DISSERTATION

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On the Limnology of High–mountain Tropical Crater Lakes Wonchi, Dendi and Ziqualla, Ethiopia

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"Love gives life within"

Hawaiian proverb

Dedication

To my darling Wife Hawi Belay and my parents Aregash Chewaka and Degefu Abera;
I'm grateful for your love, care and encouragement, I will forever cherish.

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Zusammenfassung

Die Seen Dendi, Wonchi und Ziqualla sind tropische, kalte Kraterseen im Hochland Äthiopiens und gehören zu den letzten ungestörten aquatischen Ökosystemen in dem Land. Aufgrund ihrer Abgeschiedenheit und der fehlenden Infrastruktur wurden diese Wasserkörper bisher nicht detailliert untersucht. Eingebettet in einer eindrucksvollen Landschaft stellen die Seen eine essentielle Komponente dar und spielen mittlerweile auch eine wirtschaftliche Rolle durch den wachsenden Zweig des Öko-Tourismus. Leider haben Investoren bereits den hohen Wert dieser Ökosysteme erkannt und weite Uferbereiche aufgekauft. Mit der vorliegenden Untersuchung erfolgte eine *status quo* – Erhebung, damit z.B. bei Bauvorhaben auf Grundlagendaten zurückgegriffen werden kann. Es gibt bereits einige Negativbeispiele in Äthiopien, bei denen Hotelbauten am Ufer von Kraterseen einen unglaublichen Eutrophierungsschub bewirkten, der nicht mehr rückgängig gemacht werden kann. Kraterseen stellen äußerst sensible Ökosysteme mit sehr langen Erneuerungszeiten des Wasserkörpers dar.

Die Seen Dendi und Wonchi dienen der Wasserversorgung für die lokale Bevölkerung inklusive Bewässerung von Feldern und für die Viehzucht; das Wasser des heiligen Sees Ziqualla steht nur für Taufen zur Verfügung und wird streng bewacht. In den späten 1990ern wurden die Seen Dendi und Wonchi mit Gewöhnlichem Karpfen (*Cyprinus carpio* L. 1758) und Tilapia (*Oreochromis niloticus* L.) besetzt, um die Fischereiwirtschaft zu etablieren und damit die lokale Gemeinschaft mit Eiweiß zu versorgen. Die Besatzarten konnten aber keine sich fortpflanzenden Populationen aufbauen. Als mögliche Gründe wurden genannt: (1) eine zu geringe Phytoplanktonbiomasse, die die eigentliche Hauptnahrung für planktivore Fische wie *O. niloticus* darstellt, (2) schädliche Gase und Salze aus vulkanischer Tätigkeit und (3) keine geeigneten Laichplätze. Bislang existieren keinerlei limnologische Studien, die diese Schlussfolgerungen unterstützen.

Schwerpunkt der vorliegenden Studie ist eine limnologische Beschreibung dieser abgelegenen Hochgebirgskraterseen. Zwei Probenahme-Serien stellen die Basis dar, die auch für ein zukünftiges Monitoring genutzt werden sollen. Mit dieser Datenerhebung wurde eine Basis geschaffen, um zukünftige biologische Veränderungen und Umwelteinflüsse zu erkennen. Im Wonchi-See wurden die saisonale Dynamik, Zusammensetzungen und Biomasse des Phyto- und Zooplanktons mit limnologischen Kenngrößen verglichen. Zudem liefert diese Studie plausible Erklärungen, warum die Nil-Tilapia im Wonchi-See keine sich fortplanzenden Populationen aufbauen konnte.

Im Rahmen der Studie wurde der Wonchi-See in zweiwöchigen Intervallen von Dezember 2011 bis Jänner 2013 an einer Freiwasserstation untersucht (Wassertiefe: 50 m, GPS-Koordinaten: 08°48'035"N and 37°53'592"E). Aus den Wasserproben wurden Artzusammensetzung und -biomasse des Phyto- und Zooplanktons bestimmt und mit physikalisch-chemischen Parametern verschnitten.

Die erste Studie fokussiert sich hauptsächlich auf deskriptive und vergleichende Limnologie der drei bedrohten Hochgebirgskraterseen Dendi, Ziqualla und Wonchi. Die Ergebnisse zeigen, dass alle drei Seen zwar keine erkennbaren Oberflächenabflüsse haben, aber dennoch nur geringe Ionenkonzentrationen aufweisen, die über die gesamte Wassersäule ähnlich verteilt sind (Kationen hauptsächlich Na^+/K^+, Anionen HCO_3^-). Die Sauerstoffabnahme in größeren Tiefen geht mit gesteigerten Konzentrationen von reduzierendem Fe und Mn einher, was auf das Vorkommen unterirdischer Quellen hindeutet. Basierend auf Nährstoffen, Chlorophyll *a* und Wassertransparenz können die Seen Dendi und Wonchi als oligotroph, der Ziqualla-See als oligo-mesotroph eingestuft werden. Typisch für unbelastete bis wenig eutrophierte Wasserkörper, wurde die Phytoplanktongemeinschaft in den Seen Dendi und Wonchi von kokkalen Grünalgen, Desmidiaceen und Dinoflagellaten dominiert, während chlorokokkale Algen, insbesondere *Botryococcus braunii* und benthische Diatomeen im seichten, mit Makrophyten durchsetzten Ziqualla-See vorherrschten. Die Zooplankton-Fauna war unterentwickelt und bestand aus 11 Rotatorien- und 13 Crustaceen-Taxa. In allen drei Seen bildeten Copepoden die größte Gruppe und trugen mehr als 60% zur Gesamtbiomasse des Zooplanktons bei, gefolgt von Cladoceren und Rotatorien. Aufgrund unserer Ergebnisse können diese Seen als schützenswerte und nährstoffarme Hochgebirgsseensysteme charakterisiert werden, die Biota wie Desmidiaceen und Daphniden beheimaten, die empfindlich auf Eutrophierung reagieren würden.

Die zweite Studie wurde zwischen Dezember 2011 und Jänner 2013 im Wonchi-See durchgeführt und liefert erste Daten der Phytoplankton-Dynamik mit den zugrunde liegenden Schlüsselparametern. Die Ergebnisse deuten auf eine Limitierung durch gelöste anorganische Nährstoffe hin mit jährlich gemittelten Konzentrationen von gelöstem reaktiven Phosphor (SRP) 2.4 µg L^{-1}, Totalphosphor (TP) 6.0 µg L^{-1} und gelöstem anorganischen Stickstoff (DIN) 92.4 µg L^{-1}, wobei hier interessanterweise Ammonium den Großteil stellt (> 90% des DIN).

Die Phytoplankton-Zusammensetzung besteht aus 53 Taxa aus fünf taxonomischen Großgruppen. Die Taxa konnten 15 funktionellen Einheiten zugeordnet werden. Eine partielle Atelomixis in Kombination mit auffällig niedrigen Nährstoff- Konzentrationen scheint die grundlegend treibende Kraft für die Struktur der Phytoplanktongemeinschaft im Wonchi-See zu sein. Die Community ist divers mit großen und relativ schweren und unbeweglichen, schnell sinkenden planktischen Desmidiaceen, die der N_A–Gruppe angehören (61% des gesamten Biovolumens) gefolgt von den Diatomeen (MP–Gruppe, welche 13% des Biovolumens ausmacht). Während der Nährstofflimitation im Dezember (kurz vor Umwälzung des Wasserkörpers) herrschte eine beinahe mono-spezifische Blüte von *Peridinium cinctum* (Gruppe Lo) vor, die später durch die funktionellen Codons F–J ersetzt wurden. Letztere wurden während des weiteren Beobachtungszeitraumens fortwährend von der Zusammensetzung N_A ersetzt. Die positive Korrelation zwischen Chlorophyll a und der Zooplanktonbiomasse (r = 0.482, N = 20, p = 0.037) zeigt einen "Bottom up"-Effekt an (die Menge der Algen steuert die Zooplanktonzahlen).

Die dritte Studie beschäftigte sich mit der Zooplankton-Zusammensetzung und der Biomasse, welche über siebzehn Monate mit möglichen ökologischen Einflussfaktoren verschnitten wurden. Im Wonchi-See zeigt die Zooplanktongemeinschaft eine moderate Artenzahl von vierzehn Taxa (sechs Cladoceren-, eine Copepoden- und sieben Rotatorienarten). Der Simpson's Diversitätsindex mit Werten zwischen 0.6 und 0.8 deutet klar in Richtung eines homogenen Taxavorkommens zwischen den Probenterminen hin. Die gesamte gemittelte Biomasse (±SD) des Zooplanktons betrug rund 62 ± 26 mg m^{-3} Trockenmasse, was im Vergleich zu anderen Hochland- und Grabenbruchseen in Äthiopien sehr niedrig erscheint. Der cyclopoide Copepode *Thermocyclops ethiopiensis* ist das häufigste Taxon und trägt zu mehr als 50% zur Gesamtzooplanktonabundanz bei, gefolgt von Cladoceren (38%) und Rotatorien (12%). Eine nicht-metrische multidimensionale Skalierung ergab ein 3-dimensionales Modell mit generell ähnlicher Zusammensetzung der Gemeinschaft; Ausnahmen bildeten die Monate Dezember/Jänner und Mai. Temperatur, Alkalinität, Leitfähigkeit und Nitrat-N haben einen signifikanten Einfluss auf saisonale Muster. Die signifikante positive Korrelation (r = 0.482, N = 20, p = 0.037) zwischen Chlorophyll a und Zooplanktonbiomasse spiegelt den „Bottom-up-Effekt" des Phytoplanktons auf die Zooplanktondynamik wider. Die vertikale Verteilung des Zooplanktons im Wonchi-See deutet eine Trennung der Wassersäule in Epi- und Metalimnion an. Die Ergebnisse zeigen, dass intensive, interspezifische Konkurrenz und nicht Räuber-Beute Beziehungen zwischen Fischen und Zooplanktern der Schlüsselfaktor für die vertikale Zooplanktonverteilung im Lake Wonchi sind.

Die vierte Studie beurteilt die Wachstumseffizienz von zwei indigenen Stämmen juveniler Nil-Tilapien aus geographisch abgelegenen Hochland-Regionen, welche in Käfig-Kulturen gehältert wurden. Diese Studie wurde durchgeführt, um plausible Erklärungen zu liefern, wieso die Besetzung mit *O. niloticus* im Wonchi-See nicht erfolgreich war und sich keine fortpflanzenen Populationen etablieren konnten. Unter den untersuchten Fischstämmen variierte das Wachstum nicht signifikant (t-test, $P > 0.05$), obwohl der HS-Stamm (± SD) ein höheres gemitteltes Endgewicht (25.6 ± 1.1 g pro Individuum) im Vergleich zum DZ-Stamm erreichte (20.5 ± 1,1 g).

Für den HS-Stamm betrug die Netto Gewichtszunahme und tägliches Fischwachstum pro Fisch 23.2 g und 0.2 g d^{-1} beziehungsweise 18.5 g und 0.1 g d^{-1} für den DZ-Stamm. Während der Aufzucht war die Überlebensrate aller experimenteller Fischstämme niedriger als 80% und wies keine signifikanten Unterschiede auf (ANOVA, $P > 0.05$). Alle physikalischen und chemischen Parameter deuten auf eine mögliche Etablierung einer *O. niloticus*-Population im Lake Wonchi hin, einzig die Wassertemperatur ist mit einer jährlichen Durchschnittstemperatur von 15.6° C für eine eurytherme Fischart wie Tilapia sehr tief.

Abstract

Lakes Dendi, Wonchi and Ziqualla are cold–water tropical high–mountain crater lakes in Ethiopia and are among the few remaining patches of undisturbed aquatic ecosystems in the country. They have never been investigated reliably owing to seclusion and lack of infrastructure. Nevertheless, the lakes offer a pristine environment in a beautiful landscape and play a significant economic role through increasing eco-tourism. Unfortunately, this fact was also recognized by investors thus land-grabbing increasingly becomes a serious problem for these areas. Lakes Dendi and Wonchi provide freshwater for drinking, back-yard irrigation and livestock watering to the local communities, while Lake Ziqualla is “holy” and the water is used exclusively for baptizing. Lake Ziqualla is highly protected by a local monastery. Dendi and Wonchi were stocked with common carp (*Cyprinus carpio* L. 1758) and Tilapia (*Oreochromis niloticus* L.) fish in late 1990s in an attempt to establish pelagic fishery and increase availability of protein for the local communities. However, the latter species did not establish breeding populations. For this phenomenon, three hypotheses are proposed: (1) too low plankton biomass, which is the main food source for planktivorous fish like *O. niloticus* and (2) poor water quality due to dissolved volcanic gases and salts and (3) limited spawning grounds. Nevertheless, there exist no quantitative data and rigorous studies oriented towards this implication nor are there any limnological investigations in these lakes to the best of our knowledge.

Objectives of the study were to provide a first morphometric and limnological description of these fairly pristine tropical high–mountain crater lakes during two sampling campaigns, with the aim of establishing baseline data against which future environmental and biological changes can be monitored and assessed. Moreover, we were interested in seasonal dynamics, abundance and biomass of the pelagic community in relation to the underlying limnological variables in Lake Wonchi. Besides, the study provides plausible explanations as to why the introduced fish Nile Tilapia was unable to inhabit and establish successful breeding populations in Lake Wonchi. The study in Lake Wonchi was carried out on a fortnightly basis between December 2011 and January 2013 at an open–water station marked with GPS (depth: 50 m, coordinates: 08°48’035”N and 37°53’592”E). Species composition, abundance and biomass of phyto– and zooplankton along with physico–chemical parameters were determined from net and integrated water samples.

The first investigation focused on the description and comparison of the limnology of lakes Dendi, Ziqualla and Wonchi. The results showed that all the lakes have no obvious surface outflow, but generally showed low concentrations of ions, displaying an equal distribution of readily soluble components like Na or K throughout the water column. We recognized distinct oxygen depletion in greater depths, which is linked to raising concentrations of reducing Fe and Mn pointing at subterraneous springs. Based on nutrients, chlorophyll *a,* and water transparency, lakes Dendi and Wonchi are classified as oligotrophic, whilst Ziqualla is oligo-mesotrophic. The phytoplankton community is dominated by coccal green algae, desmids and dinoflagellates in lakes Dendi and Wonchi, as 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 cladocerans and rotifers. Owing to the results, 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.

The second study provides a first record on long-term phytoplankton seasonal dynamics conducted between December 2011 and January 2013 including the underlying key environmental drivers in Lake Wonchi. Owing to the results, dissolved inorganic nutrient levels indicated oligotrophic conditions with ammonium being the dominant inorganic nitrogen form. The phytoplankton communities comprised 53 taxa distributed in five taxonomic divisions, which could be assigned to 15 codons based on the phytoplankton functional group classification. In Wonchi, as typical in other deep high–mountain tropical lakes, partial–atelomixis combined with the apparent low dissolved inorganic nutrient concentrations seem to be a fundamental driving force in structuring phytoplankton community composition, which was quite stable and characterized by high diversity of heavy, immobile and fast-sinking planktonic desmids of the N_A–codon (61% of the total biovolume) during mixis followed by diatoms MP–codon contributing 13% to the total biovolume. A near–monospecific bloom of *Peridinium cinctum* (Lo–codon) prevailed before the onset of lake turnover in December 2011 in conditions of nutrient–depletion, which was later followed by the functional groups F–J during the episode of complete mixing and then perpetually replaced by the functional group N_A. Non-metric multi-dimensional scaling resulted in a 2-dimensional solution, which revealed clear segregation of phytoplankton community to four groups. Mixing regime of the water column, specific conductivity, total phosphorus and ammonium had significant influence on the observed seasonal pattern. The strong positive relationship between chlorophyll *a* and zooplankton biomass points to bottom-up of zooplankton. Hence, the study demonstrated the significance of phytoplankton autecology for monitoring the ecological status of tropical aquatic ecosystems as it is already well-established in temperate regions.

The third study presents a first study on zooplankton taxa composition, abundance and biomass conducted over an extended period of seventeen months including underlying environmental drivers. In Lake Wonchi, the zooplankton community composition showed moderate species richness comprising a total of fourteen taxa with six cladocerans, one copepod and seven rotifers. Simpson´s index of diversity with values between 0.6 and 0.8 clearly pointed towards a homogenous taxa occurrence within the single sample units. The overall mean (±SD) standing biomass of zooplankton was 62 ± 26 mg dry mass m^{-3}, which is low compared to other highland and rift valley lakes in Ethiopia. Cyclopoid copepods, in particular *Thermocyclops ethiopiensis* were the most abundant group and contributed 50% to the total zooplankton abundance followed by cladocerans (38%) and rotifers (12%). Non-metric multi-dimensional scaling resulted in a 3-dimenensional model, which revealed similar community composition on successive sampling dates except in December/January and May. Temperature, alkalinity, conductivity and nitrate-N had significant influence on this seasonal pattern. A weak, but significant positive correlation ($r = 0.482$, $N = 20$, $p = 0.037$) between chlorophyll *a* and zooplankton biomass mirrors a bottom-up effect of phytoplankton biomass on zooplankton dynamics. Zooplankton of Lake Wonchi displayed some degree of segregation along the epi– and metalimnion during this study. The results show that intense interspecific competition, rather than fish predation, is the key factor structuring the vertical distribution of zooplankton.

The fourth study involved the evaluation of growth performance of two indigenous strains of juvenile Nile Tilapia, *O. niloticus* (L.) collected from geographically isolated regions at highland environment (Lake Wonchi) under cage culture system between July 2012 and January 2013. This study was mainly conducted to substantiate and provide plausible explanations as to why the introduced fish *O. niloticus* was unable to inhabit and/or establish successful breeding populations in Lake Wonchi. The growth of fish varied less significantly (t-test, $P > 0.05$) among the strains, although HS-strain had a higher mean (± SD) final individual size (25.6 ± 1.1 g) than DZ-strain (20.5 ± 1.1 g). The net weight gain and daily growth rate per fish were 23.2 g and 0.2 g d^{-1} for HS-strain, and 18.5 g and 0.1 g d^{-1} for DZ-strain, respectively. HS-strain was found to be in better condition than DZ-strains, which is in accordance with the relative superior growth rate of the former strain. Survival rate of fish in both treatments was below 80% and did not differ significantly (ANOVA, $P > 0.05$) among the experimental strains throughout the culture period. All the physical and chemical parameters were in the favourable range for *O. niloticus* culture except the water temperature which is very low (annual mean 15.6 ^{O}C) for the eurythermal fish species to feed and reproduce in Lake Wonchi.

Thesis outline

This dissertation summarizes the results of a doctoral study conducted in three highly threatened tropical high–mountain crater lakes in central highlands of Ethiopia which have never been investigated before. The main purpose of the research was to present first data on limnological features and biotic communities and understand the current condition of lakes Dendi, Wonchi and Ziqualla which serves as *status quo* against which future changes can be monitored. Moreover, we addressed the importance of conserving these fabulous aquatic ecosystems as surrogate reference sites, providing fairly pristine conditions for assessing and/or restoring comparable but already eutrophicated aquatic ecosystems in the region. The first chapter focuses mainly on a snapshot comparative study of the limnology of three highly threatened tropical high–mountain crater lakes Dendi, Ziqualla and Wonchi. The latter being the main study lake and the focus of this dissertation. Chapter 2 – 4 describe the detail research carried out between December 2011 and January 2013 on Lake Wonchi. These chapters are presented in form of publication papers which are submitted for publication in international peer-reviewed journals:

Chapter 1. A Comparative study of the limnology of three highly threatened tropical high–mountain crater lakes in Ethiopia– Implications for conservation. Accepted on 04/06/2014, Journal of Tropical Conservation Science.

Chapter 2. Phytoplankton communities of tropical high– mountain crater lake Wonchi, Ethiopia. Submitted to Journal of Plankton Research.

Chapter 3. Zooplankton abundance, species composition and ecology of tropical high–mountain crater Lake Wonchi, Ethiopia. Submitted to Journal of Limnology.

Chapter 4. Evaluation of growth performance of two indigenous strains of juvenile Nile tilapia, *Oreochromis niloticus* (L.) collected from geographically isolated regions at highland environment under cage culture system. Ready for submission to Journal of Aquaculture.

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General Introduction

Limnological studies in tropical African dates back to early 20th century when the British led short–term expeditions of the fisheries and limnology of lakes in Eastern Africa began between 1927 and 1928 (Graham, 1929; Worthington and Worthington, 1933). Yet, African lakes have been investigated only sporadically compared to their temperate counterparts (Ganf, 1975; Talling and Talling, 1965). This is mainly true for the high-mountain crater lakes in Ethiopia, although the Bishoftu crater lakes, a group of volcanic explosion craters in the vicinity of Debre-Zeit city some 50 km southeast of Addis Ababa have been comparatively well represented in literature owing to their geographic location and opportunities for comparative studies (Baxter *et al*. 1965; Prosser *et al*. 1968; Green, 1986; Belachew *et al*. 2012). Hydrochemistry of these lakes documented in earlier studies by Prosser *et al*. (1968), Teferra (1980), Wood and Talling (1988) and Gebre-Mariam (1994) suggest intermediate concentration of solutes, whereas the phytoplankton associations described by Talling *et al*. (1973), and Wood and Talling (1988), 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 (1968) and (Lemma, 1994, 2008). In recent years human pressures have impacted limnological features of the Bishoftu lakes (Lemma, 2002; Belachew *et al*. 2012). For instance, a significant decrease in the phytoplankton biomass and change from the mono-specific community of *Arthrospira fusiformis,* whose production previously attained the theoretical maxima of phytoplankton production for natural lakes (Talling *et al*. 1973) towards other cyanobacteria taxa such as *Anabaenopsis elenkinii* and *Chroococcus minutus* from the alkaline Lake Arenguade has been reported (Belachew *et al*. 2012). Moreover, increased eutrophication and even a mass fish kill have been reported (Teshome, 2011).

In contrast to such a remarkable build-up of literatures on the Bishoftu crater lakes, which are easily accessible, very little is known of the remote high-altitude crater lakes of Ethiopia

(Tudorancea and Taylor 2002). 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 (Löffler, 1972; Roldan-Perez, 1992; Umana, 2001). Besides, crater lakes can accumulate volcanic gases (e.g. the tragic emission of CO_2-gas from Lake Nyos in the Oku volcanic field of Cameroon), which poses serious health risk to humans (Kling, 1988; Löhr *et al*. 2005). The only detailed limnological investigations on the highland tropical crater lakes in Ethiopia was reported very recently from lake Hayq (Fetahi, 2011), focusing on food webs and energy flows and the underlying limnological variables. This study demonstrated a remarkable shift of the lake towards eutrophic conditions and subsequent mass fish kill during the episode of lake turnover (Fetahi *et al*. 2011). Apparently, the three crater lakes Dendi, Wonchi and Ziqualla in the central highlands of Ethiopia (located above 2800 m a.s.l.), situated only within 100 km radius from Addis Ababa have never been investigated reliably owing to seclusion and lack of infrastructure. Paradoxically, the latter two were stocked with common carp (*Cyprinus carpio* L. 1758) and Tilapia (*Oreochromis niloticus* L.) fish in late 1990s in an attempt to establish pelagic fishery. However, a fisheries survey by National Fisheries and Other Aquatic Life Research Center, has reported that the later species did not establish breeding populations, hypothesizing that low plankton biomass, which is the main food source for planktivorous fish like *O. niloticus* could be a cause. Nevertheless, there exist no quantitative data and rigorous studies oriented towards this implication nor are there any limnological investigations in these lakes to the best of our knowledge.

Tropical highland crater lakes are broadly known to exibit a warm–monomictic mixing regime and atelomictic events in the deep lakes of the volcanic ridge (Löffler, 1972; Roldán, 1992; Sánchez, 2001; Umana, 2001; Tavera and Martínez-Almeida, 2005). This physical process, mainly in a tropical high–mountain lakes is induced by high diel thermal heterogeneity and is recently reported to be a key driver in structuring phytoplankton assemblages and intuitively their seasonal succession, though other factors such as the availability of resources and light may take precedence (Barbosa and Padisăk, 2002; Reynolds, 2006; Zhang *et al*. 2007; Souza *et al*. 2008; Becker *et al*. 2010; Fetahi *et al*. 2014). However, the knowledge of such physical variables and the subsequent effect on phytoplankton dynamics in tropical–African high–mountain lakes, in particular in Ethiopia is meagre (Fetahi *et al*. 2014). Similarly, zooplankton research of Ethiopian lakes has been conducted earlier (e.g. Bryce, 1931; Cannicci and Almagia, 1947), yet our contemporary knowledge is far from complete. Former studies were based mainly on samples collected by expeditions, and thus provided scanty information on long-term patterns in their seasonality and dynamics. Moreover, these expeditions were predominantly focused on rift valley and Bishoftu crater lakes owing to their geographic location and opportunity for comparative studies (Tudorancea and Taylor, 2002). Therefore, no qualitative and quantitative data exist as well on the zooplankton of lakes Dendi, Wonchi and Ziqualla to the best of our knowledge. Apparently, Dejen *et al*. (2004) note that the zooplankton community composition of the highland lake Tana in Ethiopia harbours both temperate and tropical species possibly due to the high altitude at which the lake is located and the subsequent low water temperatures for a tropical lake, demonstrating the high biodiversity of tropical highland lakes compared with lakes at similar latitude in the lowland. Moreover, it is now well established that zooplankton plays a key role in channeling the transfer of energy from the primary producers to secondary consumers in aquatic ecosystems (Lampert and Sommer, 1997). Therefore, holistic understanding of zooplankton dynamics in aquatic ecosystems has an implication for a good prediction of fish yield (Melack, 1976; Tilahun and Ahlgren, 2009). Hence, this study is the first to describe the lakes and discuss the various proposed hypotheses through investigating the temporal, spatial and seasonal variations of plankton communities along with their environmental variables. The baseline information generated from this study serves as *status quo* against which future changes can be monitored. Moreover, we addressed the importance of conserving these fabulous aquatic ecosystems as surrogate reference sites, providing fairly pristine conditions for assessing, monitored and/or restoring comparable but already eutrophicated aquatic ecosystems in the region.

Aim of the study

The overall objective of this study is to provide for the first time morphometric and limnological data of the high–mountain crater lakes in the central highlands of Ethiopia which have never been investigated with due emphasis on phyto– and zooplankton including the underlying environmental variables. Besides, the study provides plausible explanations as to why the introduced fish Nile Tilapia (*Oreochromis niloticus*) was unable to inhabit and establish successful breeding populations in Lake Wonchi. To achieve these broad objectives, the investigations were guided by the following specific objectives:

- To describe and provide morphometric and limnological data on lakes Dendi and Ziqualla
- To investigate the vertical and temporal variations of physico-chemical environmental variables, elements and trace elements, major anions and dissolved inorganic nutrients in Lake Wonchi
- To determine seasonal variations in phytoplankton species composition and community structure of Lake Wonchi
- To determine phytoplankton abundance and biomass in relation with the underlying environmental variables in Lake Wonchi
- To determine seasonal variations in zooplankton species composition and community structure of Lake Wonchi
- To determine zooplankton abundance and biomass in relation with the underlying environmental variables in Lake Wonchi
- To determine the vertical distribution of zooplankton in lake Wonchi
- To identify key environmental and biological variables which are responsible to structure the vertical distribution of zooplankton in lake Wonchi
- To define the trophic state of Lakes Dendi, Ziqualla and Wonchi
- To evaluate growth performance of two indigenous strains of juvenile Nile tilapia, collected from geographically isolated regions under cage culture system in Lake Wonchi
- To construct the bathymetric map of Lake Wonchi

Guiding questions

- What is the phyto– and zooplankton composition of lakes Dendi, Ziqualla and Wonchi?
- Are there any similarities and/or differences in morphometric and limnological features among the high-mountain crater lakes Dendi, Ziqualla and Wonchi?
- Are there spatio-temporal variations in physico-chemical environmental variables, major ions and dissolved inorganic nutrients in Lake Wonchi? What causes them?
- Are there any pollutant volcanic gasses and ions in Lake Wonchi?
- Do phyto– and zooplankton composition of Lake Wonchi fluctuate on seasonal scale?

