to *Euglena gracilis* and also later replaced the dominant diatoms by Cyanoprocaryota (primarily *Merismopedia*), which was successively replaced by Chlorophyta *Oocystis*. Similarly, Mohammed et al. (2023) reported 66 phytoplankton taxa while studying the community in a Tropical Highland Lake Ardibo (Table 3). According to the author, Bacillariophyta (23 species) predominates in Lake Ardibo, followed by Chlorophyta (21 species), Cyanophyta, and other plant species (14 species). According to their research, seasonal fluctuations in the composition and density of the phytoplankton community are linked to environmental factors such as major algal nutrients, light availability, temperature, grazing pressure, water mixing regimes, and hydrological patterns.

Phytoplankton Community Structure of Ethiopian Highland Lakes

The phytoplankton community structure of Ethiopian highland lakes is dominated by green algae, desmids, diatoms, and dinoflagellates (Degefu & Schagerl, 2015; Degefu et al., 2014; Fetahi et al., 2014; Tessema et al., 2020), which are common in oligotrophic to eutrophic lakes (Li et al., 2021; Wentzky et al., 2020). The dominance of small-sized dinoflagellates and slowly-growing species (K-strategist: e.g., *Peridinium*) in Lakes Dendi

and Wonchi is due to several environmental factors such as low dissolved inorganic nutrient concentrations (Degefu & Schagerl, 2015; Degefu et al., 2014), low total ion concentrations and moderate pH. Although Flores & Sierro (2013) discussed the proliferation of the dinoflagellate community responds to low-turbulence and low-nutrient contents (oligotrophic).

In contrast, under conditions of high turbulence and high nutrient contents (eutrophic), diatoms (e.g., *Gomphonema*, *Rhoicosphenia*, and *Navicula*) are the dominant organisms; developing an r-selected ecological strategy (opportunistic; growth rate maximized) in Lake Tana (Wondie et al., 2017) and Lake Ziqualla (Degefu & Schagerl, 2015). Many studies have shown the effects of wind-induced mixing and subsequent resuspension of particles on the phytoplankton community structure and functioning of shallow lakes (Jalil et al., 2021; Mesman et al., 2022). According to Mesman et al. (2022), the resuspension of particles on the water column reduces light penetration and gives a competitive advantage to diatoms (e.g., *Gomphonema* and *Navicula*). However, diatom species are buoyant and can adapt well under low irradiance due to their ability to regulate their vertical position in the water column (Fetahi et al., 2014; Tessema et al., 2020).

The Influence of Seasonality and Nutrients in Phytoplankton Dynamics

Ethiopian highland lakes have a well-established seasonality in phytoplankton abundance, which is governed mainly by climate (Degefu & Schagerl, 2015; Fetahi et al., 2014; Mohammed et al., 2023; Tessema et al., 2020). Phytoplankton community succession

in Lake Wonchi has evidently followed the hydrodynamic processes (Degefu & Schagerl, 2015). These authors reported the non–motile and heavy plankton forms like desmids and diatoms during the extended periods of thermal instability in March–May and September–November 2012 in Lake Wonchi. According to these authors, *Pediastrum boryanum*, *Dictyosphaerium* sp., and *Closterium praelongum* dominated during the complete mixing period January–February, whereas *Xanthidium antilopaeum*, *Oocystis* sp. and *Staurastrum pingue* contributed the bulk of phytoplankton biovolume of Lake Wonchi during thermal stability June–August. The phytoplankton community of Lake Hayq is also mainly composed of chlorophytes and diatoms, with large blooms of Cyanoprocaryota (primarily *Merismopedia*) and Chlorophyta *Oocystis* also periodically observed during March and June, respectively (Fetahi et al., 2014). Mohammed et al. (2023) found that Lake Ardibo showed a seasonal pattern in the succession of its phytoplankton community, with picophytoplankton—primarily Cyanophyta and Chlorophyta—dominating during the dry and pre-rainy seasons and microphytoplankton (Bacillariophyta) contributing more during the main rainy period and less during the dry season. The ecological significance of seasonality in structuring phytoplankton communities in deep tropical high-mountain lakes was also emphasized by various authors (Barbosa & Padisák, 2002; Souza et al., 2008; Tavera & Martínez-Almeida, 2005).

In Ethiopian highland lakes, phytoplankton is typically nutrient-limited (Degefu & Schagerl, 2015) which reduces phytoplankton productivity, biomass and growth (Degefu et al., 2014; Tessema et al., 2020). Nitrogen (NO_2^-, NO_3^-, NH_3), phosphorus (Soluble Reactive Phosphorus (SRP) and TP), and dissolved silicate (SiO_2) have been identified as the major nutrients governing phytoplankton biomass and diversity in Ethiopian highland lakes (Degefu & Schagerl, 2015; Degefu et al., 2014; Fetahi et al., 2014; Tessema et al., 2020; Tibebe et al., 2019). In these lakes, planktonic desmids and dinophytes like *Cosmarium contractum*, *Cosmarium tenue*, *Cosmarium punctulatum*, *Micrasterias radians*, *C. praelongum* and *Peridinium* spp. flourish due to the limited concentrations of this nitrogen and phosphorus nutrient for other taxa in their waters (Degefu & Schagerl, 2015; Tessema et al., 2020).

