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Authors: Degefu, Fasil, Herzig, Alois, Jirsa, Franz, and Schagerl, Michael

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Research Article

First limnological records of highly threatened tropical high-mountain crater lakes in Ethiopia

Fasil Degefu[1,5]*, Alois Herzig[2], Franz Jirsa[3,4] and Michael Schagerl[5]
[1] National Fisheries and other Living Aquatic Resources Research Center. Sebeta-Ethiopia, P.O.Box 64 Sebeta, Ethiopia
[2] Biological Station Neusiedlersee, A-7142 Illmitz, Austria
[3] University of Vienna, Institute of Inorganic Chemistry, Althanstrasse 14, A-1090 Vienna, Austria
[4] University of Johannesburg, Department of Zoology, P.O.Box 524, Auckland Park, 2006 South Africa
[5] University of Vienna, Department of Limnology and Oceanography, Althanstrasse 14, A-1090 Vienna, Austria
*Corresponding author; email: fasildeg2000@yahoo.com, degefuf3@univie.ac.at
Phone: +43 6766184208

Abstract
Lakes Dendi, Wonchi and Ziqualla are among the few remnants of undisturbed crater lakes in the central highlands of Ethiopia, and have never been investigated reliably owing to seclusion and inaccessibility. As the lakes offer a pristine environment in a beautiful landscape and are located in the vicinity of the capital city Addis Ababa, they are highly threatened by unsustainable tourism, shoreline and crater rim modifications, water abstraction and land grabbing. We provide a first limnological description to establish baseline data against which future environmental and biological changes can be monitored. The lakes are located above 2,800 m elevation with no surface outflow and generally show low concentrations of ions, displaying an equal distribution of readily soluble components like Na or K throughout the water column, but distinct oxygen depletion in greater depths linked to rising concentrations of Fe and Mn, which indicates subterranean springs. Based on nutrients, chlorophyll *a,* and water transparency, lakes Dendi and Wonchi are classified as oligotrophic and Ziqualla as oligo-mesotrophic. The phytoplankton community is dominated by coccal green algae, desmids and dinoflagellates in lakes Dendi and Wonchi, typical for unpolluted dilute waterbodies; whereas chlorococcales, in particular *Botryococcus braunii* and benthic diatoms, prevail in Ziqualla. The zooplankton fauna is depauperate, comprising a total of 11 rotifer taxa and 13 crustaceans. Copepods were the most abundant group and contributed over 60% to the total zooplankton abundance in all three lakes, followed by rotifers and cladocerans. The conservation significance of these lakes lies predominantly in their representation of dilute, nutrient–poor highland lake systems that support diverse biota assemblages like desmids and daphnids, which are highly sensitive to eutrophication.

Key words: highland lake, volcanic, trophic classification, nutrient, plankton

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Introduction

Limnological expeditions to the Ethiopian crater lakes have focused almost exclusively on the Bishoftu crater lakes, a group of volcanic explosion craters in the vicinity of the emerging city Debre-Zeit, around 50 km southeast of Addis Ababa [1, 2]. Hydrochemistry of these lakes documented in earlier studies by Prosser *et al*. [2], Wood and Talling [3] and Gebre-Mariam [4] suggests intermediate concentrations of dissolved inorganic nutrients and ions. Concurrently, phytoplankton associations described by Baxter and Wood [5], Talling *et al*. [6], Wood and Talling [3], Gebre-Mariam [4] and Gebre-Mariam and Taylor [7] documented dominance by green algae, diatoms and cyanobacteria. Generally, green algae and few species of cyanobacteria, mainly *Microcystis aeruginosa* and *Chroococcus* sp., dominated algal biomass at that time, apart from a recorded unialgal bloom of a cyanobacterium, *Arthrospira fusiformis* (formerly called *Spirulina platensis*) in Lake Arenguade. Zooplankton associations and community grazing rates have been provided by Green [8] and Lemma [9]. In recent years human pressures have impacted limnological features of the Bishoftu lakes [10-12]. In the alkaline Lake Arenguade, for example, a significant decrease has been reported in the phytoplankton biomass, and the mono-specific community of *Arthrospira fusiformis,* whose production previously attained the theoretical maxima of phytoplankton production for natural lakes [6], has shifted towards other cyanobacteria taxa such as *Anabaenopsis elenkinii* and *Chroococcus minutus* [11]. Moreover, increased eutrophication and even a mass fish kill have been reported [12].

In contrast to such a remarkable amount of literature on the Bishoftu crater lakes, which are easily accessible, very little is known of the remote, high-altitude crater lakes of Ethiopia [13]. These lakes exhibit a wide range of limnological characteristics such as low water temperatures, soft waters, special mixing patterns with no stabile thermal stratifications, and unique biota [14-15].Crater lakes can also accumulate volcanic gases (e.g. the tragic emission of CO_2-gas from Lake Nyos in the Oku volcanic field of Cameroon), which pose serious health risks to humans [16]. Recently, detailed limnological investigations of the highland tropical crater lake Hayq have been initiated in Ethiopia [17], focusing on food webs and energy flows and the underlying limnological variables, demonstrating a remarkable shift towards eutrophic conditions.