- Are there temporal and spatial variability in phytoplankton abundance and biomass in Lake Wonchi? What causes them?
- To what extent do limnological conditions affect the abundance, structural and biomass of phytoplankton in the lake?
- Do zooplankton abundance and biomass in Lake Wonchi vary with time and in space?
- Why the introduced juveniles of Nile tilapia (*Oreochromis niloticus*) did not establish successful breeding populations in the lake?
- What is the trophic state of lakes Dendi, Ziqualla and Wonchi?

Study justification

Although limnological studies in Ethiopia date back to early 20th centuries, it has focused almost exclusively on the rift valley and Bishoftu crater lakes, which are easily accessible (Tudorancea and Taylor, 2002), and hence highland lakes have been investigated only sporadically (Fetahi, 2010). Nevertheless, the highlands of Ethiopia represent some of the remnants of undisturbed aquatic ecosystems; they are however highly threatened by significant socio–economic developments and associated anthropogenic impact. Lakes Dendi, Wonchi and Ziqualla, are among the few remaining fairly pristine high–mountain crater lakes in the central highlands and have never been investigated reliably owing to seclusion and lack of infrastructure. Sadly, 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 mainly focuses on the development of an 'integrated touristic, residential, commercial and recreational resort by the lake' (www.dendilake.com). Lake Wonchi is also becoming a touristic 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 do not only displace and evict riparian communities; they also stop the tradition of local people for keeping conservation and sustainable management of natural resources and jeopardize aquatic biodiversity. 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 (Ayenew and Legesse, 2007; Belachew *et al*. 2012). The current scenario of the Bishoftu and rift valley lakes in Ethiopia warrant that future developments merit Environmental Impact Assessment (EIA) including investigations of aquatic biodiversity. Lakes Wonchi and Dendi, cold–water tropical highland lakes in Ethiopia, were stocked with common carp (*Cyprinus carpio* L. 1758) and Tilapia (*Oreochromis niloticus* L.) fish in late 1990s in an attempt to establish pelagic fishery. However, the latter species did not establish breeding populations, and there have been speculations that low plankton biomass, which is the main food source for planktivorous fish like *O. niloticus* and low water temperatures could be a cause. Nevertheless, there exist no data and rigorous studies oriented towards this implication nor are there any limnological investigations in these lakes to the best of our knowledge. Therefore, this study is the first to discuss about these hypotheses through investigating the temporal, spatial and seasonal dynamics of plankton in relation with the underlying environmental variables on seasonal scale. Moreover, this research effort would addressed the importance of conserving these sensitive aquatic ecosystems as surrogate reference sites, providing fairly pristine conditions for assessing and/or restoring comparable but already eutrophicated aquatic ecosystems in the region.

References

Ayenew T., Legesse D., 2007. The changing face of the Ethiopian rift lakes and their environs: call of the time. *Lakes & Reservoirs: Research & Management* 12: 149-216.

Barbosa F.A.R., Padisák J., 2002. The forgotten lake stratification pattern: atelomixis. *Verh. Int. Ver. Limnol.* 28:1385-1395.

Baxter R.M., Prosser M.V., Talling J.F., Wood R.B., 1965. Stratification in tropical African lakes at moderate altitude (1500-2000 m). *Limnol. Oceanogr.* 10:510-520.

Becker V., Caputo L., Ordonez J., Marce R., Armengol J., Crossetti L.O., Huszar V.L.M., 2010. Driving factors of the phytoplankton functional groups in a deep Mediterranean reservoir. *Water Research* 44: 3345–3354.

Belachew M., Kifle D., Jebessa H., 2012. Deep underwater seismic explosion experiments and their possible ecological impact-The case of Lake Arenguade-Central Ethiopian highlands. *Limnological* 42: 212-219.

Bryce D.L., 1931. Report on the Rotifera: Mr. Omer-Cooper's investigation of the Abyssinian freshwater (Dr. Hugh Scott Expedition). Proceeding of the zoological Society of London: 865-878.

Cannicci G., Almagia F., 1947. Notizie sulla "Facies" planctonica di alcuni laghi della Fossa Galla. Boll. Pesca Piscicolt. *Idrobiol*. 2: 54–77.

Dejen E., Vijverberg J., Nagelkerke L.A.J., Sibbing F.A., 2004. Temporal and spatial distribution of microcrustacean zooplankton in relation to turbidity and other environmental factors in a large tropical lake (L. Tana, Ethiopia). *Hydrobiologia* 513: 39–49.

Fetahi T., Mengistu S., Schagerl M., 2011. Zooplankton community structure and ecology of the tropical-highland Lake Hayq, Ethiopia. *Limnologica* 41: 389-397.

Fetahi T., Schagerl M., Mengistu S., 2014. Key drivers for phytoplankton composition and biomass in an Ethiopian highland lake. *Limnologica* 46:77-83.

Ganf G.G., 1974c. Phytoplankton biomass and distribution in a shallow, equatorial lake (Lake George, Uganda). *Oecologia* 16: 9-24.

Grahm M., 1929. The Victoria Nyanza and its fisheries. Crown Agents for the Colonies, London.

Green J., 1986. Zooplankton associations in some Ethiopian Crater lakes. *Freshw. Biol.* 16:495-499.

Kling G.W., 1988. Comparative transparency, depth of mixing, and stability of stratification in lakes of Cameroon, West Africa. *Limnol. Oceanogr.* 33: 27-40. Amsterdam.

Lampert W., Sommer U., 1997. Limnoecology: The Ecology of Lakes and Streams. Oxford University Press, New York.

Lemma B., 1994. Changes in the limnological behavior of a tropical African explosion crater lake: Lake Hore-Kilole, Ethiopia. *Limnological* 24: 57-70.

Lemma B., 2008. Observations on the relations of some physico-chemical features and DVM of *Paradiaptomus africanus* in Lakes Bishoftu-Guda and Hora-Arsedi, Bishoftu, Ethiopia. *Limnologica* 39: 230-243.

Löffler H., 1972. Contribution to the limnology of high mountain lakes in Central America. *Int. Revue ges. Hydrobiol*. 57: 397- 408.

Löhr A., Bogaard T., Hikes A., Hendriks M., Sumartis S., Bergen vM., Kees CAM., Gestel K., Straalen vN., Vroon P., Widianarko B., 2005. Natural pollution caused by the extremely acidic crater Lake Kawahljen, East Java, Indonesia. *Environ Sci Pollut Res* 12: 89-95.

Melack J.M., 1978. Morphometrical, physical and chemical features of the volcanic crater lakes of western Uganda. *Arch. Hydrobiol.* 84: 430-453.

Prosser M.V., Wood R.B., Baxter R.M., 1968. The Bishoftu crater lakes: a bathymetric and chemical study. *Arch. Hydrobiol.* 65: 309-324.

Reynolds C., 2006. Ecology of phytoplankton. Cambridge University press, Cambridge: pp. 535-539.

Roldan-Perez G., 1992. Fundamentos de limnologia tropical. Universidad de Antioquia, Colombia.

Sánchez M., 2011. Variaction de la clorofila ‘a’ fitoplanctónica y sus mecanismos de control en un lago atalasohalino tropical. Tesis de Maestría en Ciencias del Mar y Limnología. Instituto de Ciencias del Mar y Limnología, UNAM, Mexico: 66 pp.

Souza M.B., Barros C.F.A., Barbosa .F, Hajnal E., Pádisak J., 2008. Role of atelomixis in replacement of phytoplankton assemblages in Dom Helvécio Lake, South-East Brazil. *Hydrobiologia* 607:211-224.

Talling J.F., Talling I.B., 1965. The chemical composition of African lake water. Internationale Revue Der Gesamten. Hydrobiologia 50: 421-463.

Talling J.F., Wood R.B., Prosser M.V., Baxter R.M., 1973. The upper limit of photosynthetic productivity by phytoplankton: evidence from Ethiopian soda lakes. *Freshw. Biol.* 3: 53-76.

Tavera R., Martinez-Almeida V., 2005. Atelomixis as a possible driving force in the phytoplankton composition of Zirahuén, a warm-monomictic tropical lake. Hydrobiologia 533: 199-208.

Teferra G., 1980. A limnological study on Lake Chelekleka. *SINET: Ethiop. J. Sci.* 3: 143-152.

Teshome K., 2011. The temporal variations in physico-chemical characteristics, planktonic biomass, diversity and primary productivity in three crater lakes in Ethiopia. M.Sc. Thesis. University of Bremen, Germany.

Tilahun G., Ahlgren G., 2010. Seasonal variations in phytoplankton biomass and primary production in the Ethiopian Rift Valley lakes Ziway, Awasa and Chamo-The basis of fish production. *Limnologica* 40: 330-342.

Tudorancea C., Taylor W.D., 2002. Ethiopian Rift Valley Lakes. Backhuys publisher: Leiden, Netherlands.

Umana V.G., 2001. Limnology of Boots Lake, a tropical crater lake in Costa Rica. *Rev. Biol. trop* 49: 1-10.

Wood R.G., Talling J.F., 1988. Chemical and algal relationships in a salinity series of Ethiopian inland waters. *Hydrobiologia* 158: 29-67.

Worthington E.B., Worthington S., 1933. Inland Waters of Africa. Macmillan. 259 pp.

Zinabu G-M., 1994. Long-term changes in indices of chemical and productivity status of a group of tropical Ethiopian lakes with differing exposure to human influence. *Arch. Hydrobiol.* 132: 115-125.

Chapter 1

A Comparative study of the limnology of three highly threatened tropical high–mountain crater lakes in Ethiopia– implications for conservation

From top to down:

Ziqualla, Dendi and Wonchi, Ethiopia January 2012–

'Breathtaking hidden treasures'

Chapter 1

A Comparative study of the limnology of three highly threatened tropical high-mountain crater lakes in Ethiopia

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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 their remote location. This study provides a first limnological description of these pristine tropical high-mountain crater lakes, with the aim of establishing baseline data against which future environmental and biological changes can be monitored. The lakes are located above 2800 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 raising concentrations of Fe and Mn, which points at subterraneous 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, as 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. Owing to the results, 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. Nevertheless, these lakes are currently exposed to complex human interference such as shoreline and crater rim modifications, water abstraction, land grabbing and recreational uses.

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

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 located around 50 km southeast of Addis Ababa [1, 2]. Hydrochemistry of these lakes documented in earlier studies by Prosser *et al*. [2], Teferra [3], Wood and Talling [4] and Gebre-Mariam [5] suggest intermediate concentration of dissolved inorganic nutrients and ions. Concurrently, phytoplankton associations described by Baxter and Wood [6], Talling *et al*. [7], Wood and Talling [4], Gebre-Mariam [5] and Gebre-Mariam and Taylor [8] 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 [9] and Lemma [10]. In recent years human pressures have impacted limnological features of the Bishoftu lakes [11-13]. For instance, a significant decrease in the phytoplankton biomass and change from the mono-specific community of *Arthrospira fusiformis,* whose production previously attained the theoretical maxima of phytoplankton production for natural lakes [7] towards other cyanobacteria taxa such as *Anabaenopsis elenkinii* and *Chroococcus minutus* from the alkaline Lake Arenguade has been reported [12, 13]. Moreover, increased eutrophication and even a mass fish kill have been reported [13-14].

In contrast to such a remarkable build-up of literature on the Bishoftu crater lakes, which are easily accessible, very little is known of the remote high-altitude crater lakes of Ethiopia [15]. 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 [16-18]. Besides, crater lakes can accumulate volcanic gases (e.g. the tragic emission of CO_2-gas from Lake Nyos in the Oku volcanic field of Cameroon), which poses serious health risk to humans [19-20]. Recently, detailed limnological investigations on the highland tropical crater lake Hayq have been initiated in Ethiopia [21-22] 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 only within 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 mainly focuses on the development of an 'integrated touristic, residential, commercial and recreational resort by the lake' (www.dendilake.com). Lake Wonchi is also becoming a touristic 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 do not only displace and evict riparian communities; they also stop the tradition of local people for keeping conservation and sustainable management of natural resources and jeopardize aquatic biodiversity. 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 [13, 23]. The current scenario of the Bishoftu and rift valley lakes in Ethiopia warrant that future developments merit Environmental Impact Assessment (EIA) including investigations of aquatic biodiversity. Therefore, this study aims to present first data on limnological features and biotic communities of lakes Dendi, Wonchi and Ziqualla. The baseline information generated from this study serves as *status quo* against which future changes can be monitored. Moreover, we addressed the importance of conserving these sensitive aquatic ecosystems as surrogate reference sites, providing fairly pristine conditions for assessing and/or restoring comparable but already eutrophicated 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 highly protected by monks; 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. The region is characterized by sub-humid climate with an annual rainfall of around 1200 mm. The main rainy season extends from May to September (National Meteorological Service Agency of Ethiopia), and diel air temperature varies from 14 to 26 °C during the day time and falls below 10 °C in the night (Fig. 1).

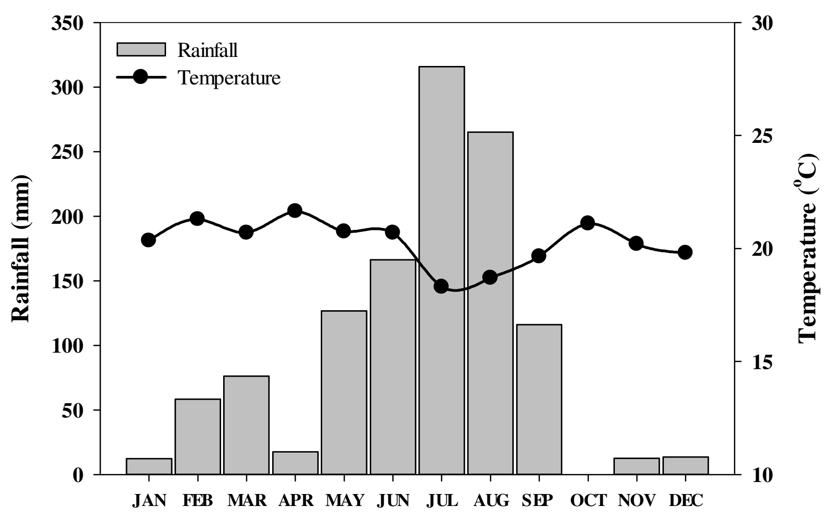

Fig.1. Mean monthly air temperature and rainfall around lakes Dendi and Wonchi during the sampling period (data provided from the Ethiopian National Meteorological Service Agency).

Lake Dendi, (Fig. 2) a double crater at an elevation of 2840 m a.s.l., is located 130 km south-west of Addis Ababa and lays 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 8 km long and 4 km wide. It has no permanent surface in- and outlets. It is mainly fed by seasonal rivers and springs during the main 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*.

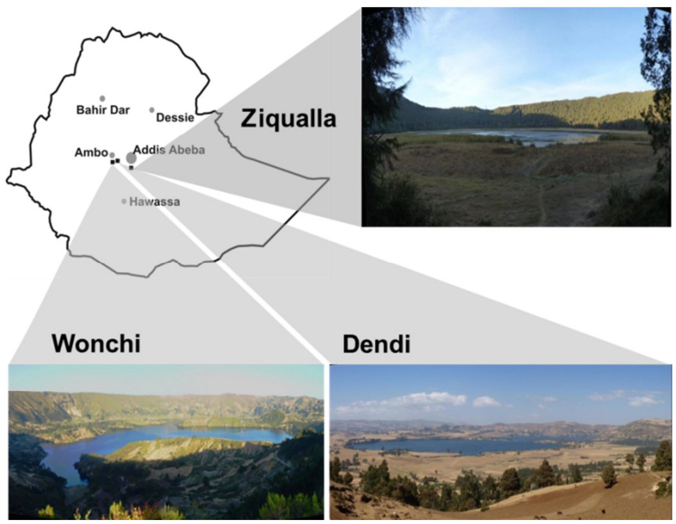

Fig. 2. Location of the lakes in the vicinity of Addis Ababa (Ethiopia).

Lake Wonchi (Fig. 2) nearby Dendi is located at an altitude of 2887 m above sea level. 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 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 the local communities [24]. 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. 2) is a crater lake located on mount Ziqualla (2989 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 and maximum depth of approximately 0.25 km^2 and 3 m, respectively, and the surface area has receded dramatically over the last 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 highly protected by the community of monks living in a nearby monastery.

Sampling protocol and analyses

All the three lakes were visited during the first week of January 2012. Physico-chemical variables 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 (Ɛ, 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, while it was taken approximately 10 cm below the surface using the same technique at the shoreline from Lake Ziqualla (boating 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 (Table 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 [25-26] were taken down to 20 m and kept in brown bottles preserved using Lugol's solution [27] 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 [28]. Algal biovolumes were then calculated using geometric formulae of the shapes similar to the respective phytoplankton cells [29]. 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 [25]. 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 [30], Korinek [31] and Fernando [32]. 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 [33].

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

Variable	Method	Reference
Total alkalinity	HCl titration	[88]
Total phosphorus (P_{tot})	Persulphate digestion and molybdenumblue-method	[88]
Soluble reactive phosphorus (SRP)	molybdeneblue-method	[89]
Total nitrogen (T_{tot})	Persulphate digestion, Cd red. and diazotization	[88]
Nitrate-nitrogen (NO_3-N)	Salicylic acid method	[88]
Nitrite-nitrogen (NO_2-N)	Diazotization	[90]
Ammonium-nitrogen (NH_4-N)	Sodium salicylate-hypochlorite method	[88]
Soluble reactive silica-a	Ammonium molybdate-EDTA method	[27]
Anions	Chromatography with suppression	[88]
Major and Trace Elements	Flame AAS and ICP OES (Perkin Elmer, Analyst 200 & Perkin Elmer Optima 5300)	[88]

Results

Physico-chemical parameters

The water temperature in lakes Dendi and Wonchi varied between 16.7 ^{o}C at the surface and 14.9 ^{o}C in deep layers and exhibited nearly isothermal conditions throughout the water column (Fig. 3). In contrast, only 8.8 ^{o}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 (Table 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 (Table 2).

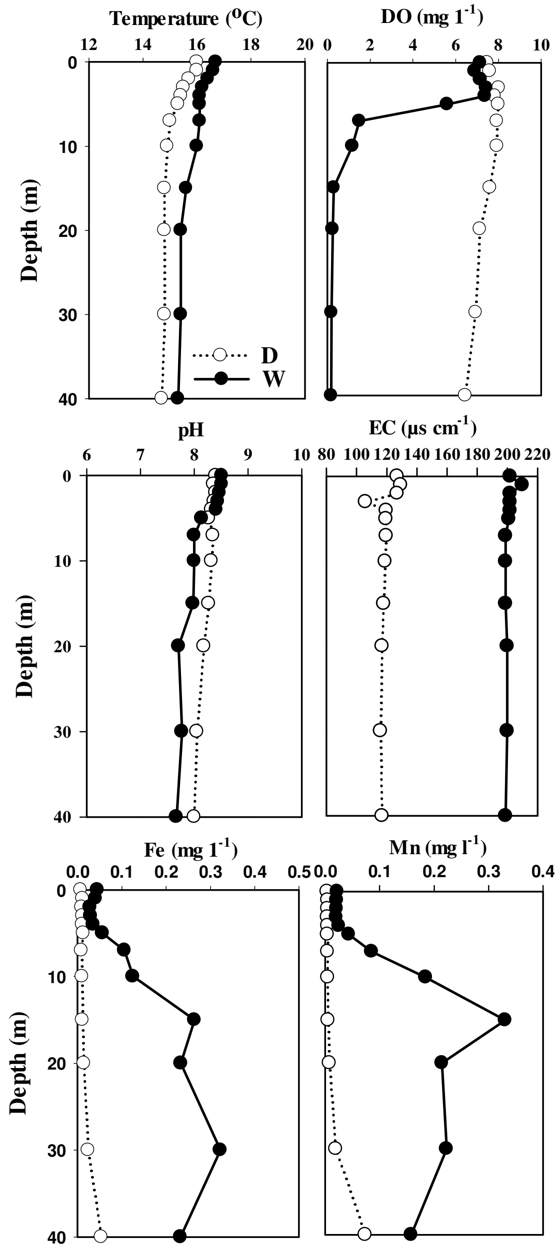

Fig. 3. Profiles of temperature, dissolved oxygen, pH, conductivity, Fe and Mn in lakes Dendi (D, open circle) and Wonchi (W, closed circle) during the sampling periods. Lake Ziqualla profile is not presented; values are only for surface water.

The rank (highest to lowest) of the predominant cation concentrations in lakes Dendi and Ziqualla were: $Ca^{2+} > Na^{+} > Mg^{2+} > K^{+}$, 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 it followed a rank of $HCO_3^- > Cl^- > F^- > SO_4^{2-}$ in Wonchi and Ziqualla (Fig. 4).

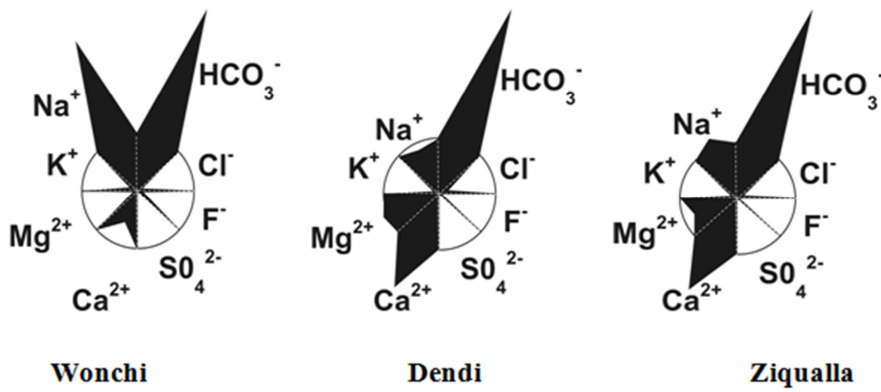

Fig. 4. Ion field diagrams of lakes Wonchi (left), Dendi (center) and Ziqualla (right). Each semicircle represents 100% of the four most abundant cat- and anions (basis mg l^{-1}).

Element concentrations of Si and trace elements are given in Table 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). For Fe and Mn, a significant increase of concentration could be noted 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.

Table 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
ε (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

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 (Table 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 (Table 2). Based on the TSI for Chl-*a*, P_{tot} and Secchi-disc readings (Table 3), the lakes are classified as oligotrophic to (oligo-) mesotrophic.

Table 3 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} (Table 1). Seven algal groups were identified during the sampling period including Cyanobacteria, green algae (Chlorophyta and Streptophyta), Bacillariophyceae, Dinophyta, Cryptophyta, Euglenophyta and Xanthophyceae (Table 4). The latter two groups were however not observed from Lake Wonchi. 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 (Table 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. 5), *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*.

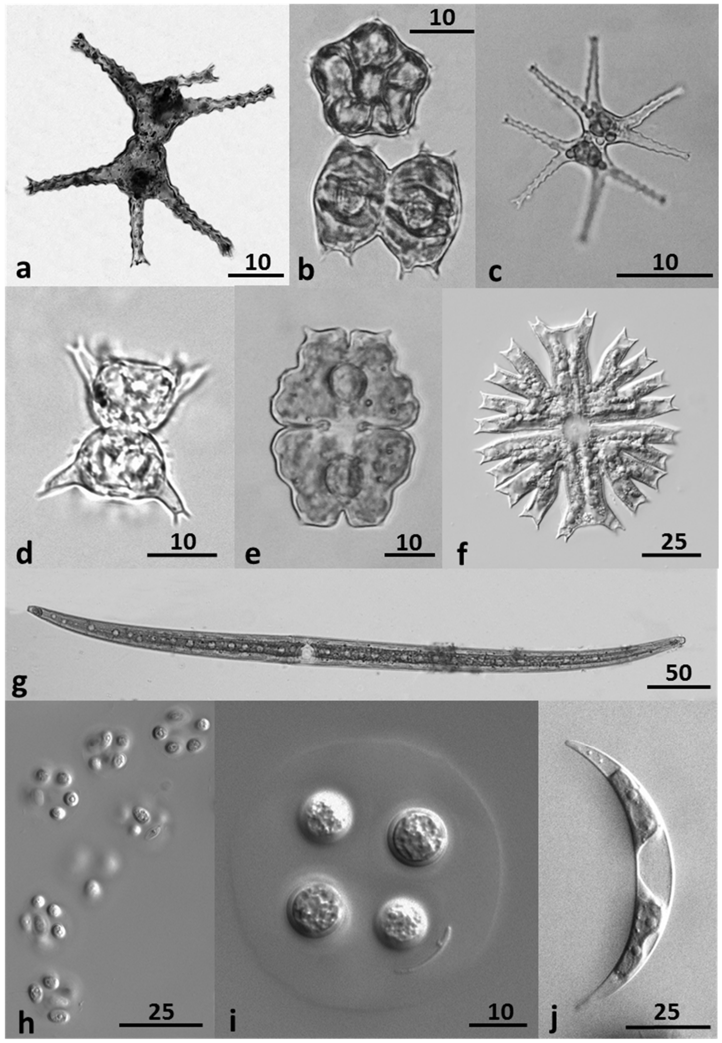

Fig. 5. Phytoplankton taxa of the lakes (occurrence see table 4) a…*Staurastrum pingue*, b… *Staurastrum quadrangulare* var. *attenuatum* f. *pentagona*, c… *Staurastrum bibrachiatum*, d… Staurastrum *laeve*, e…*Euastrum evolutum*, f…*Micrasterias radians*, g…*Closterium praelongum*, h… *Ooplanctella planoconvexa*, i…*Radiococcus polycoccus*, j… *Closterium venus.* Numbers on scale bars in µm.

Table 4 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 radians	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*	

Zooplankton species composition and abundance

A total of 11 rotifer taxa belonging to 8 genera and 13 crustacean taxa (6 genera) were identified (Table 5; Fig. 6). 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. 7, 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 (Table 5). Besides, 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* (Table 5). *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.