The low phytoplankton biomass of Ethiopian highland lakes (Table 3) has also been attributed to nitrogen and phosphorus limitations (Degefu & Schagerl, 2015). Similarly, Souza et al. (2008) noted the phosphorus limitation of phytoplankton in tropical lakes. In this case, the remarkable ability to tolerate mixing and capacity for buoyancy regulation becomes an advantage and may explain the dominance of desmids and dinophytes taxa in Ethiopian highland lakes (Degefu & Schagerl, 2015; Degefu et al., 2014; Fetahi et al., 2014; Tessema et al., 2020). Furthermore, the biomass and community structure of phytoplankton is often limited by water temperature (Ogato & Kifle, 2017), a cascading effect via trophic interactions (Arias et al., 2020; Ehrlich & Gaedke, 2020) and light availability (Rohr et al., 2020).

Phytoplankton Biomass and Trophic State of Ethiopian Highland Lakes

Even though chlorophytes accounted for high abundance in Ethiopian highland lakes, their biovolume is mainly dominated by diatoms in Lake Hayq (Fetahi et al., 2014; Tessema et al., 2020) and Lake Wonchi (Degefu & Schagerl, 2015; Degefu et al., 2014). The dominance of diatoms is also reported in tropical highland lakes and reservoirs (Souza et al., 2008; Tavera & Martínez-Almeida 2005). Degefu & Schagerl (2015) also explained the importance of atelomixis in the biomass of heavy phytoplankton like diatoms and desmids in Ethiopian highland lakes. The high contribution of planktonic desmids and diatoms in Ethiopian highland lakes also appears to be typical characteristics of oligo/meso/dystrophic water bodies (Degefu et al., 2014). Desmids are favored by several environmental factors like low dissolved inorganic nutrient concentrations (Barbosa et al., 2013), low total ion contents (Tavera & Martínez-Almeida, 2005), and moderate pH (Wood & Talling, 1988). Degefu & Schagerl (2015) and Tessema et al. (2020) reported *Peridinium spp* as a dominant species in Lake Wonchi and Hayq, which is probably attributed to nutrient depletion in the lakes and indicating the eco-physiological adaptation to limnological stress at oligotrophic and mesotrophic trophic states (Oda & Bicudo, 2006).

The biomass of phytoplankton often reflects the nutrient status of Ethiopian highland lakes with, for example, the predominance of desmids in Lakes Dendi and Wonchi suggested as indicative of oligotrophic conditions (Table 3) (Degefu et al., 2014). Low nutrient contents have also been observed in oligotrophic Lakes Dendi and Wonchi (Degefu & Schagerl, 2015; Degefu et al., 2014). Despite this, Lake Tana (Tibebe et al., 2019), Hayq (Tessema et al., 2020) and Ardibo (Mohammed et al., 2023) are now prone to nutrient enrichment from anthropogenic activities and changing environmental conditions of the lakes.

This has led to Eutrophic and Mesotrophic trophic status of the lakes (Tessema et al., 2020; Tibebe et al., 2019).

Furthermore, Ethiopian highland lakes display a considerable range in phytoplankton biomass (*Chl-a*) and ranged from 0.1 μg/L in Lake Dandi to 38 μg/L in Lake Tana (Table 2), which reflects their trophic status. Lake Dendi and Wonchi are typical examples of a nutrient-poor (oligotrophic) lake with a low value of Trophic State Index (TSI) of 23.37 and 37.84, respectively (Degefu et al., 2014). It appears that Lake Dendi and Lake Wonchi's greater water transparency played a role in the oligotrophic status of these bodies of water. Additionally, while having low nutrient levels and great water transparency, Lake Dendi and Lake Wonchi are situated in an upland area that has not yet been extensively influenced by domestic and industrial sewage inputs (Degefu et al., 2014). In contrast, both Lake Ziqualla (TSI, 45.56) and Hayq (TSI, 43.16) have mesotrophic conditions, according to Degefu et al. (2014) and Tessema et al. (2020). This is probably related to nutrient inputs from various sources, including rivers (Degefu et al., 2014; Tessema et al., 2020).

According to Carlson's TSI, the most eutrophic lakes are Lake Tana (Tibebe et al., 2019) and Lake Ardibo (Mohammed et al., 2023). The classification of the lakes as eutrophic was made possible by higher mean phosphorus contents and low Sechi depth (water transparency). An earlier analysis of nutrient levels and phytoplankton productivity labeled Lake Tana as an oligotrophic lake (Wondie et al., 2017). Tibebe et al. (2019), citing high TSI (69.77) readings and Carlson's trophic state classification criteria, observed a considerable change in Lake Tana to the eutrophic condition. Lake Tana and Ardibo receive water from their tributary rivers and streams in the catchments, which is highly impacted because of its proximity to various agricultural activities and urban centers, especially areas lacking even the most basic sanitation and having an industrial activity (Goshu & Aynalem, 2017; Mohammed et al., 2023). As a result, Lake Tana and Lake Ardibo become more eutrophic.

Conclusion

In this review, we highlighted the role of atelomix in phytoplankton dynamics, particularly in selected Ethiopian highland lakes. A total of 140 phytoplankton species have been documented in six highland tropical lakes. According to the published literature, Chlorophyceae and Bacillariophyceae were found to be the most common in Ethiopian highland lakes. From this review, it is evident that partial atelomixis

and nutrients are key variables in structuring phytoplankton community composition and abundance, which was quite stable and characterized by a high diversity of relatively heavy and non-motile desmids and diatoms.

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