Apparently, the three crater lakes Dendi, Wonchi and Ziqualla in the central highlands of Ethiopia, situated within a 100 km radius from Addis Ababa, have never been investigated reliably owing to seclusion and lack of infrastructure. A project by the so-called ALMOEZ holding groups, led by a Qatari-Egyptian investment company, has started recently to tenure Lake Dendi. This project, with a total area of 26.4 km^2, plans to develop an 'integrated residential, commercial and recreational resort by the lake' (www.dendilake.com). Lake Wonchi is also becoming a tourist destination, with a corresponding increase in newly erected resorts and tourist facilities in the lake basin, which involve modifications of the crater rim and shoreline. Such aggressive land grabbing and encroachments not only displace and evict riparian communities and jeopardize aquatic biodiversity, but also destroy local traditions for preservation and sustainable management of natural resources. This problem has been already witnessed in the Bishoftu crater lakes, which are exposed to complex human interference due to their proximity to fast-growing cities and subsequent land use and shoreline modifications [12]. Current conditions of the Bishoftu and rift valley lakes in Ethiopia warrant that future developments merit Environmental Impact Assessment (EIA), including investigations of aquatic biodiversity. Therefore, we present first data on limnological features and biotic communities of lakes Dendi, Wonchi and Ziqualla. The baseline information generated from this study serves as the *status quo* against which future changes can be monitored. Moreover, we address the importance of conserving these sensitive aquatic ecosystems as surrogate reference sites, providing fairly pristine conditions for assessing and/or restoring comparable but already eutrophic aquatic ecosystems in the region.

Methods

Study sites

All the three lakes can be reached within one day from the capital Addis Ababa and play a significant economic role through increasing eco-tourism. Lakes Dendi and Wonchi provide freshwater for drinking, back-yard irrigation, and livestock watering to the riparian communities. Lake Ziqualla is "holy" and strictly protected by monks; its water is used exclusively for baptizing.

The adjacent lakes Dendi and Wonchi (8°50'N, 38°01'E and 8°47'N, 37°53'E) are deep crater lakes formed as a result of volcanic eruption and located in the central highlands of Ethiopia (Fig. 1). The region is characterized by sub-humid climate with an annual rainfall of around 1,200 mm. The main rainy season extends from May to September (National Meteorological Service Agency of Ethiopia), and air temperature varies from 14 to 26 °C during the day and falls below 10 °C at night (Fig. 2).

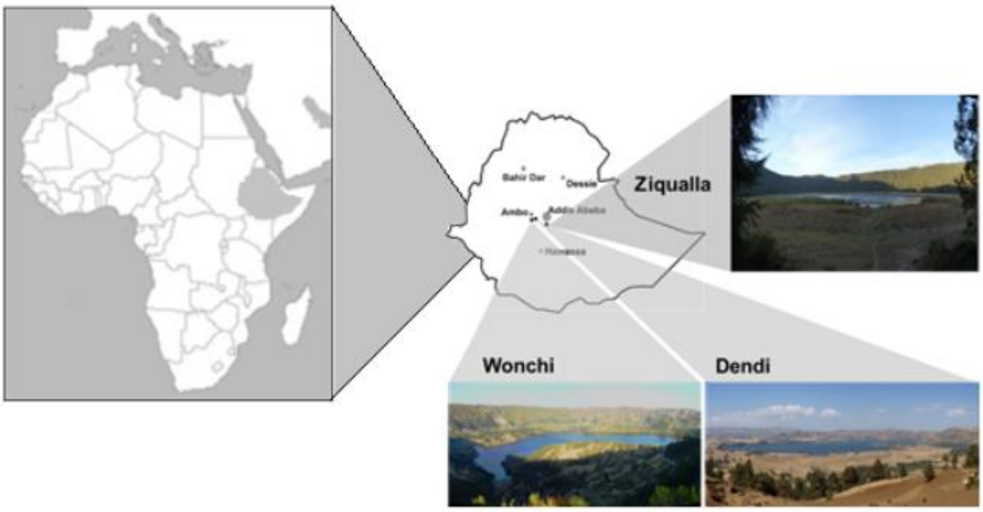


Fig. 1. Map showing location of Ethiopia, marked in grey in Africa (modified from web.worldbank.org) and the three lakes in the vicinity of Addis Ababa (Ethiopia).

Lake Dendi, a double crater at an elevation of 2,840 m a.s.l., is located 130 km south-west of Addis Ababa and 20 km north-west of Lake Wonchi. It covers an area of 7.2 km^2 and has a maximum and mean depth of 60 m and 35 m, respectively. The lake is eight km long and four km wide. It has no permanent surface inlets or outlets. It is mainly fed by seasonal rivers and springs during the rainy season. The lake is surrounded by very steep shores and vertical drop-offs that rise 50 to 120 m above the lake surface; it is only accessible at three distinct sites. The littoral zone of the lake is characterised by a belt of emergent macrophytes, mainly *Typha angustifolia*.

Lake Wonchi, near Dendi, is located at an altitude of 2,887 m a.s.l.. It is deep, steeply shelving with a surface area of 5.6 km^2, maximum and average depth of 107 and 28 m, respectively, and has maximum dimensions of 3.9 km long and 2.2 km wide. The height of its crater rim from the lake surface is about 460 m. The lake has a closed basin with no surface inlet. It receives water primarily from rainfall falling directly on its surface, and from subterranean cold and lukewarm springs. The littoral zone of the lake is characterised by submerged aquatic macrophytes, mainly *Potomageton* sp.. The fish species present in lakes Dendi and Wonchi are *Garra* sp. and *Cyprinus carpio* (common carp). The latter species was introduced in both lakes in the late 1990s, together with *Oreochromis niloticus* (Nile tilapia), by the National Fisheries and Other Aquatic Life Research Center (NFLARC) in an attempt to establish a pelagic fishery and increase availability of protein for local communities. However, *Oreochromis niloticus* did not establish breeding populations in either lake (personal observation, detailed results will be published elsewhere).

Lake Ziqualla (8°32'N, 38°51'E; Fig. 1) is a crater lake located on mount Ziqualla (2,989 m a.s.l) 100 m below the rim of the crater. It is one of the extensive series of the famous Bishoftu volcanic explosion crater lakes found 26 km south-west of Debre-Zeit town. The lake is a small, shallow endorheic lake with a surface area of approximately 0.25 km^2 and maximum depth of three m. The surface area has receded dramatically over recent decades (personal communication). The rim of the crater is covered with a natural conifer forest and other alpine type vegetation, which offers a natural habitat to various birds and mammals (e.g., the eastern black-and-white colobus monkey *Colobus guereza*). This "holy" lake is completely surrounded by a reed belt and is strictly protected by the community of monks living in a nearby monastery.