Table 5 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

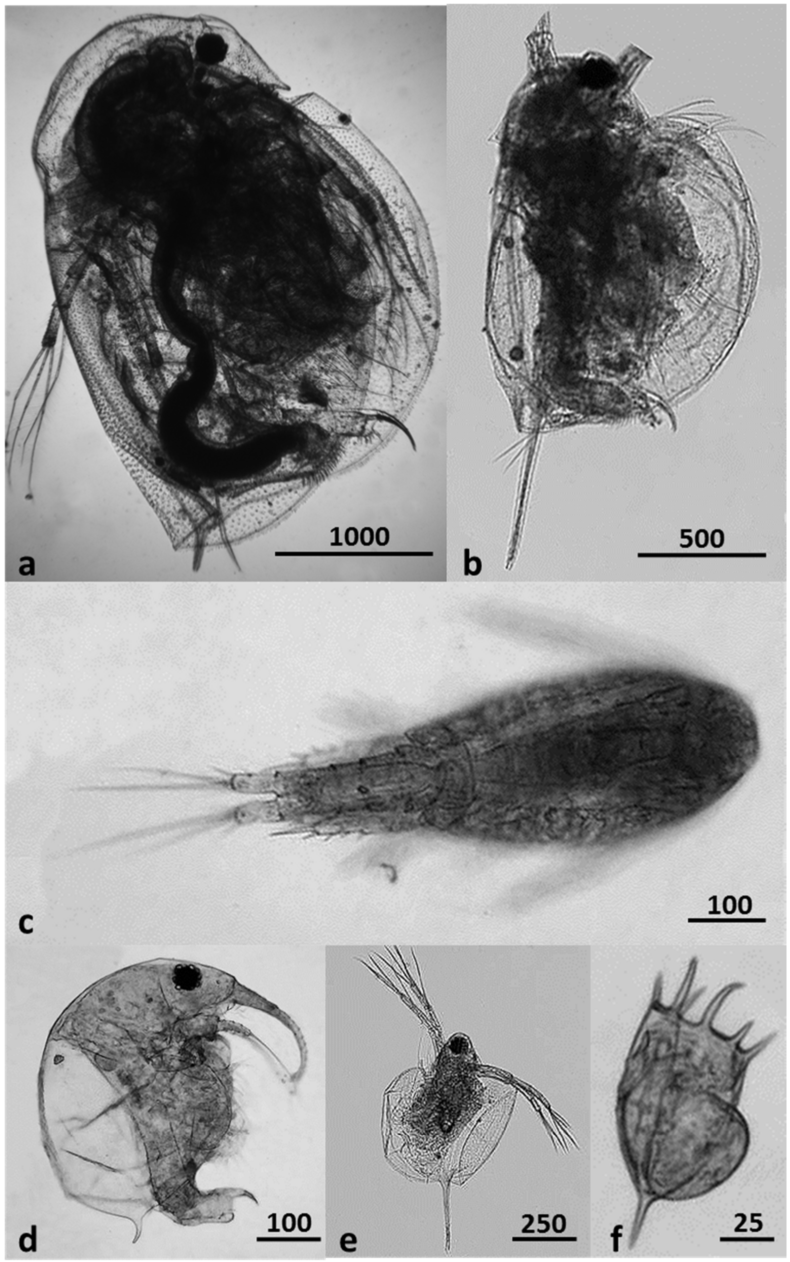

Fig. 6. Characteristic zooplankton taxa of the lakes. a…*Daphnia magna*, b, e…*Daphnia longispina*, c…*Thermocyclops ethiopiensis*, d…*Bosmina longirostris*, f…*Keratella cochlearis.* Numbers on scale bars in µm.

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, 34-35]. Beside the preliminary study of Singanan *et al*. [36] 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*. [36] did not identify sampling sites, depth and 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 (Table 2, Fig. 3). The water column temperature showed a similar pattern with 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 [37]. Nevertheless, such homogeneous DO concentration of the whole water column is a typical feature of oligotrophic lakes [35]. Although thermal stratification was not pronounced and thermocline poorly defined in Wonchi, a clinograde dissolved oxygen profile (< 1.5 mg l^{-1} below 7 m) was observed, which is unusual for an oligotrophic lake [35, 38]. Such a decrease, however, has been reported from other deep high-altitude lakes located in Cameroon, Uganda, Nepal and the United States [19, 39-41], which may reflect long-lasting stratification and – at least for eutrophicated water bodies - high oxygen consumption by decomposition of sinking labile organic matter and respiration of organisms in deeper waters [1, 16, 42-43]. 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 [44-45]. Another independent seasonal study (n=20) has also noted a comparable vertical DO profile below 10 m in Lake Wonchi [46]. 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 ^{o}C and 39.5%, respectively), probably attributed 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 highly protected by them; therefore it was impossible to get access by boat and to sample during the day. Ziqualla (77 µS cm^{-1}) had considerably lower ion contents than Dendi and Wonchi, and all the three lakes showed less ion concentrations compared with other Ethiopian lakes [1, 11, 22, 42, 47-50]. During this study, 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 (Table 2) and we classified the lakes as oligotrophic to (oligo-) mesotrophic [33, 51-52]; some accumulation of N-NH_4 and SRP was observed in deep layers of lake Wonchi. Such patterns were also recognized in other high-altitude lakes [16, 18, 40, 53] and are probably attributed to long-lasting stratification [54]. In many lakes in Africa [2, 42, 55-56], carbonate and bicarbonate are the predominant anions. Ayenew [57] documented in his extensive survey of the major ions composition of the groundwater and surface water systems in the Ethiopian volcanic terrain, that almost all highland waters are dominated by carbonate and bicarbonate in terms of anions with very few exceptions. Besides, the dominance of sodium in Wonchi (42.45 ± 0.33 mg l^{-1}) is unusual for highland lakes in contrast to rift waters, which is likely to be attributed to the dominance of acidic volcanics mainly ignimbrite, rhyolite and pumice [57]. Lake Wonchi also has an increased concentration of F^- (2.69 ± 0.01 mg l^{-1}) quite above WHO [58] guideline for drinking water (0.6 –1.5 mg l^{-1}), which was also mirrored by 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 [59-62]. The dominance of small-sized phytoplankton and slowly-growing species (K-strategist: e.g. *Peridinium*) in lakes Dendi and Wonchi are favored by several environmental factors such as low dissolved inorganic nutrient concentrations [59-60], low total ion concentrations [51, 55] and moderate pH [4]. 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 [63-64]. 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 [63- 65].

Numerically, copepods and rotifer taxa formed the major zooplankton component of all three lakes, in contrast to cladocerans which were rather more diverse (Table 5). Such a dominance of copepods and rotifers is a common pattern in tropical water bodies [22, 66-69]. The high species richness of cladocerans is most probably attributed 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 probably be transported into remote isolated waterbodies by waterbirds as they migrate between lakes, which has been often viewed elsewhere [68, 70-73].

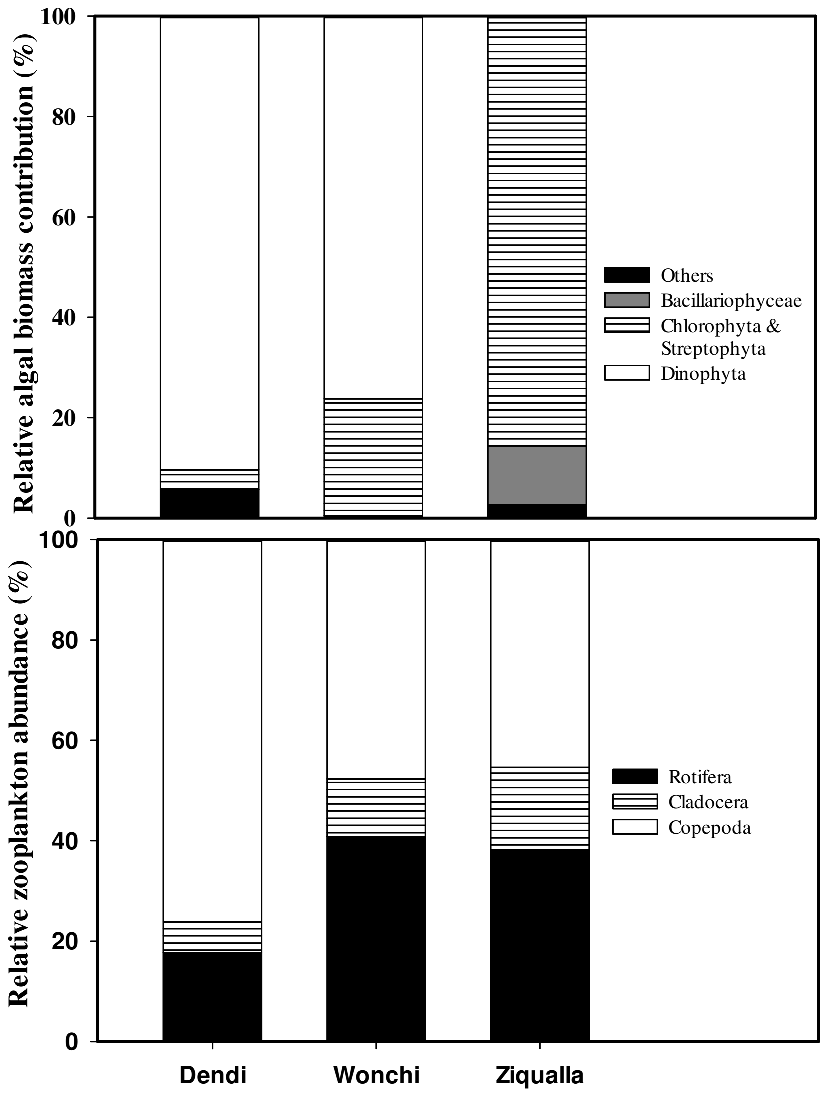

Fig. 7. Percentage algal biomass contribution (top panel) and relative zooplankton abundance based on Indl m^{-3} (lower panel) of the three lakes during the sampling period.

In contrast to other subtropical and tropical lakes [74- 80], large-bodied cladocerans such as *Daphnia magna*, *Diaphanosoma excisum* and *Daphnia longispina* (Fig. 6) were almost exclusively dominating the cladoceran communities in lakes Dendi and Wonchi. This is most probably attributed to lack of planktivorous fish (weak top-down control) in the pelagic zone [81]. 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 [65, 82-83]. The high altitude at which the lakes are located (> 2800 m) and the subsequent low water temperatures (8.8-16.7 ^{o}C) for tropical lakes agrees with the study of Dejen *et al*. [68], 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. Besides, *Daphnia magna* which was only reported from two other Ethiopian highland lakes Hayq [22] and Ashenge [84] and the predatory *Chaoborus*-larvae, recently reported from Lake Ziway [85] were recorded for the first time in Lake Dendi in the present study. Amongst rotifers, *Keratella cochlearis* was encountered in higher number (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 [86-87].

Implications for Conservation

In Africa, particularly in Ethiopia there seems to be little awareness of eutrophication and monitoring programs have barely been established for aquatic ecosystems. Such lack of monitoring systems 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 under oligotrophic status, while Lake Ziqualla is oligo- mesotrophic status. Phytoplankton assemblages were represented by the characteristic species of desmids, while the zooplankton community composition is unusually dominated by the large-bodied cladocerans, which is probably due to the high altitude and the subsequent low water temperatures for a tropical lake and the lack of strict predators. The baseline data generated from this observation document the present conditions against which future changes can be monitored. We further suggest that lakes Dendi, Wonchi and Ziqualla can be used as references 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.

Acknowledgements

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References

[1] Baxter, R.M., Prosser, M.V., Talling, J.F. and Wood, R.B. 1965. Stratification in tropical African lakes at moderate altitude (1500-2000 m). *Limnol. Oceanogr.* 10: 510-520.

[2] Prosser, M.V., Wood, R.B. and Baxter, R.M. 1968. The Bishoftu crater lakes: a bathymetric and chemical study. *Arch. Hydrobiol.* 65: 309-324.

[3] Teferra, G. 1980. A limnological study on Lake Chelekleka. *SINET: Ethiop. J. Sci.* 3: 143-152.

[4] Wood, R.G. and Talling, J.F. 1988. Chemical and algal relationships in a salinity series of Ethiopian inland waters. *Hydrobiologia* 158: 29-67.

[5] Zinabu, G-M. 1994. Long-term changes in indices of chemical and productivity status of a group of tropical Ethiopian lakes with differing exposure to human influence. *Arch. Hydrobiol.* 132: 115-125.

[6] Baxter, R.M. and Golobitsch, DL. 1970. A note on the limnology of Lake Hayq, Ethiopia. *Limnol. Oceanogr.* 15:144–148.

[7] Talling, J.F., Wood, R.B., Prosser, M.V. and Baxter, R.M. 1973. The upper limit of photosynthetic productivity by phytoplankton: evidence from Ethiopian soda lakes. *Freshw. Biol.* 3: 53-76.

[8] Zinabu, G-M. and Taylor, W.D. 1997. The bacteria-chlorophyll relationships in Ethiopian lakes of varying salinity: are soda lakes different? *J. Plankton Res.* 19: 647-654.

[9] Green, J. 1986. Zooplankton associations in some Ethiopian Crater lakes. *Freshw. Biol.* 16:495-499

[10] Lemma, B. 2008. Observations on the relations of some physico-chemical features and DVM of *Paradiaptomus africanus* in Lakes Bishoftu-Guda and Hora-Arsedi, Bishoftu, Ethiopia. *Limnologica* 39: 230-243.

[11] Zinabu, G-M., Chapman, L.J. and Chapman, C.A. 2002. Conductivity as a predictor of a total cations and salinity in Ethiopian lakes and rivers: revisiting earlier models. *Limnological* 32: 21–26.

[12] Teshome, K. 2011. The temporal variations in physico-chemical characteristics, planktonic biomass, diversity and primary productivity in three crater lakes in Ethiopia. M.Sc. Thesis, University of Bremen, Germany.

[13] Belachew, M., Kifle, D. and Jebessa, H. 2012. Deep underwater seismic explosion experiments and their possible ecological impact-The case of Lake Arenguade-Central Ethiopian highlands. *Limnological* 42: 212-219.

[14] Lemma, B. 2002. Contrasting effects of human activities on aquatic habitats and biodiversity of two Ethiopian lakes. *Ethiop. J. Natural Resources* 4: 127 – 148.

[15] Tudorancea, C. and Taylor, W.D. 2002. Ethiopian Rift Valley Lakes. Backhuys publisher: Leiden, Netherlands.

[16] Löffler, H. 1972. Contribution to the limnology of high mountain lakes in Central America. *Int. Revue ges. Hydrobiol.* 57: 397-408.

[17] Roldan-Perez, G. 1992. Fundamentos de limnologia tropical. Universidad de Antioquia, Colombia.

[18] Umana, V.G. 2001. Limnology of Boots Lake, a tropical crater lake in Costa Rica. *Rev. Biol. trop* 49: 1-10.

[19] Kling, G.W. 1988. Comparative transparency, depth of mixing, and stability of stratification in lakes of Cameroon, West Africa. *Limnol. Oceanogr.* 33: 27-40.

[20] Löhr, A., Bogaard, T., Hikes, A., Hendriks, M., Sumartis, S., Bergen, vM., Kees, CAM., Gestel, K., Straalen, vN., Vroon, P. and Widianarko, B. 2005. Natural pollution caused by the extremely acidic crater Lake Kawahljen, East Java, Indonesia. *Environ Sci Pollut Res* 12: 89-95.

[21] Fetahi, T. 2010. Plankton Communities and Ecology of Tropical Lakes Hayq and Awassa, Ethiopia. PhD thesis, University of Vienna, Austria.

[22] Fetahi, T., Mengistu, S. and Schagerl, M. 2011. Zooplankton community structure and ecology of the tropical-highland Lake Hayq, Ethiopia. *Limnologica* 41: 389-397.

[23] Ayenew, T. and Legesse, D. 2007. The changing face of the Ethiopian rift lakes and their environs: call of the time. *Lakes & Reservoirs: Research & Management* 12: 149-216.

[24] NFLARC-National Fisheries and Other Living Aquatic Resources Research Centre. 2004. Stocking based fishery enhancement programs in Ethiopia, Final Report.

[25] Wetzel, R.G. and Likens, G.E. 1991. Limnological analyses, 2nd edn. Springer-Verlag, New York.

[26] Sun, J. and Liu, D. 2003. Geometric models for calculating cell biovolume and surface area of phytoplankton. *J. Plankton Res.* 25: 1331-1346.

[27] Wetzel, R.G. and Likens, G.E. 2000. Limnological Analyses, 3rd edn. Springer Verlag, New York.

[28] Utermöhl, H. 1958. Zur Vervollkommnung der quantitativen Phytoplankton-Methodik. *Mitt. Internat. Ver. Limnol.* 9:1–38.

[29] Hillebrand, H., Durselen, D.C., Kirschtel D, Pollingher, U. and Zohary, T. 1999. Biovolume calculation for pelagic and benthic microalgae. *J. Appl. Phycol.* 35:403–424.

[30] Koste, W. 1978. Rotatoria: Die Radertiere Mitteleuropas begrundet von Max Voigt. Gebruder Borntraeger: Berlin, Germany.

[31] Korinek, V. 1999. A Guide to Limnetic Species of Cladocera of African Inland Waters (Crustacea, Branchiopoda). SIL, BTL, Geneva.

[32] Fernando, C.H. 2002. A Guide to Tropical Freshwater Zooplankton. Identification, Ecology and Impact on Fisheries. Backhuys publisher: Leiden, Netherlands.

[33] Carlson, R.E. 1977. A trophic state index for lakes. *Limnol. Oceanogr.* 22: 361-369.

[34] Mohr, P. 1961. The geology, structure and origin of the Bishoftu explosion Craters, Shoa, Ethiopia. *Bull. Geophys. Obs.* 2: 65-101.

[35] Wetzel, R.G. 2001. Limnology: Lake and River Ecosystems, 3rd edn. Academic Press, San Diego.

[36] Singanan, M., Lakew, W. and Mitiku, T. 2008. Water quality of Wonchi Crater Lake in Ethiopia. *Maejo Int. J. of Sci. Technol.* 2:361-373.

[37] Aeschbach-Hertig, W.M., Hofer, M., Schmid, R., Kipfer, D. and Imboden, M. 2002. The physical structure and dynamics of a deep, meromictic Crater Lake (Lac Pavin, France). *Hydrobiologia* 487: 111-136.

[38] Talling, J.F. and Lemoalle, J. 1998. Ecological dynamics of tropical inland waters. Cambridge University Press, UK.

[39] Britt, N.W.1955. Stratification in western Lake Erie in summer of 1953: effects on the Hexagenia (Ephemeroptera) population. *Ecology* 36: 239-244.

[40] Melack, J.M. 1978. Morphometrical, physical and chemical features of the volcanic crater lakes of western Uganda. *Arch. Hydrobiol.* 84: 430-453.

[41] Sharma, M.C., Sharma, S., Bajracharya, M.R., Gurung, S., Jüttner, I., Kang, S. and Zhang, Li. Q. 2012. First results on bathymetry and limnology of high-altitude lakes in the Gokyo Valley, Sagarmatha (Everest) National park, Nepal. *Limnology* 13: 181-192.

[42] Kebede, E. and Belay, A. 1994. Species composition and phytoplankton biomass in a tropical African lake (Lake Awasa, Ethiopia). *Hydrobiologia* 288: 13-32.

[43] Haberyan, K.A., Umana, G., Collado, C. and Horn, S. 1995. Observations on the plankton of some Costa Rican lakes. *Hydrobiologia* 312: 75-85.

[44] Kjensmo, J. 1967. The development and some main features of iron meromictic soft water lakes. *Arch. Hydrobiol.* 32: 137-312.

[45] Boehere, B. and Schultze, M. 2008. Stratification of lakes. *Rev. geophysics* 46: 11-23.

[46] Degefu, F. and Schagerl, M. Zooplankton abundance, species composition and ecology of tropical high-mountain crater lake Wonchi, Ethiopia. In preparation for submission.

[47] Kifle, D. and Belay, A. 1990. Seasonal variation in phytoplankton primary production in relation to light and nutrients in Lake Awasa, Ethiopia. *Hydrobiologia* 196: 217-227.

[48] Lemma, B. 1994. Changes in the limnological behavior of a tropical African explosion crater lake: Lake Hore-Kilole, Ethiopia. *Limnological* 24: 57-70.

[49] Demlie, M., Ayenew, T. and Wohnlich, S. 2007. Comprehensive hydrological and hydrogeological study of topographically closed lakes in highland Ethiopia: The case of Hayq and Ardibo. *J. Hydrology* 339: 145-158.

[50] Tilahun, G. and Ahlgren, G. 2010. Seasonal variations in phytoplankton biomass and primary production in the Ethiopian Rift Valley lakes Ziway, Awasa and Chamo-The basis of fish production. *Limnologica* 40: 330-342.

[51] Wetzel, R.G. 1983. Limnology, 2nd edn. Saunders College Publishing, Philadelphia.

[52] Lampert, W. and Sommer, U. 1997. Limnoecology: The Ecology of Lakes and Streams. Oxford University Press, New York.

[53] Eggermont, H. and Russell, M.J. 2007. Physical and chemical limnology of alpine lakes and pools in the Rwenzori Mountains, Uganda-DR Congo. *Hydrobiologia* 592: 151-173.

[54] Wetzel, R.G. 1975. Limnology. WB, Saunders, Philadelphia, Pennsylvania, USA.

[55] Talling, J.F and Talling, I.B. 1965. The chemical composition of African lake water. Internationale Revue Der Gesamten. *Hydrobiologia* 50: 421-463.

[56] Oduor, S.O. and Schagerl, M. 2007. Temporal trends of ion contents and nutrients in three Kenyan Rift Valley saline-alkaline lakes and their influence on phytoplankton biomass. *Hydrobiologia* 584: 59-68.

[57] Ayenew, T. 2005. Major ions composition of the groundwater and surface water systems and their geological and geochemical controls in the Ethiopian volcanic terrain. *SINET: Ethiop. J. Sci.* 28: 171-188.

[58] WHO. 2006. Fluoride in Drinking–water. In: *A series of World Health Organization monographs*. Bailey, K., Chilton, J., Dahi, E., Lennon, M., Jackson, P. and Fawell, J. (Eds.), IWA Publishing, Geneva.

[59] Hutchinson, G.E. 1967. A treatise on limnology: Introduction to lake biology and limnoplankton. John wiley and Sons, New York.

[60] Reynolds, C.S. 1984. The ecology of freshwater phytoplankton. Cambridge University Press, Cambridge.

[61] Sommer, U. 1985. Comparison between steady state and non-steady state competition: Experiments with natural phytoplankton. *Limnol. Oceanogr.* 30: 335-346.

[62] Schabetsberger. R., Drozdowski, G., Drozdowski, I., Jersabek, D.C. and Rott, E. 2004. Limnological aspects of two tropical Crater lakes (Lago Bio and Lago Loreto) on the island of Bioko, Equatorial Guinea. *Hydrobiologia* 524: 79-90.

[63] Hadas, O., Pinkas, R., Malinky-Ruchansky, N., Sukenik, A. and Kaplan, A. 2002. Cyanobacteria in Lake Kinneret: physiological and ecological adaptations. *Verh. Int. Ver Limnol.* 8: 55-74.

[64] Mwaura, F., Mavuti, K.M. and Wamicha, W.N. 2002. Biodiversity characteristics of small high-altitude tropical man-made reservoirs in the eastern Rift valley, Kenya. *Lakes & Reservoirs: lakes & Reservoirs Management* **7**: 1–12.

[65] Degefu, F., Mengistu, S. and Schagerl, M. 2011. Influence of fish cage farming on water quality and plankton in fish ponds: A case study in the Rift Valley and North Shoa reservoirs, Ethiopia. *Aquaculture* 316: 129-135

[66] Fernando, C.H., Mengistu, S. and Bely, S. 1990. The chydroid crustacean Alona diaphana (KING), limnetic in Lakes Awassa and Ziway, Ethiopia, with a discussion of littoral and limnetic zooplankton. *Int. Rev. Hydrobiol.* 75: 15–25.

[67] Mengistu, S. and Fernando, C.H. 1991. Biomass and production of major dominant crustacean zooplankton in a tropical rift valley lake, Awasa, Ethiopia. *J. Plankton Res.*13: 831–852.

[68] Dejen, E., Vijverberg, J., Nagelkerke, LA.J and Sibbing, FA. 2004. Temporal and spatial distribution of microcrustacean zooplankton in relation to turbidity and other environmental factors in a large tropical lake (L. Tana, Ethiopia). *Hydrobiologia* 513: 39–49.

[69] Wondie, A. and Mengistu, S. 2006. Duration of development, biomass and rate of production of the dominant copepods (Calanoida and Cyclopoida) in Lake Tana, Ethiopia. *SINET: Ethiop. J. Sci.* 29: 107–122.

[70] De Meester, L., Gomez, A., Okamura, B. and Schwenk, K. 2002. The monopolisation hypothesis and the dispersal-gene flow paradox in aquatic organisms. *Acta Oecologica* 23: 121-135.

[71] Figuerola, J. and Green, A.J. 2002. Dispersal of aquatic organisms by waterbirds: a review of past research and priorities for future studies. *Freshw. Biol.* 47: 483-494.

[72] Green, A.J., Figuerola, J. and Sanchez, M.I. 2002. Implications of waterbirds ecology for the dispersal of aquatic organisms. *Acta Oecologica* 23: 177- 189.

[73] Dejenie, T., Declerck, A.JS., Asmelash, T., Risch, S., Mergeay, J., Bie, T.D. and Meester, D.L. 2012. Cladoceran community composition in tropical semi-arid highland reservoirs in Tigray (Northern Ethiopia): A meta community perspective applied to young reservoirs. *Limnologica* 42: 137-143.

[74] Fernando, C.H. 1980a. The freshwater zooplankton of Sri Lanka with a discussion of tropical zooplankton composition. *Int. Rev. Hydrobiol.* **1**: 85-125.

[75] Fernando, C.H. 1994. Zooplankton, fish and fisheries in tropical freshwaters. *Hydrobiologia* 272: 105-123.

[76] Dumont, H.J.1994. On the diversity of the Cladocera in the tropics. *Hydrobiologia* 272: 27-38.

[77] Meerhoff, M., Iglesias, C., Teixeria, F.de., Mello, J., Clemente, E., Jensen, T., Lauridsen, L. and Jeppesen, E. 2007a. Effect of habitat complexity on community structure and predator avoidance behavior of littoral zooplankton in temperate versus subtropical shallow lakes. *Freshw. Biol.* 52: 1009-1021.

[78] Havens, K.E., Elia, A., Taticchi, M., and Fulton, R. 2009. Zooplankton-phytoplankton relationships in shallow sub-tropical versus temperate lakes Apopka (Florida, USA) and Trasimeno (Umbria, Italy). *Hydrobiologia* 628: 165-175.

[79] Iglesias, C., Mazzeo, N., Meerhoff, M., Lacerot, G., Clemente, J.M., Scasso, F., Kruk, C., Goyenola, G., Garcia-Alonso, J., Amsinck, S.L., Paggi, J.C., Paggi, S.J. and Jeppesen, E. 2011. High predation is of key importance for dominance of small-bodied zooplankton in warm shallow lakes: evidence from lakes, fish exclosures and surface sediments. *Hydrobiologia* 667: 133- 147.

[80] Arcifa, M.S., Gomes, E.T. and Meschiatti, A.J. 1992. Composition and fluctuations of the zooplankton of a tropical Brazilian reservoir. *Archiv für Hydrobiologie* 129: 479-495.

[81] Brooks, J.L. and Dodson S.I. 1965. Predation, body size, and composition of plankton. *Science* 150: 28-35.

[82] Carpenter, R.S. and Kitchell, F.J.1992. Trophic Cascade and Biomanipulation: Interface of research and management- A replay to the comment by DeMelo et al. *Limnol. Oceanogr.* **37**:208-213.