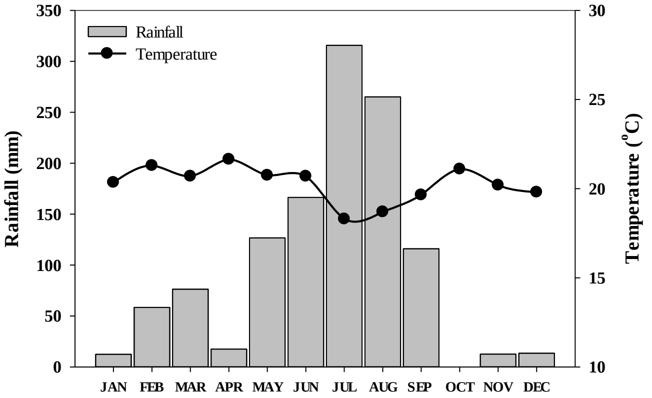


Fig.2. Mean monthly air temperature and rainfall around lakes Dendi and Wonchi during the sampling period (data provided from the Ethiopian National Meteorological Service Agency).

Sampling protocol and analyses

All the three lakes were visited during the first week of January 2012. Physico-chemical variables such as water temperature, dissolved oxygen (DO), salinity, electrical conductivity (corrected to 25 °C) and pH were measured *in-situ* in vertical profiles using a multi-probe (Model HQ40D, HACH Instruments). Underwater irradiance was measured using a light meter (Model SKP 2000, Skye Instruments); water transparency (vertical visibility) was estimated using a standard Secchi disc of 20 cm diameter. The vertical light extinction coefficient (ε, m^{-1}) was calculated using direct light irradiance measurements ($\varepsilon = (\ln I_o - \ln I_z)/Z)$), where I_o is surface light irradiance, I_z is light irradiance at a certain depth Z, and Z is depth (SKP 200, Skye company). Subsequently, euphotic depth (Z_{eu}), the depth at which 1% incident irradiance is available, was calculated using $Z_{eu} = 4.6/\varepsilon$. Water for chlorophyll-*a* (Chl-*a*), element, and nutrient analysis was collected from depth profiles (surface, 1, 2, 3, 4, 5, 7, 10, 15, 20, 30, 40, 50 m depth) of the lake center for lakes Dendi and Wonchi using a 5 L Schindler sampler, and approximately 10 cm below the surface using the same technique at the shoreline of Lake Ziqualla (boating is strictly forbidden at the holy lake). Samples were transferred to 2 L acid-prewashed plastic bottles and stored in the dark in a cooling box (4°C) until analyses of nutrients and alkalinity were made at National Fisheries and Aquaculture Research Center, Ethiopia. For water chemistry, standard methods were applied (Appendix 1). For element analyses (including trace elements) and determination of major anions, samples were acidified with nitric acid (Trace SELECT ® by FLUKA) and analyzed at the University of Vienna, Austria.

Samples for relative abundance estimations of the phytoplankton community were collected with a plankton net (30 µm mesh size) from the open water. Concurrently, water samples for algal biovolume estimations [18-19] were taken down to 20 m and kept in brown bottles, preserved with Lugol's solution, and stored in the dark. To determine biovolumes of algal taxa, cells for each taxon were first enumerated using an inverted microscope (Nikon Diaphot, Nikon, Tokyo) according to Utermöhl [20]. Algal biovolumes were then calculated using geometric formulae of the shapes similar to the respective phytoplankton cells [21]. At least thirty cells for each taxon were measured to give the average biovolume. For conversion of cell volume into biomass, a conversion factor of 1 was used [18]. For qualitative zooplankton analysis, duplicate samples were collected from two stations (shore and open-water) using plankton nets of 30 and 100 µm mesh size for rotifers and crustaceans, respectively. Subsequently, the species were examined in counting chambers under a WILD stereoscope microscope (magnification 40x). Identification was based on Koste [22], Korinek [23] and Fernando [24]. To determine numerical abundance, samples were collected by means of vertical net hauls from 20 m to the surface at open-water stations. The volume of water filtered (V) was calculated from $V = \pi r^2 h$, where "r" is radius of net ring (0.15 m) and "h" is the distance towed (20 m). The samples were stored in 250 ml plastic bottles and preserved with sugar-formalin to a final concentration of 4%. Total counts were made from subsamples and individual densities expressed as number per m^3. The trophic status of Lakes Dendi, Wonchi and Ziqualla was classified following the trophic status indices (TSI) of Carlson [25].

Results

Physico-chemical parameters

The water temperature in lakes Dendi and Wonchi varied between 16.7 °C at the surface and 14.9 °C in deep layers and exhibited nearly isothermal conditions throughout the water column (Fig. 3). In contrast, only 8.8 °C was recorded in the shallow lake Ziqualla. A striking feature was the clinograde DO profile for Wonchi, which indicated stratification below 7 m. Oxygen levels dropped from 102% relative saturation to nil (Fig. 3). Conversely, DO profiles in Dendi followed the isothermal pattern with more or less uniform oxygen distribution of 106.7% at the surface and 97% in deep water (Fig. 3). Surface-water DO saturation was 39.5% in Lake Ziqualla. All three lakes had pH values between 7.91 to 8.27 and conductivity ranging from 77 to 200 µS cm^{-1}, respectively (Appendix 2). The deep lakes are crystal-clear with a Secchi depth transparency ranging from 5 to 12 m and vertical extinction coefficients of 0.14 and 0.34 m^{-1} respectively; Ziqualla showed enhanced turbidity (Appendix 2).

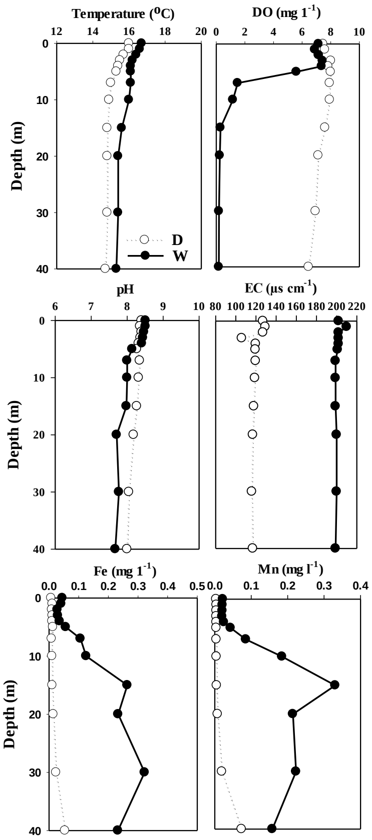


Fig. 3. Profiles of temperature, dissolved oxygen, pH, conductivity, Fe and Mn in lakes Dendi (D, open circle) and Wonchi (W, closed circle) during the sampling periods. Lake Ziqualla profile is not presented; values are only for surface water.

The rank (highest to lowest) of the predominant cation concentrations in lakes Dendi and Ziqualla was: $Ca^{2+} > Na^{+} > Mg^{2+} > K^{+}$, while it followed a rank of $Na^{+} > Ca^{2+} > K^{+} > Mg^{2+}$ in Wonchi (Fig. 4).

Anion concentrations appear in the order: HCO_3^- > Cl^- > $SO4^{2-}$ > F^- in Dendi, while they followed a rank of HCO_3^- > Cl^- > F^-> SO_4^{2-} in Wonchi and Ziqualla (Fig. 4).

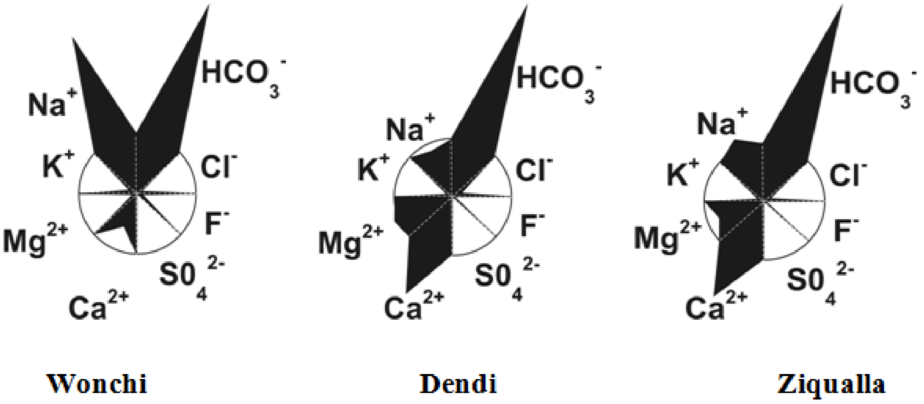


Fig. 4. Ion field diagrams of lakes Wonchi (left), Dendi (center) and Ziqualla (right). Each semicircle represents 100% of the four most abundant cat- and anions (basis mg l^{-1}).

Element concentrations of Si and trace elements are given in Appendix 2. The following element concentrations were below limit of detection (LOD) (given in parenthesis in mg l^{-1}) in all three lakes throughout the water column: Al (0.05), Be (0.001), Cd (0.010), Co (0.002), Cr (0.002), Li (0.002), Ni (0.002) Pb (0.010), Rb (0.010) , Sb (0.010), Sn (0.002), Ti (0.002), V (0.002), Zn (0.002) Zr (0.002). Concentrations of Fe and Mn significantly increased with increasing depth and increasing oxygen depletion in Lake Wonchi (Fig. 3), resulting in a fivefold increase of the two elements below 20 m compared with surface water.

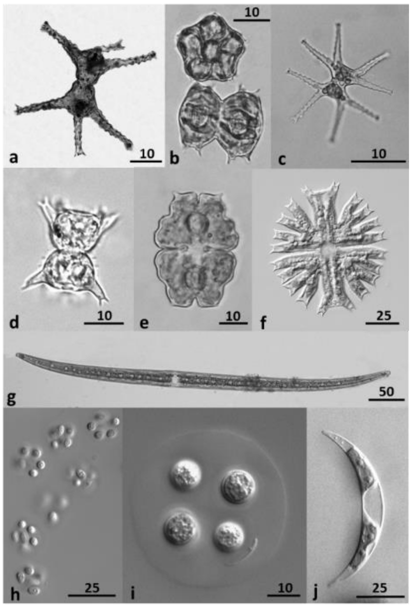
Mean SRP concentrations were < 5 µg l^{-1} for Dendi and Wonchi, while SRP was notably higher in surface water of Ziqualla (15.7 µg l^{-1}). The concentrations of P_{tot} showed a similar pattern with low values below 10 µg l^{-1} in Dendi and Wonchi, while in Ziqualla a 3-fold higher value was measured at the surface (Appendix 2). NO_3-N was generally very low with concentrations < 20 µg l^{-1}; NO_2-N was near the detection limit. In general, NH_4-N was notably higher than the other two inorganic nitrogen forms in all the water bodies (Appendix 2). Based on the TSI for Chl-*a*, P_{tot} and Secchi-disc readings (Table 1), the lakes are classified as oligotrophic to (oligo-) mesotrophic.