[83] Hall, P.O.J, Holby, O., Kollberg, S. and Samuelsson, M.O. 1992. Chemical fluxes and nitrogen mass balance in a marine fish cage farm. Mar Ecol Prog Ser 61:61–73.

[84] Haileselasie, T.H, Teferi, M., Dejenie, T., Welegerima, K., Abay, T., Hiluf, S.A. and Girmay, K. 2012. Abundance, species composition and special distribution of zooplankton in Lake Hashengae of Tigray, Northern Ethiopia. *Current Res. J. Biological Sci.* 4: 389- 393.

[85] Dagne, A. 2010. Zooplankton community structure, population dynamics and production and its relation to abiotic and biotic factors in Lake Ziway, Ethiopia. PhD thesis, University of Vienna, Austria.

[86] Walz, N. 1997. Rotifer life-history strategies and evolution in freshwater plankton communities. In: *Evolutionary ecology of freshwater animals*. Streit, B. and Städler, T. (Eds.), Lively.

[87] Primicerio, R. 2000. Seasonal changes in vertical distribution of zooplankton in an oligotrophic, subarctic Lake (Lake Takvatn, Norway). *Limnologica* 30: 301-310.

[88] APHA.1998. Standard Methods for the Examination of Water and Wastewater. 20th edn. American Public Health Association, Washington DC.

[89] Murphy, J. and Riley, J.P. 1962. A modified single solution method for the determination of phosphate in natural waters. *Analytica Chimica Acta* 27: 31–36.

[90] Legler, C. 1988. Áusgewählte Methoden der Wasseruntersuchung´, Band 1. Gustav Fischer Verlag, Jena.

Chapter 2

Phytoplankton communities of tropical high– mountain crater lake Wonchi, Ethiopia

Panoramic view of Lake Wonchi, Ethiopia

Chapter 2

Phytoplankton communities of tropical high– mountain crater lake Wonchi, Ethiopia

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ABSTRACT

Lake Wonchi is a cold–water tropical crater lake in Ethiopia located at an altitude of around 2900 m above sea level. We present a first record on phytoplankton taxa composition, abundance and biomass including underlying limnological variables; the study was conducted between December 2011 and January 2013. Dissolved inorganic nutrient levels indicate oligotrophic conditions with ammonium being the dominant nitrogen form. The phytoplankton communities comprised 53 taxa distributed in five taxonomic divisions, which could be assigned to 15 codons based on the phytoplankton functional group classification. In Wonchi, as typical in other deep high–mountain tropical lakes, partial–atelomixis combined with the apparent low dissolved inorganic nutrient concentrations seem to be a fundamental driving force in structuring phytoplankton community composition, which was quite stable and characterized by high diversity of heavy, immobile and fast-sinking planktonic desmids of the N_A–codon (61% of the total biovolume) during mixis followed by diatoms MP–codon contributing 13% to the total biovolume. A near–monospecific bloom of *Peridinium cinctum* (Lo–codon) prevailed before the onset of lake turnover in December 2011 in conditions of nutrient–depletion, which was later followed by the functional groups F–J during the episode of complete mixing and then perpetually replaced by the functional group N_A. Non-metric multi-dimensional scaling resulted in a 2-dimensional solution, which revealed clear segregation of phytoplankton community to five groups. Mixing regime of the water column, specific conductivity, total phosphorus, ammonium and zooplankton had significant influence on the observed seasonal pattern.

Key words: alga, limnology, trophic classification, nutrient, crater lake

INTRODUCTION

Although temporal variations of the incident solar radiation and water temperatures in tropical lakes are reduced compared to temperate systems, seasonal changes in phytoplankton species compositions and biomass is not trivial (Talling, 1987). This is mainly attributed to the hydrological cycle which influences the physical and chemical dynamics of the water column and consequently their biota (Sondergaard *et al*., 1990; Figueredo and Giani, 2001, 2009). Therefore, tropical lakes are not quiescent aquatic ecosystems as it has been widely thought earlier compared to their temperate counterparts. This is particularly true of tropical high–mountain lakes, which are broadly known to exibit distinict mixing regime and atelomictic events (Löffler, 1972; Roldán, 1992; Sánchez, 2001; Umana, 2001; Tavera and Martínez-Almeida, 2005). This physical process mainly occurring in a tropical high–mountain lakes is a focus of contemporary limnological investigations and is recently reported to be a key driver in structuring phytoplankton assemblages and seasonal succession, though other factors such as the availability of resources and light may take precedence (Barbosa and Padisăk, 2002; Reynolds, 2006; Souza *et al*., 2008; Becker *et al*., 2010; Fetahi *et al*., 2014). Nevertheless, the knowledge of such physical variables and the subsequent effect on phytoplankton dynamics in tropical–African high–mountain lakes is meager, even though our understanding on phytoplankton seasonal successions, abundance and biomass from rift valley lakes George (Ganf, 1974c), Tanganika (Hecky and Kling, 1981), Bogoria, Nakuru and Elmentaita (Oduor and Schagerl, 2007), Ziway (Beneberu and Seyoum, 2009; Tilahun and Ahlgren, 2010), Awasa (Kebede and Belay, 1994; Tilahun and Ahlgren, 2010), and Chamo (Tilahun and Ahlgren, 2010) in East Africa has been slowly developing. Recently, detailed limnological investigations on the highland tropical crater lake Hayq have been initiated in Ethiopia focusing on seasonal dynamics and production of phytoplankton and the underlying limnological variables (Fetahi *et al*., 2014). The authors concluded that the mixing regime plays a pivotal role in structuring phytoplankton communities and their seasonal succession.

Apparently, the limnology and phytoplankton community of Lake Wonchi, a high–mountain tropical crater lake in the central highlands of Ethiopia has never been investigated, reliably owing to seclusion and lack of infrastructure. Paradoxically, in the late 1990s, Lake Wonchi was stocked with common carp (*Cyprinus carpio* L.1758) and tilapia (*Oreochromis niloticus* L.) fish in an attempt to establish a pelagic fishery, the latter species however did not establish breeding populations. Low water temperatures and reduced phytoplankton biomass in Lake Wonchi could be causes behind the failure of *O. niloticus* to thrive in the lake, because the natural food of adult *O. niloticus* in Ethiopian lakes has been reported to be mainly phytoplankton (Tadesse, 1999). Thus, understanding of phytoplankton species composition and biomass in pelagic ecosystem has an implication for the whole community in aquatic ecosystems (Brooks and Dodson, 1965; Shapiro and Wright, 1984; Carpenter and Kitchell, 1993; Tilahun and Ahlgren, 2010). Nevertheless, no limnological research had been conducted nor are there any reports on the phytoplankton taxa composition in this lake to the best of our knowledge. Therefore, the purpose of this study is to provide a first record on algae composition, succession and biomass based on long–term observations and attempt to link the observed pattern to underlying environmental drivers. We also assessed the lake's ecological status through the application of the Carlson trophic model (Carlson, 1977) and phytoplankton functional groups.

METHODS

Study site

Lake Wonchi (8^{o}47' N, 7^{o}53' E), a high-land crater lake, is located at an altitude of 2900 m above sea level some 150 km southwest of the capital of Ethiopia, Addis Ababa. It is deep, steeply shelving with a surface area of 5.6 km^2 (Table I, Fig. 1).

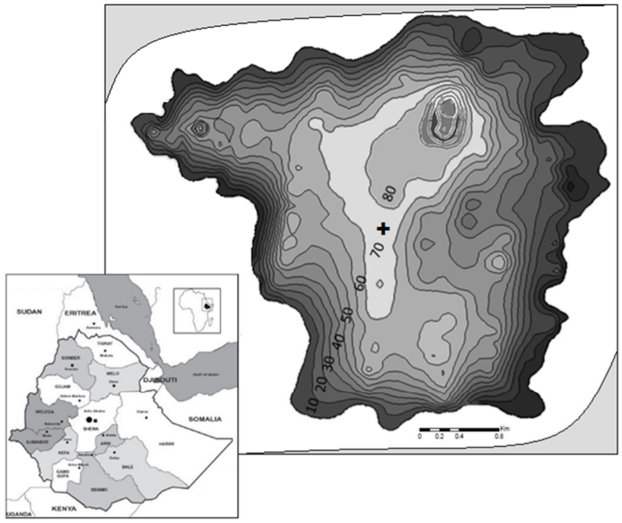

Fig. 1. Bathymetric map of Lake Wonchi in southwest escarpment of Ethiopia (✚ the primary sampling site with GPS coordinates 08^{o}48’035”N and 37^{o}53’592”E).

The shoreline is mostly rocky and gravelly, which is characterised by submerged aquatic macrophytes (mainly *Potomageton* sp.). The height of its crater rim from the lake surface is about 460 m. The lake has a closed basin with no surface inlet.

Table I: Morphometry of Lake Wonchi

Variables	Values
Location	8^{o}47' N7^{o}53' E
Max. length (east-west: 60^o from north)	3.8km
Max. width	2.2km
Max. depth	107m
Mean depth	28m
Shoreline length	13.362km
Surface area	5.6km^2
Volume	0.185km^3

It receives water primarily from rainfall and subterranean cold and lukewarm springs. The lake region is characterised by sub–humid climate with an annual rainfall of 1200 mm. There are two rainy seasons in the area: the main rainy season extends from May to September peaking during

July and August (Fig. 2), while the minor one extending roughly from February to March (Ethiopia National Meteorological Service Agency). The diel air temperature varies from 13 to 22 ^{o}C during the day time and falls below 10^{o}C in the night (Fig. 2).

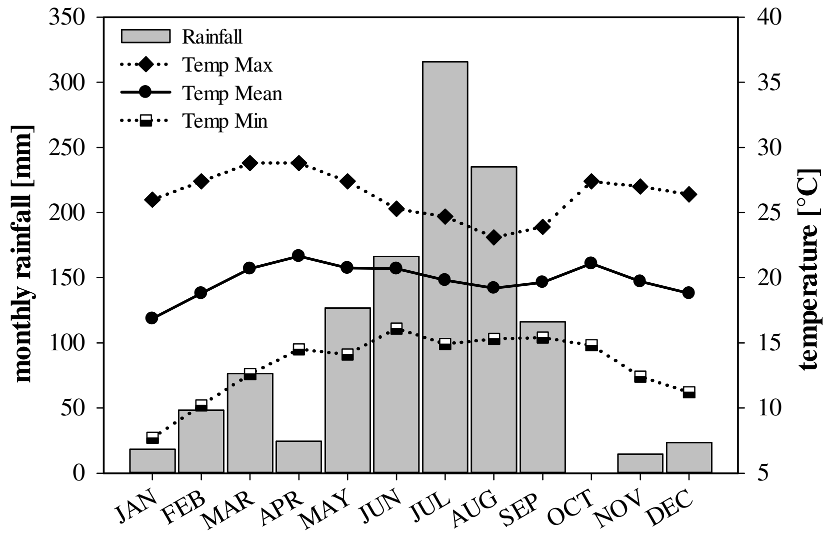

Fig. 2. Rainfall and air temperature (maximum, mean and minimum) data around Lake Wonchi during the sampling period from December 2011 to January 2013. Data provided from the Ethiopian National Meteorological Service Agency.

Field sampling and analyses

The study was carried out on a fortnightly basis between December 2011 and January 2013 at an open–water station marked with GPS (depth: 50 m, coordinates: 08^{o}48’035”N and 37^{o}53’592”E). Data on physico–chemical variables such as water temperature, dissolved oxygen (DO), conductivity (corrected to 25 ^{o}C) and pH were measured *in–situ* using a multi-probe (Model HQ40D, HACH Instruments). Lake water transparency was estimated using a Secchi disk, underwater light was measured using light meter (Model SKP 2000, Skye Instruments). The vertical light extinction coefficient (Ɛ, m^{-1}) was calculated using direct light irradiance measurements (Ɛ = $(\ln I_o - \ln I_z)/Z)$), where I_o is surface light irradiance, I_z is light irradiance at a certain depth and Z depth. Subsequently euphotic depth (Z_{eu}), the depth at which 1% incident irradiance available, was determined using Z_{eu} = 4.6/Ɛ. Water for chlorophyll-*a* (Chl-*a*), ion and nutrient analysis was collected from depth profiles (surface, 1, 2, 3, 4, 5, 7, 10, 15, 20, 30, 40, 50 m depth) using a 5 L Schindler sampler. Samples were transferred to 2 L acid–prewashed plastic bottles and transported to the laboratory, stored in dark cooling boxes. The samples were subsequently filtered within 4 h of sampling through glass fibre filters (Whatman GF/C) paper and the filtrate was used for nutrient analyses, which were done within 48 h of sample collection. Ammonium (NH_4–N) was analysed by the Indol–phenol blue method after Krom (1982), nitrate (NO_3–N) was determined with sodium–salicylate method as outlined by APHA (1998) and nitrite (NO_2–N) was analysed based on the reaction between sulphanilamide and N–naphthyl–(1)–ethylendiamin–dihydrochloride (APHA, 1998). Soluble reactive phosphorus (SRP) was determined by ascorbic acid method (APHA, 1998), while total phosphorus (P_{tot}) was determined by digesting the unfiltered water samples in an autoclave for 50 min using potassium–peroxodisulphate to convert the organically bounded phosphorus into orthophosphate. Total alkalinity was determined from the unfiltered water sample through titration with 0.01N HCl to pH 4.3 marking the end point (Wetzel and Likens, 2000). For element analyses (including trace elements) and determination of major anions, samples were acidified with nitric acid (Trace SELECT ® by Fluka) and analysed at the University of Vienna, Austria. Chl-*a* concentration was analysed spectrophotometrically after extracting GF/C glass–fibre filtered samples with 90% acetone without phaeopigments correction (Talling and Driver, 1963). The trophic status of Lake Wonchi was defined following the trophic status indices (TSI) proposed by Carlson (1977), which was computed based on Secchi–disk readings, Chl-*a* and P_{tot} concentrations. Samples for estimation of the relative abundance of the phytoplankton community were collected with a plankton net (30 µm mesh size). Phytoplankton taxa were enumerated and identified to species level under a Zeiss (computer based automated image–analyser) microscope using keys of Whitford and Schumacher (1973), Talling (1987), Popovsky and Pfiester (1990), Willen (1991) and Komarek and Anagnostidis (2005). Concurrently, integrated water samples for phytoplankton biovolume estimation were taken down to depth of 20 m and kept in brown bottles preserved using Lugol's solution (Wetzel and Likens, 2000) and stored in the dark. Subsequently, phytoplankton cell counts were done using an inverted microscope (Nikon Diaphot, Nikon, Tokyo; Utermöhl, 1958). Biovolumes of taxa were computed from the individual mean cell measurements using geometric approximations as described by Sun and Liu (2003) and Wetzel and Likens (2000). The cell biovolume was then converted into algal biomass (BM) following the procedures outlined by Wetzel and Likens (2000) and assuming a density of

1. The mean cell size was based on measurements of at least thirty cells for each taxon. Zooplankton was sampled from depth profiles (surface, 1, 2, 3, 4, 5, 7, 10, 15, 20) using a 5 L Schindler. Samples were concentrated through plankton gauze of 30 µm mesh size to ensure inclusion of all groups and preserved with 4% (final concentration) sugar–formalin solution. Total zooplankton counts were made from the concentrated original whole–samples (samples were poured into a gridded glass chamber where pre–selected grids were counted and hand–tallied) and individual densities expressed as number per m^3.

Data analysis

One–way analysis of variance (ANOVA) was used to test the differences between all the environmental variables during the sampling period followed by the Tukey–Kramer *post hoc* multiple comparisons test. SPSS 16.0 software was used in the statistical analysis and variables differences were considered significant at $P < 0.05$. For comparison of phytoplankton community similarities, non-metric multidimensional-scaling (NMDS) was performed based on Bray-Curtis similarities after square-root transformation of biomass data. NMDS resulted in a 2-dimensional solution of 0.10 minimum stress (Kruskal stress value; 1000 iterations). The Bray-Curtis similarity matrix was checked for significant pruning of groups (group average method) via the SIMPROF-routine (999 simulations; $p = 0.05$). Subsequently, the community pattern along artificial axes obtained by NMDS were post-hoc related to environmental variables, normalized prior to calculations, by LINKTREE to seek for variables and their values, which are responsible for dichotomous group separation (999 permutations, minimum group size = 1, minimum split size = 2; minimum split r = 0.0; $p = 0.05$). Community analyses were performed with the statistical package Primer V6.1.15 (Clarke and Gorley, 2006). Graphs were constructed using Sigmaplot version 12.

RESULTS

Physico-chemical characteristics of Lake Wonchi

Lake Wonchi is slightly basic (pH 7.9 – 8.9), dilute (conductivity 185 – 245 µS cm^{-1}) and can be classified as a cold-water tropical high-land lake with a temperature below18 °C (range 14.5 – 17.5 °C). Both vertical gradients and seasonal variations of water temperature were minor (only ≤ 3 °C, Fig. 3), however a strong progressive process in the formation of thermal–stratification was evident during March–December (Fig. 3). At the onset of this period, thermal discontinuity in the water column occurred between 7 and 15 m and gradually extended below 15 m. During March–October it was oscillating between 15 and 40 m, while in December the thermal discontinuity moved up to 10 m, suggesting the beginning of mixing. Complete mixing took place during the cold–dry period in January–February, leaving an isothermal column except for a superficial gradient in the uppermost 0–3 m (Fig. 3).

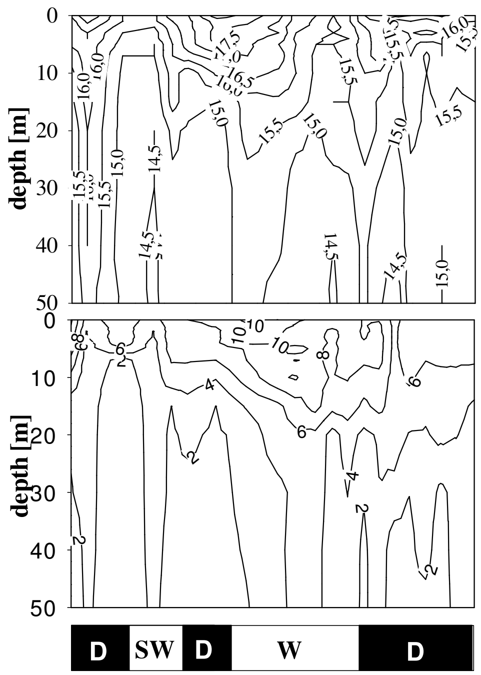

Fig. 3. Depth-time isopleths of temperature (^{O}C, top panel) and dissolved oxygen concentrations (mg L^{-1}, bottom panel) in Lake Wonchi during the sampling period, from December 2011 to January 2013. *Note*: dry season: October-January and April; Short wet season: February-March; wet season: May-September.

A striking feature was the clinograde DO profile, which indicated clear oxygen depletion in greater depths with oxygen saturation values constantly lower than 35% below 15 m (with very few exceptions during the peak rainy season, Fig. 3). There was a significant variation (ANOVA, $F_{(20, 254)}=11.412$, $P=0.00$) in DO concentration over time and depth, with the highest mean value of 8.0 mg L^{-1} recorded in June and the lowest mean value 3.4 mg L^{-1} in January 2012 (Fig. 3).

Table II: Averages and standard deviations (n=20) of physico-chemical variables in Lake Wonchi during the sampling periods (between December 2011 and January 2013).

Variables	Values
Secchi depth (m)	3.78 ± 0.52
Ɛ (m^{-1})	0.41 ± 0.10
Z_{eu} (m)	12.28 ± 4.56
pH	8.43 ± 0.50
TSI	36 ± 2.76
Conductivity (µs cm^{-1})	214.72 ± 16.75
Chlorophyll-*a* (µg L^{-1})	3.04 ± 2.17
Zooplankton biomass (mg dry mass m^{-3})	62.02 ± 25.76
SRP (µg L^{-1})	2.42 ± 2.62
TP (µg L^{-1})	6.05 ± 3.86
NO_2-N (µg L^{-1})	0.46 ± 0.50
NO_3-N (µg L^{-1})	4.72 ± 4.08
NH_4-N (µg L^{-1})	86.47 ± 98.64
Alkalinity (meq L^{-1})	2.31 ± 0.11
Hardness (meq L^{-1})	0.62 ± 0.08
Salinity (‰)	0.1± 0.05
Na (mg L^{-1})	47.74 ± 1.14
K (mg L^{-1})	6.66 ± 0.50
Ca (mg L^{-1})	8.42 ± 0.24
Mg (mg L^{-1})	1.35 ± 0.07
Si (mg L^{-1})	3.56±0.11
Fe (mg L^{-1})	0.127 ± 0.103
Mn (mg L^{-1})	0.113 ± 0.102
Ba (mg L^{-1})	<0.001
Mo (mg L^{-1})	0.031 ± 0.004
Sr (mg L^{-1})	0.020 ± 0.0005
Fluoride (mg L^{-1})	2.70 ± 0.08
Chloride (mg L^{-1})	3.20 ± 0.35
Sulfate (mg L^{-1})	1.14 ± 0.09

A mean (± SD) (n=20) Secchi depth transparency reading of 3.8 ± 0.5 m was calculated during the study period, whereas the vertical extinction coefficient varied between 0.2 and 0.5 m^{-1} (Table II). The annual mean Z_{eu} value (1% surface radiation) for this lake during this study was calculated with around 12 m. The predominant cation concentration sequence in the lake was $Na^+ > Ca^{2+} > K^+ > Mg^{2+}$, while anion concentration appears in the rank $HCO_3^- > Cl^- > F^- > SO_4^{2-}$ (Table II). Element concentrations of Si and trace elements are given in Table II. Several element concentrations were below the detection limit (LOD), nevertheless, Fe and Mn displayed significant spatial variations in concentration, resulting in a fivefold increase of the two elements below 20 m compared with surface water (depth profile data not shown).

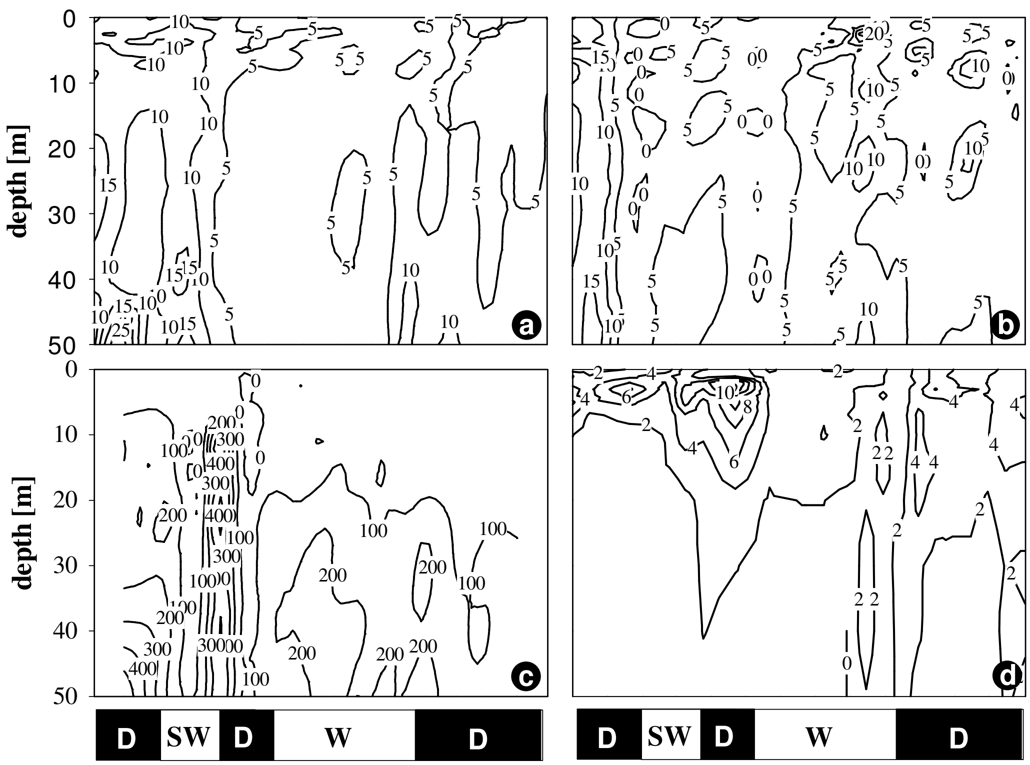

Fig. 4. Depth-time isopleths of major algal nutrients: **a**-P_{tot} (µg L^{-1}), **b**-NO_3-N (µg L^{-1}), **c**-NH_4-N (µg L^{-1}) and **d**-Chl-a (µg L^{-1}) in Lake Wonchi during the sampling period, from December 2011 to January 2013. *Note*: dry season: October-January and April; Short wet season: February-March; wet season: May-September.

Generally, the major algal nutrients showed moderate variations during the wet and dry season, except NH_4–N which significantly increased during the episode of complete mixing (mean range 52 – 220 µg L^{-1}). NO_3–N was generally very low with annual mean (± SD) concentration of 5 ± 2 µg L^{-1} (range 1–13 µg L^{-1}, Table II; Fig. 4b), while NO_2–N was close to the detection limit (Table II). Similarly, the average concentration of SRP was < 5.0 µg L^{-1} in more than 90% of the samples, the relatively highest value recorded was during the period of complete mixing. P_{tot} concentrations were generally lower than 15 µg L^{-1} with an annual mean of 6.0 ± 2.1 µg L^{-1} (Table II, Fig. 4a). Chl-*a* is concentrated in the top 15 m depth with annual average (± SD) of 3.1 ± 1.6 mg m^{-3}, however a deep chlorophyll maximum (DCM) was noted ensuing the onset of the stable stratification period in June–August (Table II, Fig. 4d). Besides, a remarkable seasonal variation in Chl-*a* was observed with a mean maximum of 7.0 mg m^{-3} along the vertical water column measured in April and a lowest mean value of 1.3 mg m^{-3} in September 2012 (Fig. 4d). Based on the Carlson model of trophic state indices for Chl-*a*, P_{tot} and Secchi–disk readings (TSI < 40), the lake is categorized oligotrophic (Table II).

Phytoplankton species composition, biomass and seasonality

We identified 53 phytoplankton taxa distributed in five groups, which were assigned to 15 coda based on the phytoplankton functional group classification (Table III). Green algae (Chlorophyta and Streptophyta) contributed 82% (with a total of 33 taxa) to the total phytoplankton biomass, followed by diatoms (12%, 11 taxa) and Dinophyta (3%, 2 taxa), whereas cyanobacteria and 'others' (taxa which could not be assigned to the taxonomic groups mentioned before) were of minor importance (Table III, Fig. 5).

Table III A checklist of phytoplankton species based on functional groups (FG) and their contribution to the total phytoplankton biomass (%BM) in Lake Wonchi, Ethiopia in 2012. Note: FG codes are from Reynolds et al. (2002) and Padisăk et al. (2009).