Table 1 Trophic State Index (TSI) for lakes Dendi, Wonchi and Ziqualla

Trophic state indices	Dendi	Wonchi	Ziqualla
TSI for P_{tot}	31.56	34.75	48.46
TSI for Chlorophyll-*a*	11.31	41.95	38.20
TSI for transparency	24.19	36.81	50.01
Mean TSI	22.37	37.84	45.56
Trophic state	**Oligotrophic**	**Oligotrophic**	**Mesotrophic**

Phytoplankton abundance and community composition

Chl-*a* was generally low with mean values < 3.2 µg l^{-1} (Appendix 2). Seven algal groups were identified during the sampling period including Cyanobacteria, green algae (Chlorophyta and Streptophyta), Bacillariophyceae, Dinophyta, Cryptophyta, Euglenophyta and Xanthophyceae (Appendix 3). The latter two groups were not observed in Lake Wonchi, however. The highest taxa number was found for green algae (21 genera, dominated by desmids, which accounted for more than 67% of the green algae) followed by Bacillariophyceae (11), Cyanobacteria (5) and Dinophyta (2), whilst Cryptophyta, Euglenophyta and Xanthophyceae were represented by only one taxon (Appendix 3). For Lake Dendi, 16 taxa were observed with the dominant (numerical abundance) ones being from Chlorophyta: cf. *Radiococcus polycoccus* and cf. *Ooplanctella planoconvexa* (Fig. 5i), *Acutodesmus acuminatus* and *Dictyosphaerium* sp.. The algae community in lakes Wonchi (comprising 26 taxa) and Ziqualla (18) were more diverse. Dominant taxa in Wonchi were *Elliptochloris* sp, *Chlorella fusca*, *Peridinium cinctum* and desmids. In Ziqualla, the dominant taxa were phytobenthic diatoms*, Botryococcus braunii* and *Scenedesmus armatus*.



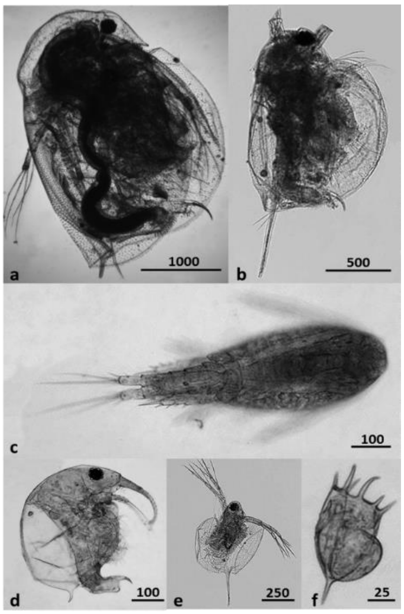


Fig. 5i (Left). Phytoplankton taxa of the lakes: a) *Staurastrum pingue*, b) *Staurastrum quadrangulare* var. *attenuatum* f. *pentagona*, c) *Staurastrum bibrachiatum*, d) Staurastrum *laeve*, e) *Euastrum evolutum*, f) *Micrasterias radians*, g) *Closterium praelongum*, h) *Ooplanctella planoconvexa*, i) *Radiococcus polycoccus*, j) *Closterium venus.* Numbers on scale bars in µm.

Fig. 5ii (Right). Characteristic zooplankton taxa of the lakes: a) *Daphnia magna*, b…*Daphnia longispina*, c) *Thermocyclops ethiopiensis*, d) *Bosmina longirostris*, f) *Keratella cochlearis.* Numbers on scale bars in µm.

Zooplankton species composition and abundance

A total of 11 rotifer taxa belonging to 8 genera and 13 crustacean taxa (6 genera) were identified (Appendix 4; Fig. 5ii). Cyclopoid copepods (17×10^3 Ind m^{-3}) were the most abundant group and contributed considerably (> 60%) to the total zooplankton abundance in all three lakes, followed by rotifers (11×10^3 Ind m^{-3}) and cladocerans (4.5×10^3 Ind m^{-3}) (Fig. 6, bottom panel). Cyclopoid copepods were represented only by *Thermocyclopes ethiopiensis* (adult: 5×10^3 Ind m^{-3}). The dominant cladoceran in Lake Dendi was *Daphnia longispina* (0.4×10^3 Ind m^{-3}), whilst *Bosmina longirostris* (9.5×10^3 Ind m^{-3}) and *Daphnia longispina* (10.2×10^3 Ind m^{-3}) were the co-dominant cladocerans in Wonchi. In contrast, Ziqualla showed a low diversity of Cladocera (2 genera); *Ceriodaphnia reticulata* was the dominant species (Appendix 4).Also, a cladoceran species, *Daphnia magna* and *Chaoborus*-larvae were identified from Lake Dendi. The rotifers in all three lakes were the typical cosmopolitan species of *Keratella, Trichocerca, Brachionus, Polyarthra* and *Lecane* (Appendix 4). *Polyarthra* sp. (2.3×10^3 Ind m^{-3}) was encountered in higher number in Dendi, while *Keratella cochlearis* (12.2×10^3 Ind m^{-3}) and *Trichocerca gracilis* were the dominant species in Wonchi and Ziqualla, respectively.

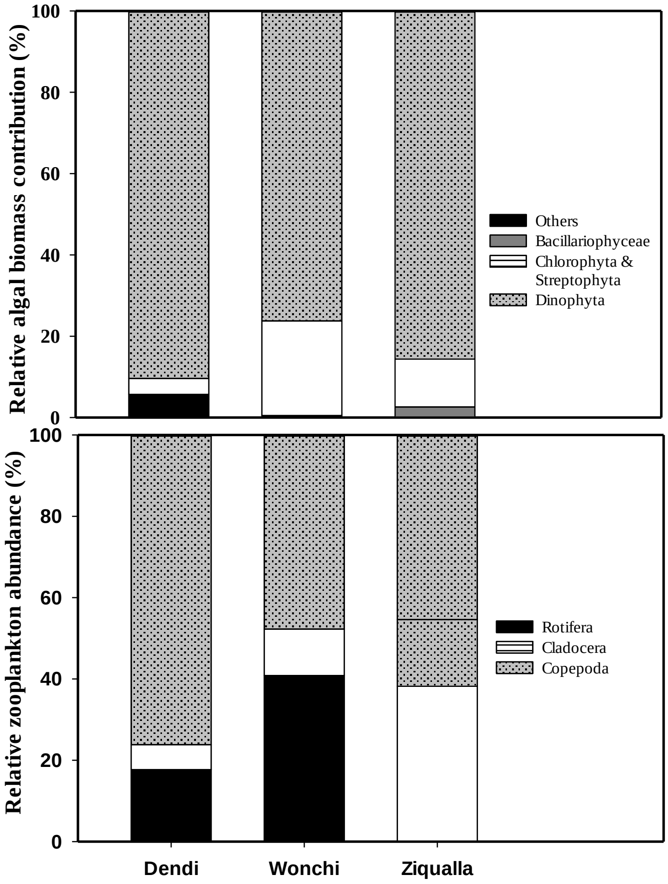


Fig. 6. Percentage algal biomass contribution (top panel) and relative zooplankton abundance based on Indl m^{-3} (lower panel) of the three lakes during the sampling period.

Discussion

The lakes studied are characterized by their confined and nearly circular catchment areas, deep (except Ziqualla: ~ 3m) and steeply shelving slopes, flat bottoms and strongly developed rim, 100 - 460 m in height, which appear to be typical features of explosion craters [1-2,]. Except for the preliminary study of Singanan *et al*. [26] on the hydrochemistry of Wonchi Crater Lake, to our knowledge no limnological data exist for the investigated lakes. Unfortunately, the work of Singanan *et al*. [26] did not identify sampling sites, depth, or the methods used to collect, identify and quantify the biotic communities. Although the biotic communities (e.g. phyto-and-zooplankton) were briefly discussed, the check-list and biomass were not provided in the article, and some of the results (e.g., F^-, Na^+ and conductivity values) are debatable.

Lakes Dendi and Wonchi exhibited marked differences with regard to DO profiles, transparency, conductivity, Chl-*a*, and major cations (Appendix 2, Fig. 3). The water column temperature showed a pattern similar to DO in Dendi, suggesting an event of seasonal mixing shortly before the measurement was taken, as these observations were made during the coldest, windy, and driest period of the year (January). Surface cooling imposes vertical circulation of water masses due to weak density differences and subsequently erodes the stratification of water properties during the cold-dry season [27]. Nevertheless, such homogeneous DO concentration of the whole water column is a typical feature of oligotrophic lakes. Although thermal stratification was not pronounced and thermocline poorly defined in Wonchi, a clinograde dissolved oxygen profile (< 1.5 mg l^{-l} below 7 m) was observed, which is unusual for an oligotrophic lake [28]. Such a decrease, however, has been reported from other deep, high-altitude lakes located in Cameroon, Uganda, Nepal, and the United States [16, 29], which may reflect long-lasting stratification and – at least for eutrophic water bodies - high oxygen consumption by decomposition of sinking labile organic matter and respiration of organisms in deeper waters [1, 14].

For the oligotrophic lake Wonchi, we attribute the strong vertical DO decrease to subterranean inflows rich in ferrous iron and manganese (Fig. 3) that deplete dissolved oxygen through oxidation processes, which has been also noted elsewhere in meromictic oligotrophic lakes [30]. Another independent seasonal study (n=20) has also noted a comparable vertical DO profile below 10 m in Lake Wonchi [31]. Dendi has a wide open basin, low rim surface walls, and a larger surface area than Wonchi (see site description) which allows wind-induced mixing of the whole water column. The low surface water temperature and DO content in Ziqualla (8.80 °C and 39.5%, respectively) are probably due to its shallowness, high respiration, and early sampling before sunrise. The lake water is believed by members of the Ethiopian Orthodox Church to be 'holy' water, used only for baptizing and strictly protected by them; therefore it was impossible to get access by boat or to sample during the day. Ziqualla (77 $\mu S\ cm^{-1}$) had considerably lower ion contents than Dendi and Wonchi, and all the three lakes showed less ion concentrations than other Ethiopian lakes [1, 11, 17, 31]. We did not measure high fluxes of volcanic gases such as CO_2 ($< 2\ mg\ l^{-1}$) and H_2S (below limit of detection) from any of the lakes.

Chl-*a* and nutrient concentrations were very low (Appendix 2) and we classified the lakes as oligotrophic to (oligo-) mesotrophic [25, 32]; some accumulation of $N\text{-}NH_4$ and SRP was observed in deep layers of lake Wonchi. Such patterns were also recognized in other high-altitude lakes [14-15, 33] and are probably attributed to long-lasting stratification [34]. In many lakes in Africa [2, 35-36], carbonate and bicarbonate are the predominant anions. In his extensive survey of the major ion composition of the groundwater and surface water systems in the Ethiopian volcanic terrain, Ayenew [37] documented that almost all highland waters are dominated by carbonate and bicarbonate anions, with very few exceptions. Also, the dominance of sodium in Wonchi ($42.45 \pm 0.33\ mg\ l^{-1}$) is unusual for highland lakes in contrast to rift waters, which is likely due to the dominance of acidic volcanics, mainly ignimbrite, rhyolite and pumice [37]. Lake Wonchi also has an increased concentration of F^- ($2.69 \pm 0.01\ mg\ l^{-1}$) quite above WHO [38] guideline for drinking water ($0.6 – 1.5\ mg\ l^{-1}$), which was reflected in mild dental fluorosis of the riparian community. The high level of F^- in Wonchi is probably due to leaching of F^- from the fluoride-rich volcanic rocks around the lake that enrich subterranean (cold and lukewarm springs) drainage into the lake with F^-.