Taxon	FG	(%BM)	Taxon	FG	(%BM)
Chlorophytes			**Chlorophytes continued**		
Staurodesmus sp.	**N_A**	0.15	*Dictyosphaerium* sp.	**F**	3.26
Staurastrum pingue	**N_A**	3.63	*Monoraphidium* sp.	**J**	0.12
Staurastrum laeve	**N_A**		*Tetraedron minimum*	**J**	0.97
Staurastrum quadrangulare	**N_A**		*Lagerheimia longiseta*	**J**	0.04
Scenedesmus armatus	**J**	0.26	*Elakatothrix* sp.	**R**	0.00
Scenedesmus quadricauda	**J**				
Acutodesmus acuminatus	**N_A**	0.00	**Bacillariophyceae**		
Cosmarium tenue	**N_A**	41.47	*Synedra* sp.	**D**	0.15
Cosmarium contractum	**N_A**		*Nitzschia* sp.	**D**	0.11
Cosmarium punctulatum	**N_A**		*Diatoma* sp.	**MP**	0.77
Chlorella fusca	**X3**	0.36	*Amphora* sp.	**MP**	1.12
Chlorella vulgaris	**X3**		*Cymbella* sp.	**MP**	0.39
Pediastrum simplex	**J**	4.81	*Navicula* sp.	**MP**	0.18
p. duplex	**J**		*Cyclotella* sp.	**A**	0.58
P. boryanum	**J**		*Tabellaria* sp.	**N**	0.04
Eudorina sp.	**G**	0.34	*Pinnularia* sp.	**MP**	0.00
Zygnema sp.	**N_A**	0.00	*Fragilaria* sp.	**P**	0.13
Closterium praelongum	**P**	7.66	*Cocconeis* sp.	**MP**	9.34
Micrasterias radians	**N_A**	4.89	**Cyanobacteria**		
Euastrum evolutum	**N_A**	0.00	*Anabaena* sp.	**H2**	0.08
Ankistrodesms gracilis	**F**	0.00	*Phormidium* sp.	**T_C**	0.04
Xanthidium antilopaeum	**N_A**	1.14	*Leptolyngbya* sp.	**R**	0.09
X. octocorne	**N_A**		*Chroococcus limneticus*	**L_O**	0.25
Ankyra sp.	**X3**	0.00	**Dinophyta**		
Oocystis sp.	**F**	2.03	*Peridinium cinctum*	**L_O**	14.47
Coelastrum sp.	**J**	0.48	*Peridinium* sp. 2	**L_O**	
Kirchneriella sp.	**F**	0.06	**Cryptophyta**		
Planktosphaeria sp.	**F**	0.00	*Cryptomonas* sp.	**Y**	0.32

Phytoplankton biomass and community succession evidently followed thermal patterns and the subsequent hydrodynamic processes (Fig. 5, top panel). Consequently, non–motile and heavy plankton forms such as desmids (N_A codon) and diatoms (mainly MP, A, N codon) prevailed during the extended periods of thermal instability in March–May and September–November 2012 (Fig. 5, middle panel). *Pediastrum boryanum* (J), *Dictyosphaerium* sp. (F), and *Closterium* *praelongum* (P) contributed significantly to the total phytoplankton biovolume during the complete mixing period January–February 2012, whereas *Xanthidium antilopaeum* (N_A), *Oocystis* sp. (F) and *Staurastrum pingue* (N_A codon) augmented during thermal stability June–August (Fig. 5, middle panel). Apparently, the highest biovolume (3.1 mm^3 L^{-1}; Fig 5, lower panel) recorded in December 2011 was associated with mono–specific occurrence of the dinoflagellate *Peridinium cinctum* (L_O codon). Nevertheless, the bulk of phytoplankton biovolume of Lake Wonchi was dominated by the functional groups N_A, mainly *Cosmarium contractum, C. tenue, C. punctulatum* and *Micrasterias radians*, MP (*Cocconeis* sp.), L_O (*Peridinium cinctum*) and P (*Closterium praelongum*) throughout the sampling period (Table III, Fig. 5); assemblages F–J mainly *Oocystis* sp., *Dictyosphaerium* sp., and *P. boryanum* were sub–dominant.

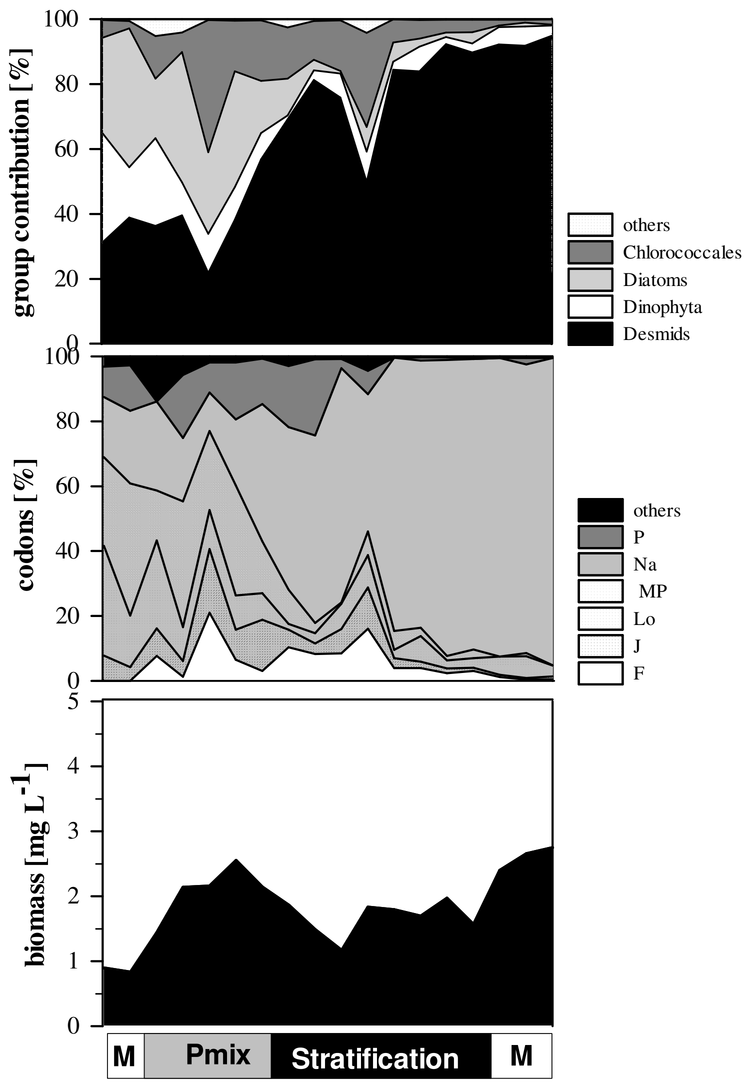

Fig. 5. Temporal changes in the biomass contribution of the main phytoplankton divisions (top), functional groups (middle) and total phytoplankton biomass (mg L^{-1}, bottom) in Lake Wonchi during December 2011 to January 2013.*Note*: complete mixing period: January-February; partial mixing periods: March-May and September-December; stable stratification period: June-August.

NMDS resulted in a 2-dimensional solution (minimum stress 0.1), which revealed clear segregation of phytoplankton community to five groups (Fig. 6), which were also reflected by cluster analysis and SIMPROF-test (data not shown).

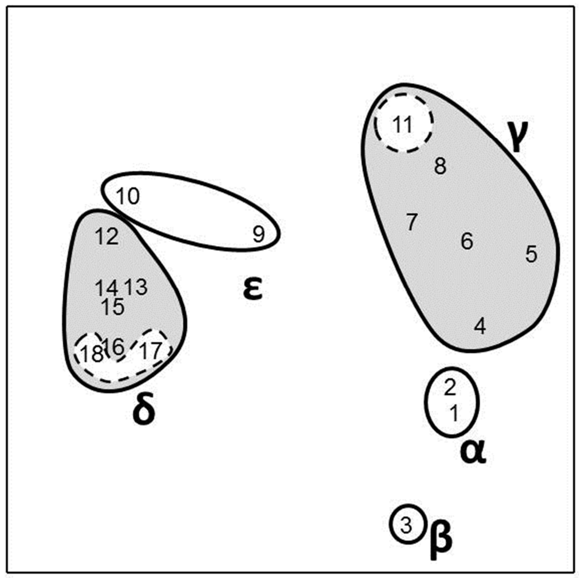

Fig. 6. NMDS-plot of algae taxa. Inclusions indicate significant groups pruned by the SIMPROF routine based on sampling dates (numbers are sampling dates).

Linking the biological data to variables of potential importance by the LINKTREE-routine showed that mixing regime of the water column, specific conductivity, P_{tot}, NH_4-N and zooplankton biomass had major influence on the pattern (Fig. 7). The first split (α) was mainly explained by specific conductivity, which separates samples with conductivity values less than 205 µS cm^{-1} from the rest of the samples with conductivity values above 218 µS cm^{-1}. Changes in *C. reticulata* and *D. excisum* biomass (grazing pressure) determined the second split β, while the third split γ separated from the other dates by elevated conductivity and P_{tot}. Group δ was pruned from the remaining sampling dates by mixing regime of the water column, slightly elevated NH_4-N and P_{tot}, changes in total zooplankton and *D. longispina* biomass; while group ε was separated from group δ and the other dates by changes in *C. reticulata* biomass and slightly elevated NO_3-N and pH (Figs. 6 and 7).

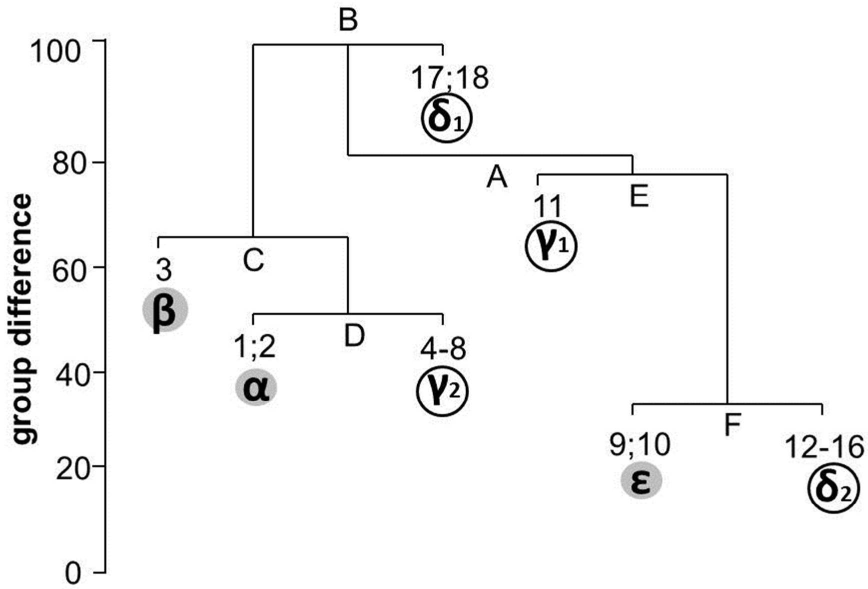

Fig. 7. LINKTREE dendrogram showing significant environmental variables for pruning groups (numbers are sampling dates); labelling corresponds to the nMDS plot (Fig. 6).

DISCUSSION

Lake Wonchi revealed distinct seasonal mixing patterns characterizing Lake Wonchi as warm-monomictic (Fig. 3). The cold-dry season circulation from January–February 2012 was complete and short–lived (Fig. 3), whereas from June to early September a relatively stable stratification developed with a maximum extension of the epilimnion down to 25 m at the end of August which coincided with the main rainy season. Partial and prolonged thermal instability restricted to the epilimnion (which was oscillating between 5 and 30 m depth) has been recognized in Lake Wonchi (Z_{max} = 107 m) during March–May and September–December 2012 (Fig. 3). Such partial–mixing pattern is mainly induced by the marked diurnal fluctuation in air temperature (mean daily air temperature variations was 13.1 °C, Fig. 1), and appears to be a typical feature in deep tropical mountain lakes (Lewis, 1996; Barbosa and Padisák, 2002; Tavera and Martínez–Almeida, 2005). The clinograde DO profile indicated clear oxygen depletion in greater depths, with saturation values constantly lower than 35% below 15 m with very few exceptions (Fig. 3), which is unusual for an oligotrophic lake (Talling and Lemoalle, 1998). Such DO profiles already have been reported from other deep high–altitude lakes located in Cameroon, Uganda, Nepal and the United States (Britt, 1955; Melack, 1978; Kling, 1988; Sharma, 2012) and may reflect long–lasting stratification and – at least for eutrophicated water bodies – high oxygen consumption by decomposition of sinking labile organic matter and respiration of organisms in deeper waters (Baxter *et al*., 1965; Löffler, 1972; Kebede and Belay, 1994; Haberyan *et al*., 1995). For the oligotrophic lake Wonchi, we attribute the strong vertical DO decrease to subterranean inflows rich in ferrous iron and manganese that deplete dissolved oxygen through oxidation processes /(Degefu *et al*. 2014), which has been also noted elsewhere in meromictic oligotrophic lakes (Kjensmo, 1967; Boehere and Schultze, 2008). While bicarbonate as predominant anion is characteristic also in many other lakes, the dominance of sodium as a major cation in Wonchi (47.7 ± 1.1 mg L^{-1}, Table II) is unusual for highland lakes in contrast to water bodies located in the rift valley, which is likely to be attributed to the dominance of acidic volcanics mainly ignimbrite, rhyolite and pumice (Ayenew, 2005). Lake Wonchi also has an increased concentration of F^{-} (2.7 ± 0.01 mg L^{-1}) quite above WHO guideline for drinking water (0.6 –1.5 mg L^{-1}; WHO, 2006), which was also mirrored by mild dental fluorosis of the riparian community. The high level of F^{-} in Wonchi is probably due to leaching from the fluoride rich volcanic rocks around the lake that enrich subterranean (cold and lukewarm springs) drainage.

Concentrations of major nutrients were generally very low with only minor variations on seasonal scale, except for NH_4–N (vertical mean range 52 to 221 µg L^{-1}) which was significantly increased during the cold–dry period of complete mixing (ANOVA, F (20, 254) =2.722, P=0.00). NO_3–N concentrations (mean 5 µg L^{-1}) were low, but are comparable with values obtained from the Ethiopian rift valley lakes Ziway (mean 3.2 µg L^{-1}), Awassa (mean 2.5 µg L^{-1}) and Chamo (mean 3.3 µg L^{-1}); these lakes are however categorized as eutrophic according to the Carlson trophic status index based on Chl-*a*, P_{tot} and Secchi–disk readings (Tilahun and Ahlgren, 2010). The remarkable high accumulation of NH_4–N in deep layers of Lake Wonchi seems to be a common pattern in tropical water bodies (Löffler, 1972; Melack, 1978; Umana, 2001; Eggermont and Russell, 2007; Fetahi *et al*., 2014). The significant increase in NH_4–N along the water column in lake Wonchi is possibly attributed to subterranean inflows rich in ferrous iron and manganese (Degefu *et al.*, 2014a), which possibly deplete dissolved oxygen through reduction processes and subsequently cease bacterial nitrification of ammonia and increases the concentration of NH_4–N (Wetzel, 1975; Talling and Lemoalle, 1998; Tilahun and Ahlgren, 2010).

Phytoplankton biomass expressed as Chl-*a* concentration (3.1 ± 1.6 mg m^{-3}) was low and somehow in the range of other Ethiopian highland lakes Ashenge (1.8 mg m^{-3}, Vijverberg *et al*., 2014) and Dendi (0.1 mg m^{-3}, Degefu *et al*., 2014). The growth of phytoplankton is often limited by several factors such as light supply (Huisman *et al*., 1999; Becker *et al*., 2010), nutrient availability (Huisman and Weissing, 2001; Reynolds, 2006), water temperature (Grover and Chrzanowski, 2006) and a cascading effect *via* trophic interactions (Spencer and King, 1984; Shurin *et al*., 2006; Iglesias *et al*., 2011). The generally low phosphorus amounts clearly indicated P–limitation of phytoplankton (Reynolds, 1997). Another limiting factor for phytoplankton growth is irradiance supply. The ratio of mixed depth to euphotic depth (Z_{mix}/Z_{eu}) of 1.4 suggests that phytoplankton cells are not light-limited; Strickland (1965) and Wood *et al*. (1978) have proposed a ratio of 4 to 5 above which light availability limits phytoplankton production.

The phytoplankton community composition of Lake Wonchi is characterized by high diversity of the N_A–P codon contributing > 60% to the total phytoplankton biovolume, with *Cosmarium contractum, C. tenue, C. punctulatum*, *Micrasterias radians* and *Closterium praelongum* being the most abundant taxa (Table III). Such high contribution of planktonic desmids appears to be typical of oligo/meso/dystrophic water bodies (Hutchinson, 1967; Reynolds, 1984; Sommer, 1985; Gerrath, 2003; Schabetsberger *et al*., 2004). Desmids are favoured by several environmental factors such as low nutrient concentrations (Hutchinson, 1967; Reynolds, 1984), low total ion contents (Talling and Talling, 1965; Wetzel, 1983) and moderate pH (Wood and Talling, 1988). Additionally, circulation patterns of the water column may take precedence and possibly favors the relatively heavy, immobile and fast-sinking planktonic species to remain within the epilimnion extending over several m (Gunkel and Casallas, 2002; Martínez–Almeida and Tavera, 2005; Fetahi *et al*., 2014). This process was first recognised by Lewis (1973) in Lake Lanao, the Philippines, as strong progressive process in the formation of unstable layers of different densities on a daily basis, due to marked diurnal fluctuation in air temperature and the subsequent daytime heating and nocturnal cooling. Later on, the phenomenon was widely recognised as partial–atelomixis *sensu* Barbosa and Padisăk (2002), and its ecological significance in structuring phytoplankton communities and intuitively their seasonal succession, mostly in favour of the planktonic desmids and diatoms in deep tropical high–mountain lakes was emphasized (Barbosa and Padisăk, 2002; Tavera and Martinez-Almeida, 2005; Betânia, *et al*., 2008; Souza *et al*., 2008; Fetahi *et al*., 2014). We found a higher diurnal range of air temperatures (13.1 °C, Fig. 1) than annual variations on a daily basis (≤ 4 °C, Fig. 2), which possibly imposed short-time layers of different densities that explain the persistence of high diversity and dominance of desmids (N_A codon) together with oligotrophic conditions. Similar observations were noted in Lake Dom Helvécio, South-East Brazil by Betânia *et al*. (2008), who found perpetual dominance of the functional group N_A. The almost monospecific occurrence of the slowly growing K–strategist *Peridinium cinctum* shortly before the onset of complete mixing in December 2011 (Fig. 5, top panel) was probably attributed to nutrient–depletion and indicates the ecophysiological adaptation of codon L_O to limnological stress at oligotrophic conditions (Oda and Bicudo, 2006). Nonetheless, *P. cinctum* biomass crashed during complete mixing (Fig.5, bottom panel) and was replaced by N_A–MP–F–J codons. Based on NMDS, the primary factor that regulates desmids (N_A codon) and coccal green algae (F-J codon) were the mixing regime of the water column, conductivity, Nitrate-N and pH, which probably indicate the prolonged dry season (Fig. 8). The significant association of diatoms (MP codon) with total zooplankton and *D. longispina* biomass represented in the NMDS suggested seasonal variation in the strength of community grazing rates, which also determine phytoplankton assemblages (McQueen *et al*., 1986).

The pelagic zooplankton standing biomass in Lake Wonchi showed a significant seasonal variation and positive correlation with Chl-*a* concentrations ($r = 0.5$, $N = 20$, $p = 0.037$), suggesting a strong effect of zooplankton on phytoplankton biomass, which has also been observed elsewhere (Brooks and Dodson 1965; Jeppesen *et al*. 1997b). Therefore, zooplankton grazing rate also plays a pivotal role in regulating phytoplankton biomass in the system. Nonetheless, the overall mean standing biomass of zooplankton was 62 mg m^{-3} dry mass, which is low compared to the results obtained from the East African lakes Ziway (133.5 mg m^{-3}, Dagne *et al*., 2008), Hayq (236.4 mg m^{-3}, Fetahi *et al*., 2011), Kivu (188 mg m^{-3}, De Iongh *et al*. 1995), George (368 mg m^{-3}, Burgis, 1974) and Chad (333 mg m^{-3}, Carmouze *et al*., 1983), but it is in the range obtained from Lake Awasa (Mengestou *et al*., 1991). In general, Cladocerans form the major zooplankton biomass (53%) in Lake Wonchi, contrasting to copepods which accounted over 50% to the total abundance (Degefu and Schagerl, Submitted). Apparently, the contribution of rotifers to the total zooplankton standing biomass during this study was tenfold less than other zooplankton components.

CONCLUSIONS

In Wonchi, partial–atelomixis combined with the apparent low nutrient supply are key variables in structuring phytoplankton community composition, which was quite stable and characterized by high diversity of relatively heavy, immobile and fast-sinking planktonic desmids (N_A codon) followed by diatoms (MP codon). Such a high diversity and the stable biovolume of N_A codon indicate oligotrophic conditions highly sensitive to stable thermal stratification and nutrient enrichment, demonstrating the significance of phytoplankton autecology for monitoring the ecological status of tropical aquatic ecosystems as it is in temperate region. The lake can be classified as a cold-water tropical high–mountain lake with a temperature below18 ^{O}C; as a result the eurythermal planktivorous fish species, *O. niloticus* (optimum range for recruitment 22–28 ^{O}C) might not able to establish breeding populations irrespective of the apparent diverse desirable phytoplankton taxa and high biomass of large–bodied cladocerans in the lake.

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REFERENCES

APHA. (1998) Standard Methods for the Examination of Water and Wastewater. 20th edn. American Public Health Association, Washington DC, USA.

Ayenew, T. (2005) Major ions composition of the groundwater and surface water systems and their geological and geochemical controls in the Ethiopian volcanic terrain. *SINET: Ethiop. J. Sci.,* **28**,171-188.

Barbosa, F.A.R. and Padisák, J. (2002) The forgotten lake stratification pattern: atelomixis. *Verh. Int. Ver. Limnol.,* **28**, 1385-1395.

Baxter, R.M., Prosser, M.V., Talling, J.F. *et al*. (1965) Stratification in tropical African lakes at moderate altitude (1500-2000 m). *Limnol. Oceanogr.*, **10**,510-520.

Becker, V., Caputo, L., Ordonez, J. *et al*. (2010) Driving factors of the phytoplankton functional groups in a deep Mediterranean reservoir. *Water Research,* **44**, 3345–3354.

Beneberu, G. and Mengistou, S. (2009) Oligotrophication trend of Lake Ziway, Ethiopia. *SINET: Ethiop. J. Sci.,* **32**,141-148.

Betânia, M., Souza, G., Cristiane, F. *et al*. (2008) Role of atelomixis in replacement of phytoplankton assemblages in Dom Helvécio Lake, South-East Brazil. *Hydrobiologia,* **607,** 211-224.

Boehere, B. and Schultze, M. (2008) Stratification of lakes. *Rev. Geophysics,* **46**, 11-23.

Britt, N.W. (1955) Stratification in western Lake Erie in summer of 1953: effects on the Hexagenia (Ephemeroptera) population. *Ecology,* **36**, 239-244.

Brooks, J.L. and Dodson, S.I. (1965) Predation, body size, and composition of plankton. *Science,* **150**, 28-35.

Burgis, M.J. (1971) The ecology and production of copepods, particularly *Thermocyclopes hyalinus*, in the tropical Lake George, Uganda. *Freshw. Biol.*, **1**, 169-192.

Carlson, R.E. (1977) A trophic state index for lakes. *Limnol. Oceanogr.,* 22: 361-369.

Carpenter, R.S. and Kitchell, F.J. (1993) Cascading trophic interactions. In Carpenter, R.S. and Kitchell, F.J. (eds), *The Trophic Cascade in Lakes*. Cambridge University Press, Cambridge: pp. 385.

Carmouze, J.P., Durand, J.R. and Leveque, C. (1983) Ecology and productivity of a shallow tropical ecosystem. Monographiae Biologicae, Dr W Junk Publishers, The Hague, pp. 575.

Clarke, R.J. and Gorley, R.N. (2006) Primer V6: user manual/tutorial. PRIMER-E, Plymouth.

Dagne, A., Herzig, A., Jersabek, C. *et al*.(2008) Abundance, species composition and spatial distribution of planktonic rotifers and crustaceans in Lake Ziway (Rift Valley, Ethiopia). *Int. Rev. Hydrobiol.,* **93**, 210-226.

Degefu, F., Herzig, A., Jirsa, F. *et al*. A limnological snapshot of three, highly threatened tropical high-mountain crater lakes in Ethiopia. *Tropical Conservation Science*, submitted for publication.

De Iongh, H.H., Spliethoff, P.C. and Roest, F. (1995) The impact of an introduction of sardine into Lake Kivu. In Pitcher, T.J. and Hart, P.J.B. (eds), *The Impact of Species Change in African Lakes*. Chapman and Hall, Fish and Fisheries Series pp. 277-297.

Eggermont, H. and Russell, M.J. (2007) Physical and chemical limnology of alpine lakes and pools in the Rwenzori Mountains, Uganda-DR Congo. *Hydrobiologia,* **592**,151-173.

Fetahi, T., Mengistu, S. and Schagerl, M. (2011) Zooplankton community structure and ecology of the tropical-highland Lake Hayq, Ethiopia. *Limnologica,* **41,** 389-397.

Fetahi, T., Schagerl, M. and Mengistu, S. (2014) Key drivers for phytoplankton composition and biomass in an Ethiopian highland lake. *Limnologica,* **46**, 77-83.

Figueredo, C.C. and Giani, A. (2001) Seasonal variation in the diversity and species richness of phytoplankton in a tropical eutrophic reservoir. *Hydrobiologia*, **445**, 165-174.

Figueredo, C.C. and Giani, A. (2009) Phytoplankton community in the tropical lake of Lagoa Santa (Brazil): Conditions favouring a persistent bloom of *Cylindrospermopsis raciborskii*. *Limnologica*, **39**, 264-272.

Ganf, G.G. (1974c) Phytoplankton biomass and distribution in a shallow, equatorial lake (Lake George, Uganda). *Oecologia*, **16**, 9-24.

Gerrath, J.F. (2003) Conjugating green algae and desmids. In Wehr, J.D. and Sheath, R.G. (eds), *Freshwater algae of North America*: *Ecology and Classification*. Academic Press, New York, pp.918.

Grover, J.P. and Chrzanowski, T.H. (2006) Stoichiometry and growth kinetics in the “smallest zooplankton” Phagotrophic flagellates. *Arch. Hydrobiol.,* **167,** 467–487.

Gunkel, G. and Casallas, J. (2002) Limnology of an equatorial high mountain lake—Lago San Pablo, Ecuador: the significance of deep diurnal mixing for lake productivity. *Limnologica*, **32**, 33–43.

Haberyan, K.A., Umana, G., Collado, C. *et al*. (1995) Observations on the plankton of some Costa Rican lakes. *Hydrobiologia*, **312**, 75-85.

Hecky, R.E. and Kling, H.J. (1981) The phytoplankton and protozooplankton of the euphotic zone of Lake Tanganyika: species composition, biomass chlorophyll content, and spatio-temporal distribution. *Limnol. Oceanogr.,* **26**, 548-564.

Huisman, J., van Oostveen, P. and Weissing, F.J. (1999) Critical depth and critical turbulence: two different mechanisms for the development of phytoplankton blooms. *Limnol. Oceanogr.,* **44,** 1781-1787.

Huisman, J. and Weissing, F.J. (2001) Competition for nutrients and light in a mixed water column: a theoretical analysis. *Am.Nat.,* **146**, 536-564.