The algal composition of lakes Dendi and Wonchi was dominated by coccal green algae, desmids, and dinoflagellates, which are common in oligo- to mesotrophic environments [39-40]. The dominance of small-sized phytoplankton 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 [39-40], low total ion concentrations [35] and moderate pH [3]. In contrast, the algal community of Lake Ziqualla is dominated by Chlorococcales (e.g. *Botryococcus braunii*) and diatoms (e.g. *Gomphonema, Rhoicosphenia* and *Navicula*). We attributed this finding to the shallowness and subsequent resuspension of particles into the water column through wind-induced mixing. This, in turn, reduces light penetration and gives competitive advantage to some taxa (e.g. *Botryococcus*), which have established an evolutionary adaptation to low underwater irradiance [41-42]. Although cyanobacteria were not dominant in terms of numerical abundance, their diversity was relatively high in Lake Ziqualla. Some species of this group are buoyant and can adapt well under low irradiance due to their ability to regulate their vertical position in the water column [41, 43].

Numerically, copepods and rotifer taxa formed the major zooplankton component of all three lakes, in contrast to cladocerans, which were rather more diverse (Appendix 4). Such a dominance of copepods and rotifers is a common pattern in tropical water bodies [17, 44-45]. The high species richness of cladocerans is most probably attributable to their high dispersal rate compared with copepods. Cladocerans are well-known to produce resting eggs (ephippia) during unfavorable conditions, and hence viable resting eggs could be transported into remote isolated waterbodies by waterbirds as they migrate between lakes, which has been often observed elsewhere [45, 46-49].

In contrast to other subtropical and tropical lakes [50-54], large-bodied cladocerans such as *Daphnia magna*, *Diaphanosoma excisum,* and *Daphnia longispina* (Fig. 5ii) almost exclusively dominated the cladoceran communities in lakes Dendi and Wonchi. This is likely due to lack of planktivorous fish (weak top-down control) in the pelagic zone [55]. The riverine benthic fish *Garra* was the only indigenous and dominant fish in the lakes during our sampling campaign. Some authors have also presented evidence that predation by invertebrates is an important factor influencing the size structure of the whole zooplankton community [43, 56-57]. The high altitude at which the lakes are located (> 2,800 m) and the subsequent low water temperatures (8.8-16.7^{o}C) for tropical lakes agrees with the study of Dejen *et al*. [45], who also reported high diversity of cladocerans and the co-occurrence of both temperate and tropical species in Lake Tana due to comparatively low water temperatures. *Daphnia magna,* which was only reported from two other Ethiopian highland lakes Hayq [17] and Ashenge [58], and the predatory *Chaoborus*-larvae, recently reported from Lake Ziway [59], were recorded for the first time in Lake Dendi in the present study. Amongst rotifers, *Keratella cochlearis* was encountered in greater numbers (12.2×10^{3} Ind m^{-3}), which is probably linked to its evolutionary adaptation to low food concentration in such oligotrophic environments (range of Chl-*a* between 0.2 – 3.2 µg l^{-1}), as was also noted from similar oligotrophic lakes elsewhere in the world [60-61].

Implications for Conservation

In Africa, particularly in Ethiopia, there seems to be little awareness of eutrophication, and few monitoring programs have been established for aquatic ecosystems. Such lack of monitoring on freshwater lakes has contributed to the continuous degradation of their biodiversity. Therefore, in order to protect biodiversity, it is essential to document the natural states of reference ecosystems before deleterious effects have become evident. Lakes Dendi and Wonchi are categorized as oligotrophic, while Lake Ziqualla is oligo- mesotrophic. Phytoplankton assemblages were represented by the characteristic species of desmids, while the zooplankton community composition is unusually dominated by the large-bodied cladocerans, probably due to the high altitude and subsequent low water temperatures for a tropical lake and the lack of strict predators. The baseline data generated from this study document the present conditions against which future changes can be monitored. We further suggest that lakes Dendi, Wonchi and Ziqualla be used as reference sites in the region, providing fairly pristine conditions for assessing and/or restoring the natural state of the Bishoftu crater lakes, a group of volcanic explosion craters (which had already undergone cultural eutrophication) located southeast of Addis Ababa.

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Appendix 1 Specific methods used for the determination of alkalinity, major and trace elements, major anions and nutrients

Variable	Method	Reference
Total alkalinity	HCl titration	[62]
Total phosphorus (P_{tot})	Persulphate digestion and molybdenumblue-method	[62]
Soluble reactive phosphorus (SRP)	molybdeneblue-method	[63]
Total nitrogen (T_{tot})	Persulphate digestion, Cd red. and diazotization	[62]
Nitrate-nitrogen (NO_3-N)	Salicylic acid method	[62]
Nitrite-nitrogen (NO_2-N)	Diazotization	[64]
Ammonium-nitrogen (NH_4-N)	Sodium salicylate-hypochlorite method	[62]
Soluble reactive silica	Ammonium molybdate-EDTA method	[62]
Anions	Chromatography with suppression	[62]
Major and Trace Elements	Flame AAS and ICP OES (Perkin Elmer, Analyst 200 & Perkin Elmer Optima 5300)	[62]

Appendix 2 Physico-chemical characteristics of lakes Dendi, Wonchi and Ziqualla for the respective sampling dates. For parameters where sampling was made as a depth profile, values given are mean ± SD (n=13), for Ziqualla only data from surface samples available