Hutchinson, G.E. (1967) A treatise on limnology: *Introduction to lake biology and limnoplankton*. John wiley and Sons, New York.

Iglesias, C., Mazzeo, N., Meerhoff, M. *et al*. (2011) High predation is of key importance for dominance of small-bodied zooplankton in warm shallow lakes: evidence from lakes, fish exclosures and surface sediments. *Hydrobiologia,* **667**,133- 147.

Jeppesen, E., Jensen, T.P., Søndergaard, M. *et al*. (1997b) Top-down control in freshwater lakes: the role of nutrient state, submerged macrophytes and water depth. *Hydrobiologia,* **343**, 151-164.

Kebede, E. and Belay, A. (1994) Species composition and phytoplankton biomass in a tropical African lake (Lake Awasa, Ethiopia). *Hydrobiologia,* **288**, 13-32.

Kjensmo, J. (1967) The development and some main features of iron meromictic soft water lakes. *Arch. Hydrobiol.,* **32,** 137-312.

Kling, G.W. (1988) Comparative transparency, depth of mixing, and stability of stratification in lakes of Cameroon, West Africa. *Limnol. Oceanogr.,* **33,** 27-40.

Komărek, J. and Anagnostidis, K. (2005) Freshwater Flora of Central Europe: *Cyanoprokaryota 19/2*. Elsevier GmbH, München, pp.759.

Krom, M.D. (1982) Spectrophotometric determination of ammonia: a study of a modified Bertholet reaction using salicylate and dichlorisocyanurate. *Analyst,* **105**, 305–316.

Lewis, Jr. W.M. (1973) The thermal regime of Lake Lanao (Philippines) and its theoretical implications for Tropical Lakes. *Limnol. Oceanogr.,* **18**, 200-217.

Lewis, Jr. W.M. (1996) Tropical lakes: how latitude makes a difference. In Schiemer, F. and Boland, K.T. (eds), *Perspectives in Tropical Limnology*.SPB Academic Publishing, Amsterdam.

Löffler, H. (1972) Contribution to the limnology of high mountain lakes in Central America. *Int. Revue ges. Hydrobiol*., **57**, 397- 408.

Martínez-Almeida, V. and Tavera, R. (2005) A hydrobiological study to interpret the presence of desmids in Lake Zirahuén, México. *Limnologica*, **35**, 61-69.

McQueen, D.J., Post, J.R. and Mills, E.L. (1986) Trophic relationships in freshwater pelagic eco-systems. *J. Fish Aquat. Sci*., **43,** 1571-1581.

Melack, J.M. (1978) Morphometrical, physical and chemical features of the volcanic crater lakes of western Uganda. *Arch. Hydrobiol.,* **84,** 430-453.

Mengistu, S., Green, J. and Fernando, C.H. (1991) Species composition, distribution and seasonal dynamics of Rotifera in a Rift Valley lake in Ethiopia (Lake Awasa). *Hydrobiologia,* **209**, 203-214.

Oda, A.C.R. and Bicudo, C.E.M. (2006) Ecology of *Peridinium gatunense* and *Peridinium umbonatum* (Dinophyceae) in a shallow, tropical, oligotrophic reservoir (IAG pond), Sao Paulo, southeast Brazil. *Acta Limnol. Bras*. **18**, 165-180.

Oduor, S.O. and Schagerl, M. (2007) Temporal trends of ion contents and nutrients in three Kenyan Rift Valley saline-alkaline lakes and their influence on phytoplankton biomass. *Hydrobiologia*, **584,** 59-68.

Popovsky, J. and Pfiester, L.A. (1990) *Freshwater Flora of Central Europe*: Dinophyceae (Dinoflagellida). Gustav Fischer Verlag, Stuttgart, pp. 272.

Reynolds, C.S. (1984) *The ecology of freshwater phytoplankton*. Cambridge University Press, Cambridge.

Reynolds, C.S. (1997) Vegetation process in the pelagic: a model for ecosystem theory. In Kinne, O. (eds), *Excellence in Ecology*. ECI, Oldendorf.

Reynolds, C. (2006) *Ecology of phytoplankton*. Cambridge University press, Cambridge, pp. 535-539.

Roldán, G. (1992) *Fundamentos de Limnología Neotropical*. Fen-Universidad de Antioquia, Medellín: pp. 529.

Sánchez, M. (2011) Variaction de la clorofila 'a' fitoplanctónica y sus mecanismos de control en un lago atalasohalino tropical. Tesis de Maestría en Ciencias del Mar y Limnología. Instituto de Ciencias del Mar y Limnología, UNAM, Mexico, pp.66.

Schabetsberger, R., Drozdowski, G., Drozdowski, I. *et al*. (2004) Limnological aspects of two tropical Crater lakes (Lago Bio and Lago Loreto) on the island of Bioko, Equatorial Guinea. *Hydrobiologia,* **524**, 79-90.

Shapiro, J. and Wright, D.I. (1984) Lake restoration by biomanipulation round Lake, Minnesota, the first two years. *Freshw. Biol.,* **14**, 371-384.

Sharma, M.C., Sharma, S., Bajracharya, M.R. *et al*. (2012) First results on bathymetry and limnology of high-altitude lakes in the Gokyo Valley, Sagarmatha (Everest) National park, Nepal. *Limnology*, **13,** 181-192.

Shurin, J.B., Gruner, D.S. and Hillebrand, H. (2006) *All wet or dried up? Real differences between aquatic and terrestrial food webs*. Proceedings of the Royal Society, pp. 1-9.

Sommer, U. (1985) Comparison between steady state and non-steady state competition: Experiments with natural phytoplankton. *Limnol. Oceanogr.,* **30**, 335-346.

Sondergaard, M., Jeppesen, E., Mortensen, E. *et al*. (1990) Phytoplankton biomass reduction after planktivorous fish reduction in a shallow, eutrophic lake: a combined effect of reduced internal P-loading and increased zooplankton grazing. *Hydrobiologia*, **200**, 229-240.

Souza, M.B., Barros, C.F.A., Barbosa, F. *et al*. (2008) Role of atelomixis in replacement of phytoplankton assemblages in Dom Helvécio Lake, South-East Brazil. *Hydrobiologia*, **607**, 211-224.

Spencer, C.N. and King, D.L. (1984) Role of fish in regulating of plant and animal communities in eutrophic ponds. *Can.J.Fish.Aquat.Sci.*, **41**, 1851-1855.

Strickland, J.D. (1965) Phytoplankton and marine primary production. *Ann. Rev. Microb.*, **19**, 127-162.

Sun, J. and Liu, D. (2003) Geometric models for calculating cell biovolume and surface area of phytoplankton. *J. Plankton Res.*, **25,** 1331-1346.

Tadesse, Z. (1999) The nutritional status and digestibility of Oreochromis niloticus L. diet in Lake Langano, Ethiopia. *Hydrobiologia,* **417,** 97-106.

Talling, J.F. (1987) The phytoplankton of Lake Victoria (East Africa). *Arch. Hydrobiol.,* **25**,229-256.

Talling, J.F. and Driver, D. (1963) Some problems in the estimation of chlorophyll a in phytoplankton. In: proceedings of a Conference on Primary Productivity Measurements, Marine and Freshwater, US Atomic Energy Commission, TID 7633: pp. 142-146.

Talling, J.F. (1971) The underwater light climate as a controlling factor in the production ecology of freshwater phytoplankton. *Mitt.Int.Ver.Limnol.* **19**, 214-243.

Talling, J.F. and Lemoalle, J. (1998) *Ecological dynamics of tropical inland waters*. Cambridge University Press, UK.

Talling, J.F. and Talling, I.B. (1965) The chemical composition of African lake water. *Internationale Revue Der Gesamten. Hydrobiologia*, **50,** 421-463.

Tavera, R. and Martinez-Almeida, V. (2005) Atelomixis as a possible driving force in the phytoplankton composition of Zirahuén, a warm-monomictic tropical lake. *Hydrobiologia*, **533**, 199-208.

Tilahun, G. and Ahlgren, G. (2010) Seasonal variations in phytoplankton biomass and primary production in the Ethiopian Rift Valley lakes Ziway, Awasa and Chamo-The basis of fish production. *Limnologica*, **40**, 330-342.

Umana, V.G. (2001) Limnology of Boots Lake, a tropical crater lake in Costa Rica. *Rev. Biol. Trop.,* **49**, 1-10.

Utermöhl, H. (1958) Zur Vervollkommnung der quantitativen Phytoplankton-Methodik. *Mitt. Internat. Ver. Limnol*., **9**, 1–38.

Vijverberg, J., Dejen, E., Getahun, A. *et al*.(2014) Zooplankton, fish communities and the role of planktivory in nine Ethiopian lakes. *Hydrobiologia,* **722**, 45-60.

Wetzel, R.G. (1975) *Limnology*. WB, Saunders, Philadelphia, Pennsylvania, USA.

Wetzel, R.G. (1983) *Limnology*. 2nd edn. Saunders College Publishing, Philadelphia.

Wetzel, R.G. and Likens, G.E. (2000) *Limnological Analyses.* 3rd edn. Springer Verlag, New York.

Willen, E. (1976) A simplified method of phytoplankton counting. *J. Br. Phycol.* **11**, 265-278.

Whitford, L.A. and Schumacher, G.J. (1973) A Manual of Freshwater Algae. Sparks Press, Raleigh, NC, pp.324.

WHO. (eds) (2006) *Fluoride in Drinking–water*. A series of World Health Organization monographs. IWA Publishing, Geneva.

Wood, R.B., Prosser, M.V. and Baxter, R.M. (1978) Optical characteristics of the Rift Valley Lakes of Ethiopia. *SINET: Ethiop. J. Sci.*, **1**, 73-85.

Wood, R.B. and Talling, J.F. (1988) Chemical and algal relationships in a salinity series of Ethiopian inland waters. *Hydrobiologia*, **158**, 29-67.

Chapter 3

Zooplankton abundance, species composition and ecology of tropical high–mountain crater Lake Wonchi, Ethiopia

Zooplankton– *indispensable channel*

in the transfer of energy from the primary producers to secondary consumers

Chapter 3

Zooplankton abundance, species composition and ecology of tropical high-mountain crater Lake Wonchi, Ethiopia

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ABSTRACT

The highlands of Ethiopia represent some of the remnants of undisturbed aquatic ecosystems; they are however highly threatened by significant socio–economic developments and associated anthropogenic impact. Lake Wonchi is one of the few remaining fairly pristine high–mountain crater lakes in the central highlands and has never been investigated. We present a first study on zooplankton taxa composition, abundance and biomass conducted over more than one year including the underlying environmental drivers. The lake is slightly basic (pH 7.9 – 8.9), dilute (specific conductivity 185 – 245µS cm^{-1}) and oligotrophic with mean trophic status index of 36. The zooplankton community composition showed moderate species richness comprising a total of fourteen taxa with six cladocerans, one copepod and seven rotifers. Simpson´s index of diversity with values between 0.6 and 0.8 pointed towards a homogenous taxa occurrence within the single sample units. The overall mean (±SD) standing biomass of zooplankton was 62.02 ± 25.76 mg dry mass m^{-3}, which is low compared to other highland and rift valley lakes in Ethiopia. Cyclopoid copepods, in particular *Thermocyclops ethiopiensis* were the most abundant group and contributed 50% to the total zooplankton abundance followed by cladocerans (38%) and rotifers (12%). Non-metric multi-dimensional scaling resulted in a 3-dimenensional model, which revealed similar community composition on successive sampling dates except in December/January and May. Temperature, alkalinity, conductivity and nitrate-N had significant influence on this seasonal pattern. A weak, but significant positive correlation ($r = 0.482$, $N = 20$, $p = 0.037$) between Chlorophyll *a* and zooplankton biomass mirrors a bottom-up effect of phytoplankton biomass on zooplankton dynamics. The zooplankton of Lake Wonchi displayed

some degree of segregation along the epi– and metalimnion during this study. The results show that intense interspecific competition, rather than fish predation, is the key factor structuring the vertical distribution of zooplankton.

Keywords: Lake Wonchi, zooplankton, competition, vertical distribution, trophic classification

INTRODUCTION

Although zooplankton research of Ethiopian lakes has been conducted earlier (e.g. Bryce, 1931; Cannicci and Almagia, 1947), our contemporary knowledge is far from complete. Former studies were based mainly on samples collected by expeditions, and thus provided scanty information on long-term patterns in their seasonality and dynamics. Our understanding on zooplankton in East Africa has been slowly developing (Defaye, 1988; Fernando *et al*., 1990; Mengestou *et al*., 1991; Dagne *et al*., 2008). Some studies were able to explore zooplankton associations along ecosystem gradients mainly in the rift valley region (Wodajo and Belay, 1984; Mengestou and Fernando, 1991; Vijverberg *et al*., 2014). Later on, an account of information on zooplankton of Ethiopian crater lakes, particularly from Bishoftu in the vicinity of Debre-Zeit city some 50 km southeast of the capital Addis Ababa, was documented by Green (1986), Green and Mengestou (1991) and Lemma (2007, 2008, 2009). Nevertheless, contemporary limnological studies with special emphasis on zooplankton in Ethiopia are shifting from the southeastern rift valley region to the highland lakes in the northern escarpments. For instance, Dejen *et al*. (2004) have documented the temporal and spatial distribution of zooplankton in relation to turbidity and other environmental factors from Lake Tana, while Wondie and Mengistu (2006) investigated the developmental stages, biomass and rate of production of copepods in the lake. Imoobe and Akoma (2008, 2009) investigated spatial variations in the composition and abundance of zooplankton in the Bahir Dar Gulf of lake Tana. Furthermore, Fetahi *et al*. (2011) have been recently initiated detailed limnological investigations on the highland tropical Crater Lake Hayq in the northernmost part of Ethiopia focusing on food webs and energy flows and the underlying limnological variables. More recently, abundance, species composition and spatial distribution of zooplankton in Lake Hashengae were described by Haileselasie *et al*. (2012), whilst Dejene *et al*. (2012) gave a detailed account of data on the cladoceran community composition in a series of 32 tropical reservoirs in the highlands of northern Ethiopia.

In contrast to such a remarkable build-up of literature on zooplankton fauna of lakes in the rift valley region and northern escarpments of Ethiopia, the Crater Lake Wonchi in the central highlands has never been investigated, presumably due to seclusion and lack of infrastructure. Ironically *Cyprinus carpio* and *Oreochromis niloticus* were introduced in Lake Wonchi by the National Fisheries and Other Aquatic Life Research Centre (NFLARC) in the late 1990s in an attempt to establish a pelagic fishery and to increase availability of protein for the local communities. Degefu *et al*. (unpublished) did a snap-shot survey recently on the ichthyofauna of the lake and reported that the latter species did not establish breeding populations. We hypothesize that low plankton biomass and water temperature could probably be the cause behind the failure of *O. niloticus* to inhabit this water body.

The productivity of aquatic ecosystem is strongly influenced by the amount of available resources (bottom-up control), however, it is often the food web structure, particularly the abundance and size structure of the zooplankton (top-down grazing effect), which suppress phytoplankton biomass (Carpenter *et al*., 1985; Lampert and Sommer, 1997; Scheffer, 1998; Dejene *et al*., 2012). In this regard, zooplankton plays a key role in channeling the transfer of energy from the primary producers to secondary consumers in aquatic ecosystems (Lampert and Sommer, 1997). Hence, holistic understanding of zooplankton dynamics in aquatic ecosystems has an implication for fish recruitment and production (Brooks and Dodson, 1965; Shapiro and Wright, 1984; Carpenter and Kitchell, 1993).

We studied for the first time the seasonal dynamics of zooplankton in relation to underlying environmental variables over a year in a deep tropical–highland Crater Lake. It was also interesting to corroborate the *'visual predator avoidance hypothesis'* in the lake where strict–planktivorous fish is absent, which may imply that there is no need of performing diurnal vertical movement of the zooplankton. Our study will additionally provide baseline data against which future changes can be monitored. Virtually no information is available on this lake, whereas exploitation of the lake is undergoing without comprehensive understanding of its physico–chemical and biological limnology.

METHODS

Study area

The deep oligotrophic crater lake Wonchi, is located at $8^{o}47'$ N and $37^{o}53'$ E at an altitude of 2887 m above sea level some 150 km southwest of the capital city of Ethiopia Addis Ababa. It is deep, steeply shelving with a surface area of 5.6 km^2 (Tab. 1; Fig. 1).

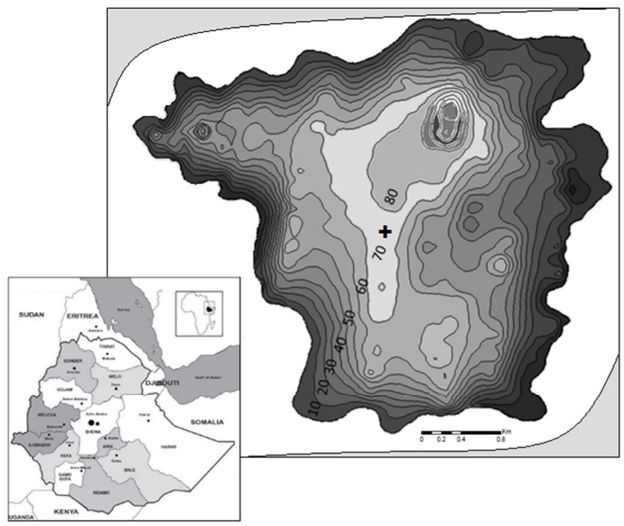

Fig. 1. Bathymetric map of Lake Wonchi in southwest escarpment of Ethiopia (✚ the primary sampling site with GPS coordinates $08^{o}48'035''$N and $37^{o}53'592''$E).

The shoreline is mostly rocky and gravelly and inhabited by beds of submerged aquatic macrophytes mainly *Potomageton* sp.. The height of its crater rim from the lake surface is about 460 m. The Lake has a closed basin with no surface inlet.

Tab. 1. Morphometry of Lake Wonchi

Variables	Values
Location	$8^{o}47'$ N$7^{o}53'$ E
Max. length (east-west: 60^{o} from north)	3.8km
Max. width	2.2km
Max. depth	107m
Mean depth	28m
Shoreline length	13.362km
Surface area	5.6km^2
Volume	0.185km^3

It receives water primarily from rainfall falling directly on its surface, and subterranean cold and lukewarm springs. The lake region is characterised by sub–humid type of climate with an annual rainfall of 1200 mm. The diel air temperature varies from 13 to 22 ^{o}C during the day time and falls below 10^{o}C in the night (Fig. 2; Ethiopia National Meteorological Service Agency).

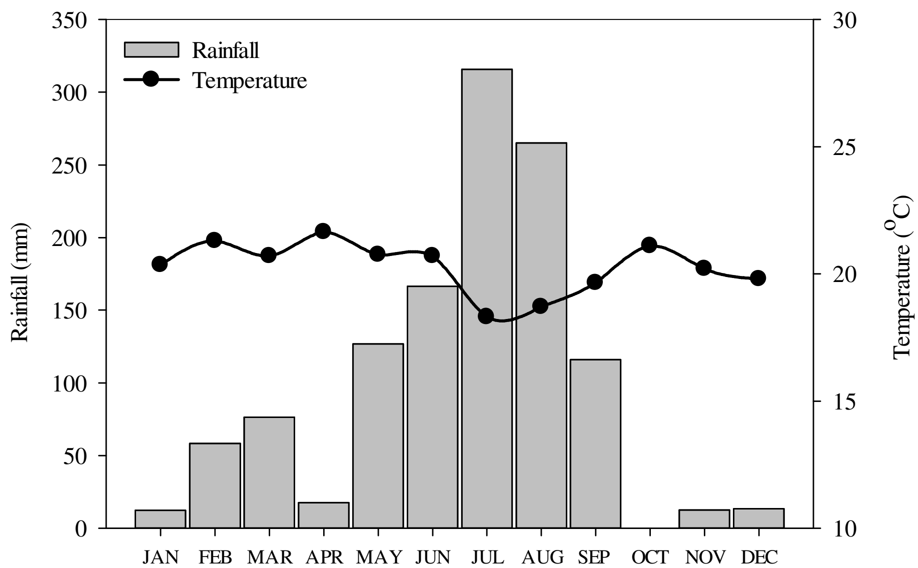

Fig. 2. Air temperature and rainfall data around Lake Wonchi during the sampling period. Data provided from the Ethiopian National Meteorological Service Agency.

Field sampling and analyses

The study was carried out on a fortnightly basis between December 2011 and January 2013 at an open–water station marked with GPS (depth: 50 m, coordinates: 08^{o}48’035”N and 37^{o}53’592”E). Physico–chemical variables such as water temperature, dissolved oxygen (DO), salinity, specific conductivity (corrected to 25 ^{o}C) and pH were measured *in-situ* in vertical profiles using a multi-probe (Model HQ40D, HACH Instruments). 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) using 5 L Schindler sampler. Samples were transferred to 2 L acid–prewashed plastic bottles and stored in the dark in a cooling box (4^{O}C) until analyses of nutrients and alkalinity were made at National Fisheries and Aquaculture Research Center, Ethiopia. For water chemistry, standard methods were applied (Tab. 2).

Tab. 2. Specific methods used for the determination of alkalinity, major ions and nutrients.

Variables/ions, nutrients	Analytical method	Reference
Total alkalinity	HCl titration	APHA (1998)
Total phosphorus (P_{tot})	Persulphate digestion and ascorbic acid method	APHA (1998)
Soluble reactive phosphorus (SRP)	Ascorbic acid method	Murphy and Riley (1962)
Total nitrogen (T_{tot})	Persulphate digestion, Cd reduction and diazotization method	APHA (1998)
Nitrate-nitrogen (NO_3-N)	Sodium salicylate method	APHA (1998)
Nitrite-nitrogen (NO_2-N)	Diazotization	Legler (1988)
Ammonium-nitrogen (NH_4-N)	Sodium salicylate-hypochlorite method	APHA (1998)
Soluble reactive silica (SiO_2-Si)	Ammonium molybdate-EDTA method	Wetzel and Likens (2000)
Major ions	Suppressed ion chromatography	APHA (1998)

For ions, samples were acidified with nitric acid (Trace SELECT ® by FLUKA) and analyzed at the University of Vienna, Austria. Water transparency (vertical visibility) was estimated using a standard secchi disc of 20 cm diameter. For Chl-*a* analysis, raw samples were gently filtered through Whatman GF/C filters. Filters were stored at –20° C to assist cell bursting. Filters were then homogenized in 90% cold acetone using a tissue grinder and stored in a refrigerator at 4° C overnight. After centrifugation, the supernatant was measured spectrophotometrically (Talling and Driver, 1963; Wetzel and Likens, 2000). Subsequently, the Trophic State Index (TSI) proposed by Carlson (1977) was computed based on transparency, Chl-*a*, total dissolved nitrogen (TDN) and total phosphorus (P_{tot}).

For qualitative zooplankton analysis, triplicate samples were collected from two stations (littoral and pelagic zone) using plankton nets of 30 and 100 µm mesh size for rotifers and crustaceans, respectively. Zooplankton was enumerated and identified to species level under a WILD stereoscope microscope (magnification 100-400x) using keys of Koste (1978), Defaye (1988), Korovchinsky (1992), korinek (1999) and Fernando (2002). To determine numerical abundance, samples were collected from depth profiles at open–water station using 5 L Schindler sampler (surface, 1, 2, 3, 5, 7, 10, 15 and 20 m). Water samples were filtered and concentrated through plankton gauze of 30 µm mesh size to ensure inclusion of rotifers and preserved with sugar–formalin solution to a final concentration of 4%. Total counts were made from the concentrated original whole-samples (samples were poured into a gridded glass chamber where pre-selected grids were counted and hand- tallied) and individual densities expressed as number per m^3. All developmental stages of copepod species were pooled together and counted as total copepodites and nauplii stages, while for cladocerans all stages were counted together as one age class. For biomass estimation, the entire samples during the study periods were pooled, 50-100 (based on their densities) individuals with different size class were arbitrarily sorted and body lengths measured. The body size of crustaceans was measured excluding the caudal setae, spines and projections and converted into biomass according to Dumont *et al*. (1975) via length–weight regression equations, using the linear form:

$$\text{Ln}\,(W) = \ln a + b\ln\,(L) \qquad \text{(eq. 1)}$$

Where L is body length in mm, a is estimate of intercept, b is estimate of the slope and W is body mass in µg dry mass (DM). Biovolumes of rotifers were computed from individual size measurements using geometric approximations as described by Ruttner-Kolisko (1977). These volumes were subsequently used to estimate fresh mass, assuming a density of 1.0 (volume of 10^6 μm^3 = 1 µg fresh weight). A wet–dry mass conversion factor of 0.1 was used for all genera except for *Asplanchna*, for which a factor of 0.039 was considered (Dumont *et al*., 1975). Zooplankton species standing biomass was computed based on the product of species specific dry mass and mean abundance of species for the sampling date.

A 24 h sampling program was carried out to consider zooplankton diel vertical migration (DVM) in June 21-22, 2012 (weather condition: rainy; new moon). Samples were collected at 4 h intervals, between 6:00 a.m. in the first day and 2:00 a.m. the following day from surface, 1, 2, 3, 5, 7, 10, 15 and 20 m using a 5 L Schindler sampler. Subsequently, the samples were filtered, preserved and counted as described earlier.

Data analysis

To identify the dominance of single species/even taxa distribution, Simpson´s index of diversity was estimated following McCune and Grace (2002). Similarity of species composition between consecutive sampling dates (pre-treatment of abundances 4^{th} root transformation for down weighting dominant taxa; Clarke & Gorley 2006) was assessed by Bray–Curtis similarity index. Non-metric multi-dimensional scaling (nMDS) was performed based on Bray–Curtis similarities in order to display succession patterns in the species composition during the sampling period. Subsequently, the community pattern along artificial axes obtained by nMDS were post-hoc related to environmental variables, normalized prior to calculations, by BIO-ENV (999 permutations, $p = 0.001$; Rho = 0.359). LINKTREE was employed to seek for variables and their values, which are responsible for dichotomous group separation (minimum group size = 1; minimum split size = 2; minimum split r = 0.0; $p = 0.1$). All the statistical analyses were performed using the statistical package Primer 6 version 6.1.15 (Clarke and Gorley, 2006). One–way analysis of variance (ANOVA) was used to test the differences between all the environmental variables during the sampling period followed by the Tukey–Kramer *post hoc* multiple comparisons test. SPSS 16.0 software was used in the statistical analysis and variables differences were considered significant at $P < 0.05$. Graphs were constructed using sigmaplot version 12.

RESULTS

Climatic and physico–chemical variables

Meteorological data such as rainfall and air-temperature showed a clear seasonality in Lake Wonchi. There are two rainy seasons in the area: the main rainy season is between May and September peaking during July and August, while the minor one extending from February to March (Fig. 2). The cold-dry season is distinguished between October and January. The lake was characterized by high underwater transparency (annual mean Secchi-depth 4 m) and low water temperatures with a maximum of 17.5 ^{O}C in April and a minimum of 14.8 ^{O}C in January (Fig. 3). The vertical and seasonal variation of water temperature during the study period was small (≤ 3 ^{O}C, Fig. 3).

There was a significant variation (ANOVA, F (20, 254)=11.412, P=0.00) in DO concentration over time and depth, with the highest mean value of 8.0 mg L^{-1} (116%) recorded in June and the lowest mean value 3.4 mg L^{-1} (46%) in February 2012 (Fig. 3).

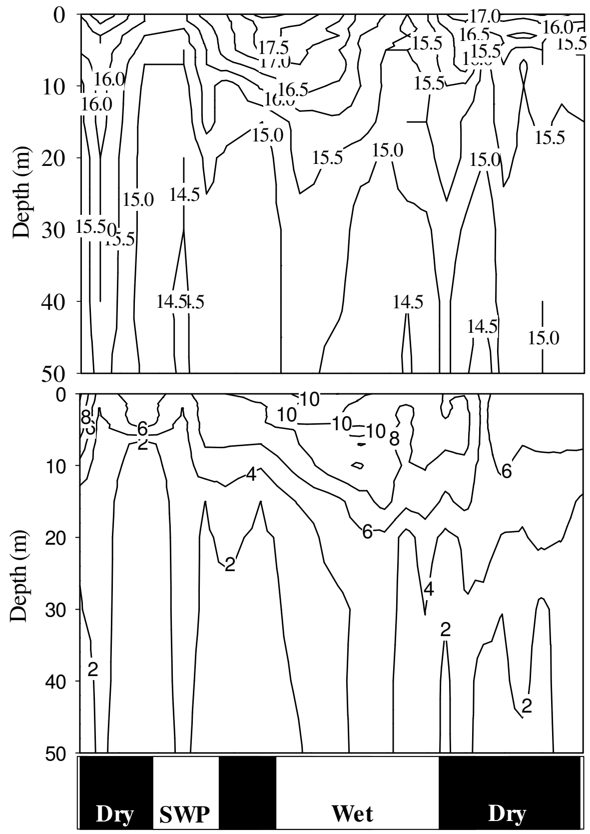

Fig. 3. Depth-time isopleths of temperature (^{O}C, top panel) and dissolved oxygen concentrations (mg L^{-1}, bottom panel) in Lake Wonchi during the sampling period, from December 2011 to January 2013. *Note*: dry season: October-January and April; Short wet season: February-March; wet season: May-September.

The lake water was generally basic and dilute with a relatively narrow range of pH 7.9 to 8.9 and conductivity ranging from 186 to 245 µS cm^{-1}, respectively. TDN and P_{tot} showed significant variation along the water column with annual mean (±SD) values of 91 ± 46 and 6 ± 3 µg L^{-1} respectively, but the seasonal variation was not significant. Apparently, Chl-*a* exhibited marked variations coupled with seasonality. The maximum value (7.0 µg L^{-1}) was recorded in April during the dry period and decreased progressively to a lowest value (1.3 µg L^{-1}) in September during the main rainy season (Fig. 4). Based on the TSI for Chl-*a*, $P_{tot,}$ Secchi-depth and TDN values, the lake is categorized oligotrophic.

Spatio-temporal patterns in the zooplankton community and biomass

The pelagic zooplankton standing biomass in Lake Wonchi showed significant seasonal variations with the highest total biomass in the dry and short-wet seasons (November, March and April) and the lowest biomass during peak rainy season, July-August, 2012 (Figs. 4 and 5). The overall mean (±SD) standing biomass of zooplankton for Lake Wonchi was 62.02 ± 25.76 mg DM m^{-3}. Cladocerans contributed 53% to the total zooplankton biomass, whereas copepods and rotifers contributed 39% and 8%, respectively (Fig.4, top-panel).

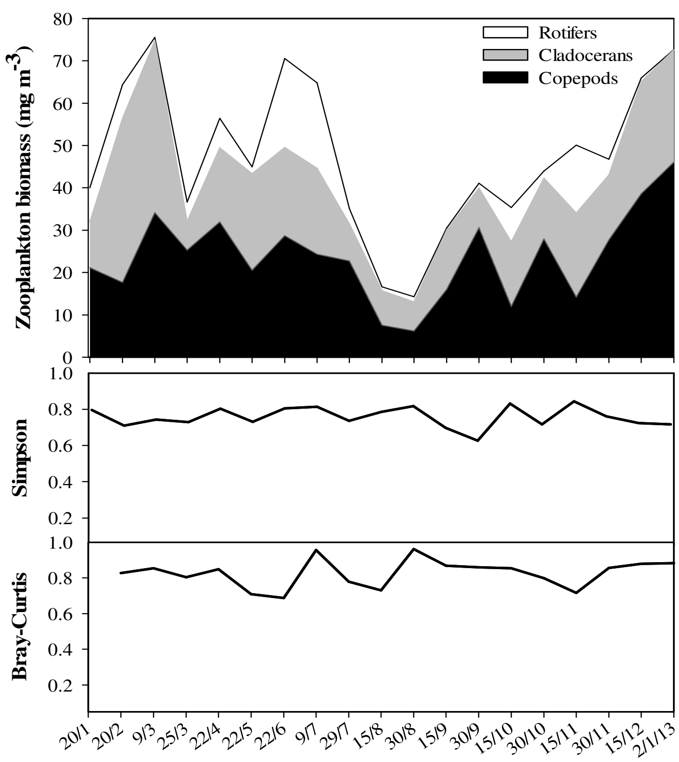

Fig. 4. Zooplankton biomass (groups; top), Simpson´s index of diversity (center) and Bray-Curtis similarity (bottom).

The highest biomass of cladocerans (89.96 mg DM m^{-3}) was recorded in March 2012, while the lowest biomass (12.42 mg DM m^{-3}) was recorded during the last week of July 2012, respectively (Fig. 4, top-panel). In contrast, highest biomass (42 mg DM m^{-3}) of copepods was recorded during the dry and short-wet seasons, however its relative importance declined substantially during the rainy-season (Fig.4, top-panel). The contribution of rotifers to the total zooplankton standing biomass during this study (range: 0.25 – 30.52 mg DM m^{-3}) was far less. Apparently, there was a weak, but significant positive correlation between Chl-*a* and zooplankton biomass ($r = 0.482$, $N = 20$, $p = 0.037$) throughout the study period (Fig. 5).

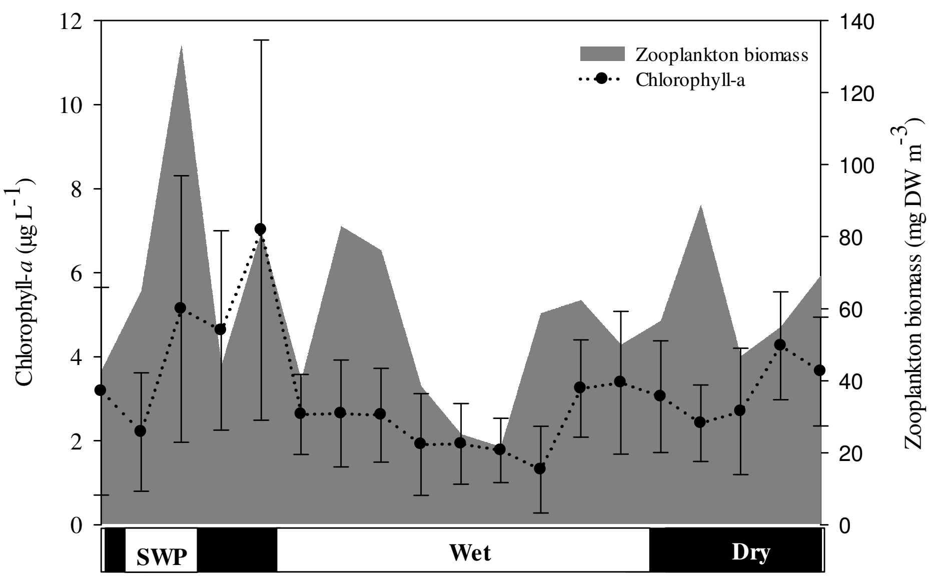

Fig. 5. Temporal trends in mean (± SD) phytoplankton biomass (Chl-*a,* µg L^{-1}) and total zooplankton standing biomass (mg DW m^{-3}) in Lake Wonchi during the study period. *Note*: dry season: October-January and April; Short wet season: February-March; wet season: May-September.

A total of fourteen zooplankton taxa were identified indicating moderate species richness: six cladocerans, one copepod and seven rotifers. Seven species comprised more than 95% of the total zooplankton abundance (Tab. 3). Copepods were the most abundant group and contributed considerably (50%) to the total zooplankton abundance followed by cladocerans (38%) and rotifers (12%, Tab. 3). Nevertheless, copepods were the least in terms of species richness and represented only by *Thermocyclops ethiopiensis* (Tab. 3). Simpson´s index of diversity with values between 0.6 and 0.8 (Fig.4, center panel) pointed towards a homogenous taxa occurrence within the single sample units. However, zooplankton abundance exhibited temporal variations in concomitance with hydrological cycle, with copepods ranging from 3 x 10^3 to 118 x10^3 and from 0.6 x 10^3 to 63 x 10^3 Ind m^{-3} during dry and peak rainy season, respectively. Amongst the cladocerans, *Daphnia longispina, Ceriodaphnia reticulata* and *Bosmina longirostris* (which accounted for 40%, 22% and 31% of total cladocerans, respectively) were dominant throughout the sampling period (Tab. 3). Other cladoceran species such as *Diaphanosoma excisum* and *Moina micrura* (which made up to 7% of the cladoceran community) were common, whereas *Chydorus sphaericus* was very rare (Tab. 3). Apparently, *D. longispina, C. reticulata* and *Diaphanosoma excisum* did not co-exist in higher number: *D. longispina* significantly dominates (40%) the cladoceran community and the latter two species were either absent or present at very low abundance. The rotifers in Lake Wonchi were typical cosmopolitan species (Tab. 3). The annual mean abundance of rotifers (8 x 10^3 Ind m^{-3}) was 5-fold lower than crustaceans (42 x 10^3 Ind m^{-3}). *Keratella cochlearis* and *Asplanchna sieboldii* were the dominant rotifer species and accounted more than 88% to the total rotifer abundance. *K. cochlearis* attained the highest mean abundance (19x10^3 Ind m^{-3}) in June/July 2012 and almost disappeared during the short-wet period when the cladocerans abundance peaked (41 x 10^3 Ind m^{-3}). Apparently, the omnivorous invertebrate *A. sieboldii* (mean: 4-6x10^3 Ind m^{-3}) predominated the total rotifer community in November and April 2012 during the cold-dry months.

Tab. 3. Zooplankton species found in Lake Wonchi with their mean relative abundance based on Ind m^{-3} during December 2011 to January 2013.

Zooplankton groups	Relative abundance (%)
Copepoda	
Thermocyclops ethiopiensis Kiefer, 1934	29.60
Copepod nauplii	20.45
Cladocera	
Daphnia longispina (O.F. Müller, 1776)	14.33
Diaphanosoma excisum Sars, 1885	1.43
Bosmina longirostris (O.F. Müller, 1776)	13.64
Ceriodaphnia reticulata Jurine	7.04
Moina micrura Kurz, 1874	1.51
*Chydorus sphaericus (*Müller, 1785)	< 0.1
Rotifera	
Asplanchna sieboldii (Leydig, 1854)	2.23
Trichocerca gracilis (Tessin, 1890)	0.26
Filinia longiseta	< 0.1
Keratella cochlearis (Gosse, 1855)	9.06
Polyarthra sp.	< 0.1
Brachionus caudatus Barrois & Daday, 1894, 1766	0.41
Brachionus dimidiatus Bryce, 1931	< 0.1

Zooplankton displayed some dispersion along the epi– and metalimnion. The dominant cladoceran *D. longispina* was almost exclusively aggregated in the narrow band of 1– 4 m (Fig. 6). In contrast, *C. reticulata* was relatively evenly distributed down to 10 m exhibiting its peak abundance at 3.5 m of water column, while *B. longirostris* was clustered between 4 and 9 m of depth (Fig. 6). *Thermocyclops ethiopiensis* and copepod nauplii were found along the entire epilimnion, however, 50% of their relative biomass was recorded around 3 m (Fig.6). The dominant rotifers *K. cochlearis* and *A. sieboldii* occupied different depth-habitats during the study period, with *K. cochlearis* dwelling between 1 and 8 m, and *A. sieboldii* staying closer to the upper layers of the water column between 0 and 4 m, respectively. The DVM data did not show significant migration patterns between day and night for all zooplankton taxa during our 24 h sampling (Fig. 7). Interestingly, the dominant species displayed a bimodal vertical distribution, with a shallow peak at 3–5 m, and a deeper one at the depth of 10–15 m (Fig. 7).

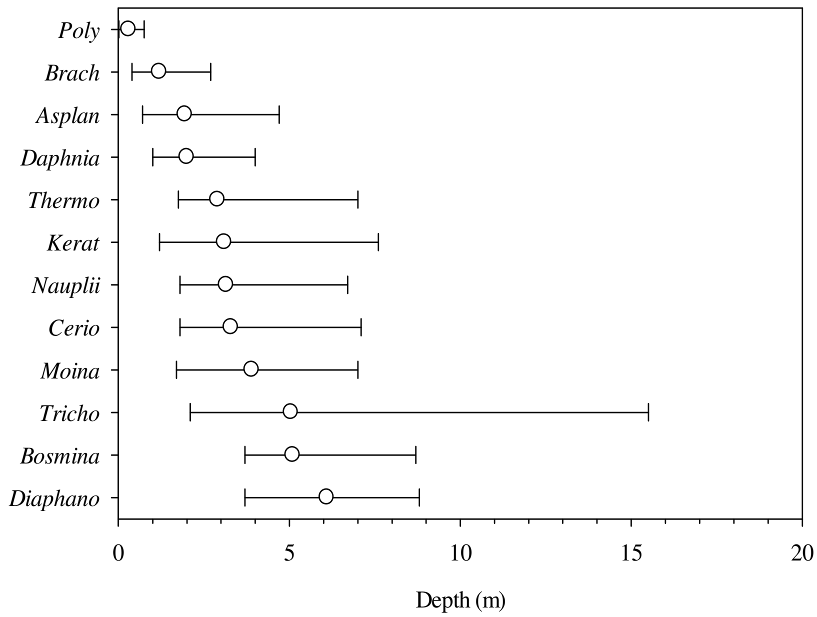

Fig. 6. The vertical distribution of zooplankton taxa summarized over the sampling period. 25-50-75% of relative abundance at certain depths based on mg m^{-3} (n, %) (N = 20).

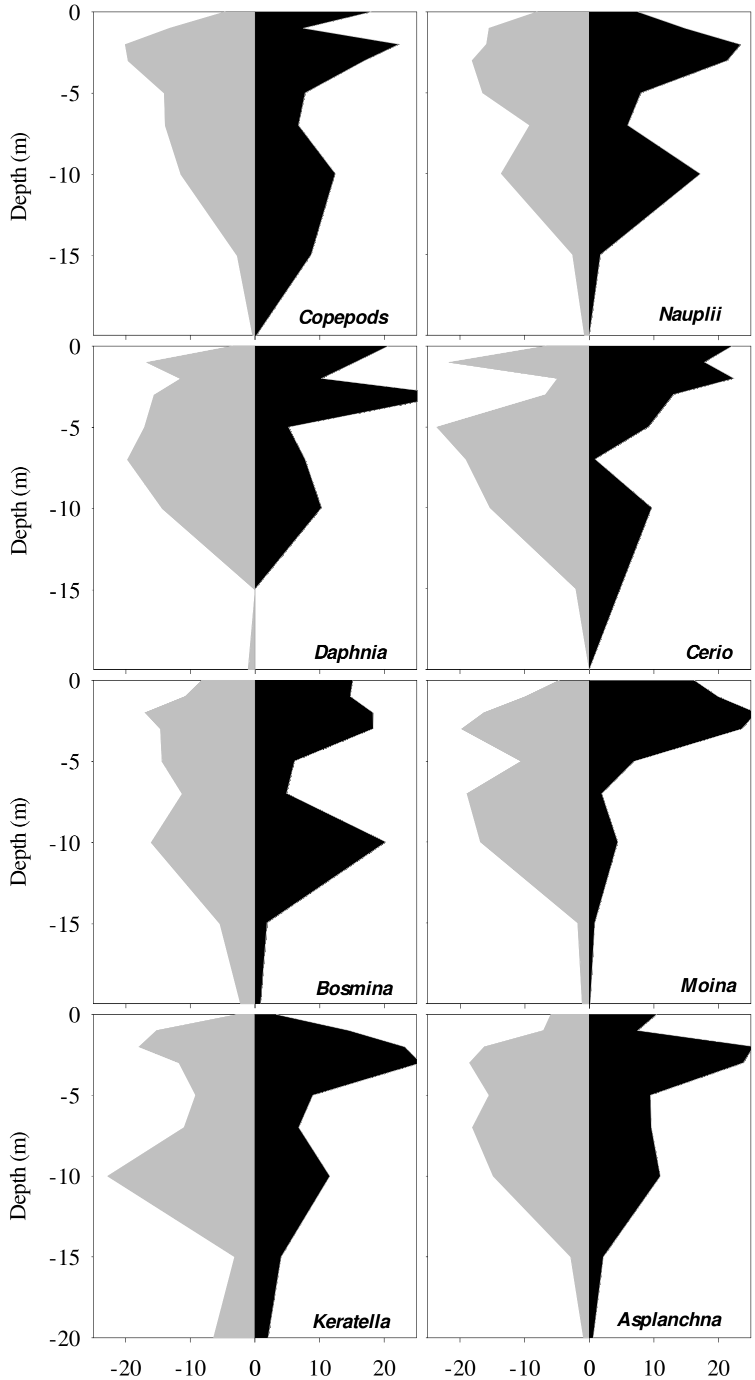

Fig. 7. Day (grey; mean of 6, 10, 14 hr) and night (black; mean of 18, 22, 2 hr) distribution of taxa during a 24 hr sampling. Data presented as percentage over depth.

nMDS resulted in a 3-dimensional model (minimum stress 0.1), which revealed similar community composition on successive sampling dates except May (group A) and December–January (group B; Fig. 8). Linking the biological data to variables of potential importance showed that temperature, alkalinity, specific conductivity and NO_3-N had major influence on the pattern (BIOENV-test routine) and revealed that group A (Fig. 8) was separated from the other dates by a slightly elevated temperature of 16.6°C and alkalinity of 2.52 meq L^{-1} (LINKTREE; $p < 0.05$), while group B was pruned from the remaining sampling dates by conductivity < 185 µS cm^{-1} (LINKTREE; $p < 0.10$).

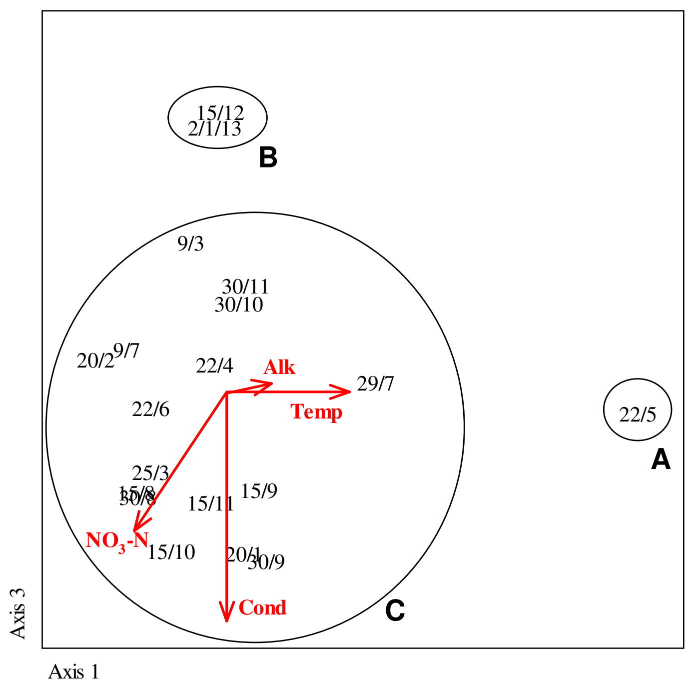

Fig. 8. nMDS-plot of zooplankton taxa with post-projected variables and grouping according to LINKTREE routine (arrows: Alk-total alkalinity, Temp-temperature, Cond- conductivity).

DISCUSSION

Zooplankton species composition, abundance and biomass

The pelagic zooplankton standing biomass in Lake Wonchi showed a significant seasonal variation and positive correlation with Chl-*a* concentrations, which mirrors a bottom-up effect of phytoplankton on zooplankton dynamics in the lake, which has also been documented elsewhere (Brooks and Dodson, 1965; Jeppesen *et al*., 1997). The drop of zooplankton biomass during the rainy season was likely caused by low abundance of post-nauplii during this period due to the significant decrease in algal biomass and the subsequent intense competition by *D. longispina* for limited food sources. The overall mean standing biomass of zooplankton around 62.02 mg DM m^{-3} is low compared to the results obtained from other East African lakes (Tab. 4).

The zooplankton abundance of Lake Wonchi was dominated by cyclopoid copepods, *Thermocyclops ethiopiensis* (50%) and cladocerans (38%), which is in agreement with several other authors, who also reported low rotifer abundance and high crustacean diversity in other high-mountain tropical lakes (Gillooly and Dodson, 2000; Dejen *et al*., 2004; Fetahi *et al*., 2011; Dejenie *et al*., 2012; Haileselasie *et al*., 2012). Comparison of zooplankton species composition from Lake Wonchi with the data from other high-mountain lakes in Ethiopia revealed some remarkable trends (Tab. 4).

Tab. 4. Zooplankton numerical abundance, biomass and chlorophyll-*a* content of Lake Wonchi in comparison to other highland and rift valley lakes in Ethiopia.([a] present study; [b] Fetahi *et al*., 2011; [c] Wondie and Mengistu, 2006; [d] Dagne *et al*., 2008; [e] Mengistou, 1989; [f] Haileselasie *et al*., 2012).

Lake	Copepod (Ind m^{-3})	Copepod biomass (mg DM m^{-3})	Cladoceran (Ind m^{-3})	Cladoceran biomass (mg DM m^{-3})	Total biomass (mg DM m^{-3})	Mean Chl-*a* µg l^{-1}
Wonchi	23,852[a]	23.30[a]	18,091[a]	32.81[a]	62.02[a]	3.1[a]
Hayq	67,280[b]	161.46[b]	8,422[b]	75[b]	236.4[b]	12.9[b]
Tana	37,210[c]	34.43[c]	__	__	__	9.8[c]
Ziway	220,000[d]	43.74[d]	__	27.22[d]	133.5[d]	23.6[d]
Awasa	59,929[e]	36.93[e]	2,616[e]	__	44.9[e]	19.0[e]
Hashengae	328,000[f]	__	218,800[f]	__	__	1.1[f]

For instance, a seasonal study on zooplankton community composition from the high altitude tropical Lake Hayq showed that the species composition is depauperate and was dominated by *Thermocyclops ethiopiensis* and *D. magna* (Fetahi *et al*., 2011), which is in accordance with this study. Similarly, Dejen *et al*. (2004) and Haileselasie *et al*. (2012) reported the dominance of crustaceans and the co-occurrence of temperate and tropical species in lakes Tana and Hashengae. The dominance of crustaceans is quite exceptional to the scenario observed in most lowland tropical water bodies, where the less competitive and smaller planktonic species, mostly rotifers, predominating (Burgis, 1971; Fernando, 1980b; Nilssen, 1984; Fernando *et al*., 1990; Dumont, 1994; Dagne *et al*., 2008; Lemma, 2009). The possible explanations for the paucity of rotifers in Lake Wonchi could be either high predation from the abundant *Thermocyclops ethiopiensis* or strong competition from *D. longispina* for limited food sources (mean algal biomass Chl-*a*: 3.1 ± 1.6 µg l^{-1}). Such exploitative competition between crustaceans and rotifers and the mechanism by which especially large-bodied cladoceran (e.g. *Daphnia*) suppress rotifer populations have already been well documented (Brooks and Dodson, 1965; Gilbert, 1988; Fernando *et al*., 1990; Walz, 1995; Shurin *et al*., 2006). In this regard, cladocerans are considered to be the most effective grazers in freshwater lakes and at times tend to ingest over 80% of the phytoplankton biomass (Lampert, 1988; Jeppesen *et al*., 1997b; Shurin *et al*., 2006; Iglesias *et al*., 2011). *Daphnia* are more efficient exploiters of shared, limited resources in such oligotrophic lakes and significantly suppress the phytoplankton biomass and hence other inferior competitors like rotifers (Brooks and Dodson, 1965; Gilbert, 1988; Lampert and Rothhaupt, 1991). Indeed, this was evident in Lake Wonchi, where rotifers (in particular *K. cochlearis*) were almost vanished during the short-wet period when the cladocerans (mainly *D. longispina*) abundance peaked to their mean maxima for the study period (Fig. 5, top panel). However, they recurred and exhibited peaks during the dry periods (April and December), where increasing temporal variation in the phytoplankton abundance was also observed coupled with the lake mixing period (Figs. 3 and 5, top panel). Therefore, exploitative competitions between the obligate grazers significantly dictate their seasonal succession in Lake Wonchi, probably to avoid similar food niches. Nevertheless, nMDS analysis indicated comparable community composition on consecutive sampling dates except during December, January and April (Fig. 7), which coincided with the dry season. BIOENV-test routine also revealed that group A was separated from the other dates by a slightly elevated temperature and alkalinity, while Group B was pruned from the remaining sampling dates by slight change in conductivity.

Contrasting to copepods, our investigations revealed relatively high diversity of the limnetic cladocerans (Tab. 3), which is probably attributed to their high dispersal rate as compared with copepods. Cladocerans have a special ability to produce resting eggs parthenogenetically during unfavorable conditions and hence viable resting eggs are transported into remote isolated waterbodies by waterbirds as they migrate between lakes (Brooks, 1957; De Meester *et al*., 2002; Figuerola and Green, 2002; Green *et al*., 2002). Besides, *D. longispina* was copious in Lake Wonchi (40% of total cladoceran abundance), which is in contrast with the general opinion that large-bodied species of cladocerans are sporadic or lacking in tropical water bodies (Dumont, 1994; Gillooly and Dodson, 2000; Meerhoff *et al*., 2007; Dejenie *et al*., 2012). The plausible explanations are: (1) the lack of strict zooplanktivorous in the pelagic zone. Degefu et al. (unpublished) reported that *Cyprinus carpio* (a facultative zooplanktivorous species) and *Garra* sp. (a riverine, strict benthic species) are the only fish species inhabited Lake Wonchi with very low abundance. This further pointed towards a weak top-down control of zooplankton, which was also observed elsewhere in a series of mesocosm experiments using *Garra* sp. as sole zooplanktivorous organism (Dejenie *et al*., 2012); (2) the high altitude (2887 m) at which the lake is located and the subsequent low water temperature (annual mean: 15.7 ± 0.6 ^{O}C) for a tropical lake. Similar evidence was documented from the highland Lake Tana in Ethiopia, where high abundance and diversity of large-bodied cladocerans including temperate species such as *D. hyaline* and *C. dubia* were identified (Dejen *et al*., 2004). At a first glance, the occurrence of large-bodied cladocerans is contradicting the findings of decreasing size with latitude. Gillooly and Dodson (2000) demonstrated the decrease in the body size of limnetic cladocerans across latitude, suggesting that water temperature difference is pivotal factor for the observed pattern, since the upper thermal tolerance of large-bodied cladocerans (mainly *Daphnia*) is surpassed in tropical and subtropical lakes. Besides, size-selective predation of fish is substantial in tropical lakes due to the indirect effect of high water temperature on fish recruitment and the subsequent predation impact of high biomass of 0+ fishes on daphnids (Flik, 2000; Lemma, 2007). Interestingly, high-mountain lakes in tropical regions appear to be exceptional to the general view of latitudinal patterns of cladoceran body size recounted. For instance, Fernando *et al*., (1987) and Green (1995) reported large-bodied cladocerans from both temperate and high-mountain tropical lakes. In these studies, the authors found more similarities in the thermal regimes of tropical high-mountain lakes with those lakes at higher latitude, than lakes at lower elevations at the same latitude. Therefore, we assume that low water temperatures rather than fish predation is the key factor for the observed dominance of the daphnids in Lake Wonchi. Also Dejen *et al*., (2004), Fetahi *et al*., (2011) and Dejenie *et al*. (2012) noted similar evidence from the high-altitude water bodies in Ethiopia, despite tilapia fish (strict planktivorous) dominating the pelagic fisheries.