Parameter	Dendi	Wonchi	Ziqualla
Secchi (m)	12.0	5.0	1.0
Ɛ (m^{-1})	0.14	0.34	1.70
Z_{eu} (m)	33.0	14.0	2.7
Conductivity (µS cm^{-1})	120 ± 6	201 ±3	78
pH	8.27 ± 0.13	8.10 ± 0.31	7.91
Chlorophyll-*a* (µg l^{-1})	0.1 ± 0.4	3.2 ± 2.5	2.2
Zooplankton density (Ind m^{-3})	13,500	35,600	50,000
NO_2-N (µg l^{-1})	1.0 ± 0.4	0.3 ± 0.2	2.4
NO_3-N (µg l^{-1})	18 ± 2	1 ± 1	15
NH_4-N (µg l^{-1})	90 ± 16	79 ± 68	48
SRP (µg l^{-1})	2.9 ± 1.1	3.4 ± 2.3	15.7
P_{tot} (µg l^{-1})	6.7 ± 1.4	8.4 ± 2.4	21.6
Alkalinity (meq l^{-1})	1.50 ± 0.01	2.32 ± 0.03	1.50
Hardness (meq l^{-1})	1.18 ± 0.03	0.53 ± 0.09	0.64
Salinity (‰)	0.10 ± 0.00	0.10 ± 0.00	0.24
Na (mg l^{-1})	7.8±0.1	42.5±0.3	12.7
K (mg l^{-1})	3.4±0.2	6.8±0.7	2.0
Ca (mg l^{-1})	14.7±0.1	8.4±0.1	17.43
Mg (mg l^{-1})	5.1±0.04	1.4±0.03	4.22
Si (mg l^{-1})	7.97 ± 0.04	3.56±0.11	2.28
Fe (mg l^{-1})	0.015 ± 0.013	0.127 ± 0.103	1.773
Mn (mg l^{-1})	0.012 ± 0.020	0.113 ± 0.102	0.116
Ba (mg l^{-1})	<0.001	<0.001	0.025
Mo (mg l^{-1})	0.009 ± 0.003	0.031 ± 0.004	<0.010
Sr (mg l^{-1})	0.081 ± 0.0004	0.020 ± 0.0005	0.065
Fluoride (mg l^{-1})	0.3±0.00	2.7±0.01	0.4
Chloride (mg l^{-1})	3.2±0.04	3.3±0.5	3.4
Sulfate (mg l^{-1})	0.9±0.01	1.09±0.04	0.15

Appendix 3 Phytoplankton species found in lakes Dendi, Wonchi and Ziqualla during the sampling period. Categories: 1-sporadic, 2-rare, 3-frequent, 4-very frequent, 5-copious

Phytoplankton	Dendi		Wonchi		Ziqualla	
Chlorophyta & Streptophyta	*Acutodesmus acuminatus*	3	*Acutodesmus acuminatus*	3	*Scenedesmus armatus*	5
	Chlorella fusca	2	*Scenedesmus armatus*	3	*Closterium praelongum*	3
	Pediastrum duplex	2	*Scenedesmus quadricauda*	3	*Closterium venus*	3
	Dictyosphaerium sp.	4	*Staurastrum pingue*	4	*Botryococcus braunii*	5
	Cosmarium contractum	2	*Staurastrum laeve*	4	*Chlorella fusca*	2
	Radiococcus polycoccus	5	*Staurastrum quadrangulare*	2		
	Ooplanctella planoconvexa	5	*Euastrum evolutum*	5		
			Cosmarium contractum	4		
			Xanthidium sp.	1		
			Elliptochloris sp.	5		
			Micrasterias crux-melitensis	4		
			Closterium praelongum	4		
			Botryococcus braunii	2		
			Pediastrum boryanum	3		
			Chlorella fusca	4		
Bacillariophyceae	*Cyclotella* sp.	1	*Navicula* sp.	2	*Navicula* sp.	3
	Nitzschia sp.	1	*Nitzschia* sp.	2	*Craticula* sp.	1
	Tabellaria sp.	1	*Diatoma* sp.	1	*Aulacoseria* sp.	2
			Cymbella sp.	2	*Pinnularia* sp.	2
			Cyclotella sp.	2	*Cymbella* sp.	1
					Gomphonema sp.	3
					Rhoicospheria abbreviata	4
Cyanobacteria	*Microcystis aeruginosa*	1	*Chroococcus limneticus*	2	*Chroococcus limneticus*	1
			Anabaena sp.	1	*Oscillatoria* sp.	1
					Scytonema sp.	1
					Microcystis aeruginosa	1
Xanthophyceae	*Xanthonema* sp.	1			*Xanthonema* sp.	1
Cryptophyta			*Cryptomonas* sp.	1		
Dinophyta	*Peridinium cinctum*	2	*Peridinium cinctum*	5	*Peridinium cinctum*	2
			Peridinium sp.2	4		
Euglenophyta	*Euglena* sp.	1				
Others	*Picoplankton*		*Picoplankton*		*Picoplankton*	

Appendix 4 Zooplankton species found in lakes Dendi, Wonchi and Ziqualla during the sampling period. Categories: 1-sporadic, 2-rare, 3-frequent, 4-very frequent, 5-copious

Zooplankton	Dendi		Wonchi		Ziqualla	
Copepoda (Post-nauplii)	*Thermocyclopes ethiopiensis*	5	*Thermocyclopes ethiopiensis*	5	*Cyclopoid- copepods*	5
Cladocera	*Daphnia magna*	3	*Daphnia longispina*	4	*Ceriodaphnia reticulata*	4
	Daphnia longispina	4	*Daphanosoma excisum*	2	*Chydorus* sp.	3
	Diaphanosoma excisum	2	*Bosmina longirostris*	3		
	Ceriodaphnia quadrangula	2	*Ceriodaphnia reticulata*	2		
			Moina micrura	2		
			Chydorus sphaericus	1		
Rotifera	*Keratella tropica*	2	*Asplanchna sieboldii*	2	*Trichocerca* sp.	5
	Trichocerca smilis	2	*Trichocerca gracilis*	2	*Lecane* sp.	3
	Polyarthra sp.	3	*Filinia longiseta*	1	*Platias* sp.	2
			Keratella cf. cochlearis	3		
			Polyarthra sp.	1		
			Brachionus caudatus	2		
Chaoboridae	*Chaoborus*-larvae	1				
Ostracoda					Ostracoda	2
Others					Water mites	1