Vertical distribution of zooplankton

It is generally accepted that the vertical distribution patterns of zooplankton is induced by factors such as water temperature, UV-radiation, food availability, oxygen saturation, competition and predation (Stich and Lampert, 1981; Dagg, 1985; Loose and Dawidowicz, 1994; Winder *et al*., 2004). Zooplankton of Lake Wonchi displayed some degree of segregation along the epi- and metalimnion during the study period, which is probably stimulated by strong interspecific competition among the obligate grazers to avoid similar niches for limited food sources. This was mainly evident among the herbivorous filter-feeders (Fig. 7). *D. longispina* almost exclusively occupied the upper section of the epilimnion, where food is more abundant (annual mean Chl–*a* ~ 4 µg L^{-1} in the top 10 m, data not shown) and did not descend below 4 m in higher number. *D. excisum* and *C. reticulata* displayed relatively broader vertical distribution and occupied the lower boundaries of the epilimnion, whereas *B. longirostris* was restricted to the upper section metalimnion (Fig. 7). As the water column did not display apparent vertical gradients in the key physico-chemical variables (e.g. DO concentrations 0-15 m was fairly above 2 mg O_2 L^{-1}, a threshold concentration for cladocerans), competitive exclusion for limited resources probably accounted for the vertical distribution of the herbivorous filter-feeders. It was evident that inferior competitors such as *B. longirostris* circumvented the upper section of the epilimnion (Fig. 7). Such intense exploitative competition has already been reported earlier: DeMott and Kerfoot (1982) indicated that *Bosmina* is strongly suppressed by competition from *Daphnia.* Besides, Johnsen and Jakobsen (1987) have also noted earlier that daphnids remain in the surface and exhibit small amplitude of vertical migration when food is limiting, irrespective of the risk of predation and high fluxes of damaging UV- radiation. This is in agreement with our observations, as *D. longispina* was restricted to the upper section of the water columns, attaining maximum annual mean density at 2 m. Apparently, copepods almost co-existed with *D. longispina* along the entire epilimnion irrespective of their wide overlap in food spectrum. Nevertheless, copepods can ingest large food particles and select between food items to avoid competitive exclusion from cladocerans, as has been well-documented earlier (Gliwicz, 1980; De Moott, 1988).

In Lake Wonchi, the dominant rotifer species displayed a clear-cut spatial segregation during the entire study period. Interestingly, the invertebrate predator *A. sieboldii* occupied the uppermost section of epilimnion, whereas the herbivorous *K. cochlearis* was restricted to the lower boundaries of epilimnion (Fig. 7). The extended distribution of *K. cochlearis* to the metalimnion is probably a behavioral response to evade both competition (exploitative and interference) and predation at the surface from *D. longispina* and *A. sieboldii*, respectively. Apparently, *K. cochlearis* survived in the metalimnion probably due to its evolutionary adaptation to low food concentrations, which is also a characteristic feature for oligotrophic conditions (Ruttener-Kolisko, 1974, Walz 1995, 1997). Additionally, *K. cochlearis* can ingest small particles such as bacteria (Boon and Shiel, 1990), which are probably abundant in the meta– and hypolimnion of Lake Wonchi owing to lukewarm subterranean inflows rich in ferrous iron below 7 m depth (Degefu *et al*., unpublished). Interestingly, the DVM study during our 24 hr sampling displayed bimodal distribution of zooplankton abundance in Lake Wonchi (Fig. 8). The first peak (at 3–5 m) was associated with algal biomass maxima (annual mean Chl-*a* in upper epilimnion, data not shown), while a deeper one at the depth of 10–15 m was probably attributed to increased bacteria numbers. This remains however speculative until further research will be conducted to quantify bacteria abundance and elucidate the trophic role and interaction of zooplankton grazing on bacteria in the lake.

CONCLUSIONS

The zooplankton community composition of Lake Wonchi harbours both temperate and tropical species possibly due to the high altitude at which the lake is located. Numerical abundance is approximately an order of magnitude lower than in other comparable Ethiopian highland lakes owing to low trophic status of the lake (TSI < 36). The seasonal dynamics of zooplankton biomass in Lake Wonchi was mainly correlated with Chl-*a* concentration, which reflects a bottom-up effect of algal biomass on zooplankton. It can be assumed that intense interspecific competition for limited food sources, rather than fish predation pressure, is the key factor structuring the vertical distribution of zooplankton in Lake Wonchi.

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RERERENCES

APHA, 1998. Standard Methods for the Examination of Water and Wastewater. 20th edn. American Public Health Association, Washington DC, USA.

Boon PL, Shiel RJ, 1990. Grazing on Bacteria by Zooplankton in Australian Billabongs. Aus J Mar Freshwt Res 41: 247-257.

Brooks JL, 1957. The systematic of North American *Daphnia*. Mem. Conn. Acad. Arts Sci. 13, 1-180.

Brooks JL, Dodson SI, 1965. Predation, body size, and composition of plankton. Science 150: 28-35.

Bryce DL, 1931. Report on the Rotifera: Mr. Omer-Cooper's investigation of the Abyssinian freshwater (Dr. Hugh Scott Expedition). Proceeding of the zoological Society of London: 865-878.

Burgis MJ, 1971. The ecology and production of copepods, particularly *Thermocyclopes hyalinus*, in the tropical Lake George, Uganda. Freshw. Biol. 1:169-192.

Cannicci G, Almagia F, 1947. Notizie sulla "Facies" planctonica di alcuni laghi della Fossa Galla. Boll. Pesca Piscicolt. Idrobiol. 2: 54–77.

Carlson RE, 1977. A trophic state index for lakes. Limnol. Oceanogr. 22: 361-369.

Carpenter RS, Kitchell FJ, Hodgson JR, 1985. Cascading trophic interactions and lake productivity. Bio-science 35: 634-639.

Carpenter RS, Kitchell FJ, 1993. Cascading trophic interactions. In: R.S. Carpenter and F.J. Kitchell (eds.), The Trophic Cascade in Lakes. Cambridge University Press, Cambridge: pp 385.

Clarke RJ, Gorley RN, 2006. Primer V6: user manual/tutorial. PRIMER-E, Plymouth.

Dagg MJ, 1985. The effect of food limitation on diel migratory behavior in marine zooplankton. Ergeb. Limnol. 21: 247-255.

Dagne A, Herzig A, Jersabek C, Tadesse Z, 2008. Abundance, species composition and spatial distribution of planktonic rotifers and crustaceans in Lake Ziway (Rift Valley, Ethiopia). Internat. Rev. Hydrobiol. 93: 210-226.

Defaye D, 1988. Contribution a la connaissance des Crustaces Copepodes d'Ethiopie. Hydrobiologia 164: 103-147.

Dejen E, Vijverberg J, Nagelkerke LAJ, Sibbing FA, 2004. Temporal and spatial distribution of microcrustacean zooplankton in relation to turbidity and other environmental factors in a large tropical lake (L. Tana, Ethiopia). Hydrobiologia 513: 39–49.

Dejenie T, Declerck AJS, Asmelash T, Risch S, Mergeay J, Bie TD, Meester DL, 2012. Cladoceran community composition in tropical semi-arid highland reservoirs in Tigray (Northern Ethiopia): A meta community perspective applied to young reservoirs. Limnological 42: 137-143.

De Meester L., Gomez A, Okamura B, Schwenk K, 2002. The monopolisation hypothesis and the dispersal-gene flow paradox in aquatic organisms. Acta Oecologica 23: 121-135.

DeMott WR, Kerfoot WC, 1982. Competition among cladocerans: Nature of the interaction between *Bosmina* and *Daphnia*. Ecology 63: 1949-1966.

DeMott WR, 1988. Discrimination between algae and artificial particles by freshwater and marine copepods. Limnol. and Oceano. 33: 397–408.

Dumont HJ, Van De Velde I, Dumont S, 1975. The dry weight estimate of biomass in a selection of Cladocera, Copepoda and Rotifera from the plankton, periphyton and benthos of continental waters. Oecolgia (Berl.) 19: 75-97.

Dumont HJ, 1994. On the diversity of the Cladocera in the tropics. Hydrobiologia 272: 27-38.

Fernando CH, 1980b. The species and size composition of tropical freshwater zooplankton, with special reference to the oriental region (South East Asia). Int. Revue ges. Hydrobiol. 65:411- 426.

Fernando CH, Paggi J, Rajapaka R, 1987. Daphnia in tropical lowlands. In: R.H. Peters and R. De Bernardi (eds.), Daphnia, 45: 107-141, Memorie Dell' Instituto Italiano Di Idrobiologia Dott. Marco Di Marchi., Verbania Pallanza.

Fernando CH, Mengistu S, Bely S, 1990. The chydroid crustacean *Alona diaphana* (KING), limnetic in Lakes Awasa and Ziway, Ethiopia, with a discussion of littoral and limnetic zooplankton. Int. Revue ges. Hydrobiol. 75: 15–25.

Fernando CH, 2002. A Guide to Tropical Freshwater Zooplankton. Identification, Ecology and Impact on Fisheries. Backhuys publisher: Leiden, Netherlands.

Fetahi T, Mengistu S, Schagerl M, 2011. Zooplankton community structure and ecology of the tropical-highland Lake Hayq, Ethiopia. Limnologica 41: 389-397.

Figuerola J, Green AJ, 2002. Dispersal of aquatic organisms by waterbirds: a review of past research and priorities for future studies. Freshw. Biol. 47: 483-494.

Flik BJG, 2000. Size selective feeding of 0+ perch during a period of diel vertical migration of *Daphnia*. Verh. Internat. Verein. Limnol. 27: 3019.

Gilbert JJ, 1988. Suppression of rotifer population by *Daphnia*: a review of the evidence, the mechanisms, and the effects on zooplankton community structure. Limnol. Oceanogr. 33: 1286-1303.

Gillooly JF, Dodson SI, 2000. Latitudinal patterns in the size distribution and seasonal dynamics of new world, freshwater Cladocerans. Limnol. Oceanogr. 45: 22-30.

Gliwicz ZM, 1980. Filtering rates, food size selection, and feeding rates in cladocerans – another aspect of interspecific competition in filter-feeding zooplankton. In: W.C. Kerfoot (eds.), Evolution and ecology of zooplankton communities. University Press of New England.

Green J, 1986. Zooplankton associations in some Ethiopian Crater lakes. Freshw. Biol. 16: 495-499.

Green J, Mengstou S, 1991.species diversity and community structure of Rotifera in a salinity series of Ethiopian inland waters. Hydrobiologia 209: 95-106.

Green J, 1995. Altitudinal distribution of tropical planktonic Cladocera. Hydrobiologia 3307: 75-84.

Green J, Figuerola J, Sanchez MI, 2002. Implications of waterbirds ecology for the dispersal of aquatic organisms. Acta Oecol. 23: 177- 189.

Haileselasie TH, Teferi M, Dejenie T, Welegerima K, Abay T, Hiluf SA, Girmay K, 2012. Abundance, species composition and special distribution of zooplankton in Lake Hashengie of Tigray, Northern Ethiopia. Current Research journal of Biological Sciences 4: 389- 393.

Iglesias C, Mazzeo N, Meerhoff M, Lacerot G, Clemente JM, Scasso F, Kruk C, Goyenola G, Garcia-Alonso J, Amsinck SL, Paggi JC, Paggi SJ, Jeppesen E, 2011. High predation is of key importance for dominance of small-bodied zooplankton in warm shallow lakes: evidence from lakes, fish exclosures and surface sediments. Hydrobiologia 667: 133- 147.

Imoobe TOT, Akoma OC, 2008. Assessment of zooplankton community structure of Lake Tana, Bahir Dar Gulf of Ethiopia. Ethiopian Journal of Environmental Studies and Management 1: 247-255.

Imoobe TOT, Akoma OC, 2009. Spatial variations in the composition and abundance of zooplankton in the Bahir Dar Gulf of Lake Tana, Ethiopia. Afr. J. Ecol. 48: 72-77.

Jeppesen E, Jensen TP, Søndergaard M, Lauridsen T, Pedersen LJ, Jensen L, 1997. Top-down control in freshwater lakes: the role of nutrient state, submerged macrophytes and water depth. Hydrobiologia 343: 151-164.

Johnsen GH, Jakobsen PJ, 1987. The effect of food limitation on vertical migration in Daphnia longispina. Limnol. Oceanogr. 32: 873- 880.

Korinek V, 1999. A Guide to Limnetic Species of Cladocera of African Inland Waters (Crustacea, Branchiopoda). SIL, BTL, Geneva.

Korovchinsky NM, 1992. *Sididae* and *Holopedidae*: guides to the identification of microinvertebrates of the continental waters of the world. SPB academic publishing, The Netherlands.

Koste W, 1978. Rotatoria: Die Radertiere Mitteleuropas begrundet von Max Voigt. Gebruder Borntraeger: Berlin, Germany.

Lampert W, 1988. The relationship between zooplankton biomass and grazing: a review. Limnologia 19: 11-20.

Lampert W, Rothhaupt KO, 1991. Alternating dynamics of rotifers and Daphnia magna in a shallow lake. Arch. Hydrobiol. 120: 447-456.

Lampert W, Sommer U, 1997. Limnoecology: The Ecology of Lakes and Streams. Oxford University Press, New York.

Lemma B, 2007. Diel vertical migration of *Daphnia barbata* in a shallow tropical lake, Ethiopia. SINET: Ethiop. J. Sci. 30: 117-126.

Lemma B, 2008. Observations on the relations of some physico-chemical features and DVM of *Paradiaptomus africanus* in Lakes Bishoftu-Guda and Hora-Arsedi, Bishoftu, Ethiopia. *Limnologica* 39: 230-243.

Lemma B, 2009. Observations on the relations of some physico-chemical features and DVM of *Paradiaptomus africanus* in lakes Bishoftu-Guda and Hora-Arsedi, Bishoftu, Ethiopia. Limnologica 39: 230-243.

Legler C, 1988. Áusgewählte Methoden der Wasseruntersuchung´, Band 1. Gustav Fischer Verlag, Jena.

Loose CJ, Dawidowicz, P., 1994. Trade-offs in Diel Vertical Migration by Zooplankton: The Costs of Predator Avoidance. Ecology 75: 2255-2263.

McCune B, Grace JB, 2002. Analysis of Ecological Communities. MJM Software Design, Gleneden Beach, Oregon, USA.

Meerhoff M, Iglesias C, Teixeria de Mello F, Clemente JM, Jensen E, Lauridsen TL, Jeppesen E, 2007a. Effect of habitat complexity on community structure and predator avoidance behavior of littoral zooplankton in temperate versus subtropical shallow lakes. Freshw. Biol. 52: 1009-1021.

Mengistu S, Fernando CH, 1991. Biomass and production of major dominant crustacean zooplankton in a tropical rift valley lake, Awasa, Ethiopia. J. Plankton Res. 13: 831–852.

Mengistu S, Green J, Fernando CH, 1991. Species composition, distribution and seasonal dynamics of Rotifera in a Rift Valley lake in Ethiopia (Lake Awasa). Hydrobiologia 209: 203-214.

Murphy J, Riley JP, 1962. A modified single solution method for the determination of phosphate in natural waters. Analytica Chimica Acta 27: 31–36.

Nilssen JP, 1984. Tropical lakes-functional ecology and future developments: the need for a process-oriented approach. Hydrobiologia 113: 231-242.

Ruttner -Kolisko A, 1974. Plankton Rotifers, Biology and Taxonomy. Die Binnengewasser XXVI/1 146. Schweizerbart´sche Verlagsbuchhandlung, Stuttgart.

Ruttner-Kolisko A, 1977. Suggestions for biomass calculation of plankton rotifers. Arch. Hydrobiol. Beih. 8: 71-76.

Shapiro J, Wright DI, 1984. Lake restoration by biomanipulation round Lake, Minnesota, the first two years. Freshw. Biol. 14: 371-384.

Sheffer M, 1998. Ecology of shallow Lakes. Chapman and Hall, London.

Shurin JB, Gruner DS, Hillebrand H, 2006. All wet or dried up? Real differences between aquatic and terrestrial food webs. In: Proceedings of the Royal Society, series B 273: 1-9 pp.

Stich HB, Lampert W, 1981. Predator evasion as an explanation of diurnal vertical migration by zooplankton. Nature 293: 396-398.

Talling JF, Driver D, 1963. Some problems in the estimation of chlorophyll a in phytoplankton. In: proceedings of a Conference on Primary Productivity Measurements, Marine and Freshwater, US Atomic Energy Commission, TID 7633: 142-146 pp.

Vijverberg J, Dejen E, Getahun A, Leopold A, Nagelkerke J, 2014. Zooplankton, fish communities and the role of planktivory in nine Ethiopian lakes. Hydrobiologia 722:45–60.

Walz N, 1995. Rotifer populations in plankton communities: Energetics and life history strategies. Experiential 51: 437-453.

Walz N, 1997. Rotifer life-history strategies and evolution in freshwater plankton communities. In: B. Streit, and T. Städler (eds.), Evolutionary ecology of freshwater animals, Lively.

Wetzel RG, Likens GE, 2000. Limnological Analyses, 3rd edn. Springer.

Winder M, Spaak P, Mooij WM, 2004. Trade-offs in *Daphnia* habitat selection. Ecology 85: 2027-2036.

Wodajo K, Belay A, 1984. Species composition and seasonal abundance of zooplankton in two Ethiopian Rift valley lakes, Lakes Abiata and Langano. Hydrobiologia 113: 129-136.

Wondie A, Mengistu S, 2006. Duration of development, biomass and rate of production of the dominant copepods (Calanoida and Cyclopoida) in Lake Tana, Ethiopia. SINET: Ethiop. J. Sci. 29: 107–122.

Chapter 4

Evaluation of growth performance of two indigenous strains of juvenile Nile Tilapia, *Oreochromis niloticus* (L.) from geographically isolated regions in highland environment

Prototype of fish cage plot fixed on floating pier used during this experiment

Chapter 4

Evaluation of growth performance of two indigenous strains of juvenile Nile Tilapia, *Oreochromis niloticus* (L.) from geographically isolated regions in highland environment

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Abstract

Lake Wonchi is a deep highland crater-lake in Ethiopia and classified as oligotrophic. The lake was stocked with common carp, *Cyprinus carpio* L. 1758 and Nile Tilapia, *Oreochromis niloticus* L., fish in late 1990s in an attempt to establish pelagic fishery. A recent survey however reported that the latter species did not establish a breeding population. Possible causes are (1) dissolved volcanic gases and salts, (2) low plankton biomass, which are the main feed for *O. niloticus,* (3) missing spawning areas and (4) low temperature. To prove our hypotheses, we evaluated growth performance of two indigenous strains of *O. niloticus* collected from geographically isolated regions (Hashengae-highland = HS; and Debre Zeit-lowland = DZ) in cage culture over a 6-month period. Juveniles weighing 2.5–3.0 g were stocked in the cages with stocking density of 20 fish m^{-3} and fed a formulated diet composed of brewery waste (40%), wheat bran (13%) and Noug cake (47%) at a daily feeding rate of 5% of their body weight. Results indicated that the between-strain difference in growth performance of juvenile *O. niloticus* was not significant ($P > 0.05$), HS-strain had however superior final body weight at harvest than DZ-strain. The survival rate of fish in both treatments was below 80% and did not differ significantly ($P > 0.05$). Generally, the daily growth rate per fish (0.23 and 0.14 g d^{-1} for HS- and DZ-strain, respectively) observed in the present study was very low compared to the growth rates reported from other natural lakes and reservoirs in Ethiopia. All the key water quality parameters were within the optimum range for tilapia culture except water temperature (mean 15.6 ± 0.7 ^{O}C) which seems to be too low for the warm-water species to feed and reproduce.

Key words: growth, *Oreochromis niloticus*, strains, highland lake, Lake Wonchi

1. Introduction

Growth of human world population increases the demand for high–proteins in Sub–Saharan Africa, where over three–hundred million people and over one–third of African children are affected by malnutrition (World Bank, 2006). In Ethiopia, about 29% of the population lives below the national poverty line (MoFED, 2012) and over 85% of the population (i.e. over seventy million people) inhabit rural areas depending totally on agriculture, mainly cereal crop farming (World Bank, 2012). Population growth (annual growth rate 2.9%, World Bank, 2013) coupled with the apparent climate change and erratic rainfall events are highly likely to exacerbate crop failures, shortage of livestock feeds, food insecurity and subsequently results in chronic hunger which leads to losses of many lives particularly in the dry-lowlands of Ethiopia. Apparently, the country is gifted with numerous inland water bodies covering an estimated surface area of 18487 km^2 (Ethiopian Environmental Protection Authority, 2010), which provides ample opportunity to develop culture-based aquaculture. The central highlands of the country (> 2,500 m above sea level) represent about 11 % of the total land area, which could be appropriate for farming of cold-water species, while the lowlands (about 33% of total land area) offers optimal environmental conditions for warm-water species such as *Oreochromis niloticus* (Balarin, 1986). There exist more than 180 species of fish in Ethiopia, of which over 57 species are endemic to the country (Golubstov and Mina, 2003); some of them could be used for protein supply. Fish farming has enormous potential as a means of livelihood diversification, income generation for the smallholder farmers and subsequently improves food security. In this regard, *O. niloticus* has been well farmed in a broad range of culture conditions in most parts of the globe, particularly in African countries like Ethiopia (Bentsen *et al*., 1998; Gjedrem, 2005; Pillay and Kutty, 2005; El-Sayed, 2006; Dagne *et al*., 2013). *O. niloticus* are considered to be resistant to many stresses, fast in growth with better Feed Conversion Ratio (FCR) and high fecundity under captivity (Balarin and Hatton, 1979; Lowe-McConnel, 1982). These characteristics coupled with their capability to utilize a broad range of natural food stuff originating from planktons make tilapia a suitable species for semi–intensive fish farming in most developing countries (Liti *et al.*, 2005; El-Sayed, 2006). Besides, *O. niloticus* matures earlier under captivity and reproduces in different culture conditions (Balarin and Hatton, 1979; Lowe-McConnel, 1982; Tsadik and Bart, 2007). Therefore *O. niloticus* has been the predominant candidate species for stock enhancement of fishless and overexploited natural water bodies in Ethiopia.

Introduction of fish species into a natural water body is debatable and has enormous impact on the aquatic biodiversity; yet a great deal of economic benefits has been reported due to stock enhancement through knowledge based fish introduction programs (Tigabu, 2010). Lake Wonchi, a cold–water tropical highland lake in central Ethiopia, was stocked with common carp (*Cyprinus carpio* L. 1758) and Nile Tilapia (*O. niloticus*) in late 1990s in an attempt to establish pelagic fishery and increase availability of protein for the local community (Degefu *et al*., 2014a). Frequent fisheries surveys conducted by National Fisheries and Other Aquatic Life Research Center (NFLARC) have however reported that the latter species did not establish a breeding population. For this phenomenon, we propose four hypotheses: (1) too low plankton biomass, which is the main food source for planktivorous fish like *O. niloticus* (Tudorancea *et al*., 1988; Fernando, 1994; Tadesse, 1999); (2) too low water temperature: although tilapia is classified as eurythermal fish species, it does not grow and feed at temperature below 17 ^{O}C (Fryer and Iles, 1972; Philippart and Ruwet, 1982; Khater and Smitherman, 1988); reproduction stops at temperature below 22 ^{O}C (Chervinski, 1982; Dan and Little, 2000). Further reasons could be (3) toxic gases and salts released into the water column by volcanic activity and (4) limited spawning areas in the deep crater-lake. It has been well established that *O. niloticus* is generally restricted to the shallow littoral zones for breeding (Ita,1978; Philippart and Ruwet,1982; Wudneh, 1998), which is probably attributed to their physiological need such as elevated water temperature, availability of food resources, and protection from predators (Caulton and Hill, 1973). Nevertheless, there exist no quantitative data and rigorous studies oriented towards these implications nor are there any limnological investigations available for this lake to the best of our knowledge. This study is the first to discuss about the failure of Nile Tilapia to establish a breeding population through evaluating the growth performance of two indigenous strains of juveniles *O. niloticus* at highland environmental conditions collected from geographically isolated regions. We used cage culture system to corroborate the aforementioned speculations why *O. niloticus* is unable to thrive in Lake Wonchi. Moreover, we discussed the potential key water quality parameters which mainly influenced the survival rate of *O. niloticus* in Lake Wonchi.

2. Material and methods

2.1. Study site

Lake Wonchi (8^{o}47' N, 7^{o}53' E), a highland oligotrophic crater lake, is located at an altitude of 2900 m above sea level some 150 km southwest of the capital city of Ethiopia, Addis Ababa. The general morphometric features (Table 1) of Lake Wonchi were recently described by Degefu *et al*. (2014a) and a summary of its limnological features are provided in Table 2.

Table 1
Morphometry of Lake Wonchi from Degefu *et al*., 2014a

Variables	Values
Location	8^{o}47' N7^{o}53' E
Max. length (east-west: 60^{o} from north)	3.8km
Max. width	2.2km
Max. depth	107m
Mean depth	28m
Shoreline length	13.362km
Surface area	5.6km^2
Volume	0.185km^3

2.2. Origin of experimental strains

Two sources of Nile Tilapia (*O. niloticus*) wild brood stock namely Hashengae–strain (HS) and Debre–Zeit–strain (DZ) from geographically isolated natural water bodies were used in this study. The HS strain used in this experiment was collected from Lake Hashengae, a highland crater lake (mean annual temperature 19°C) located at an altitude of 2449 m above sea level some 630 km north of the capital city of Ethiopia, Addis Ababa (Melaku *et al*., 2013). DZ strain was collected from Lake Hora, a lowland crater lake (mean annual temperature 25 ^{O}C) located at 1850 m above sea level about 50 km southeast of Addis Ababa and transported to Sebeta National Fisheries and Aquaculture Research Center (NFARC), which is located at 2200 m above sea level about 24 km southwest of Addis Ababa. The mean annual air temperature of Sebeta area is about 21°C. Brood stocks of both strains were then acclimatized in separate ponds (50 m^2) for about two weeks prior to the start of successive fry (F_1 and F_2 generation) production at Sebeta–NFLARC. Subsequently, broodfish were selected randomly, manually sexed and stocked into separate spawning ponds each with an area of 200 m^2. Each pond was stocked with 60 founder individuals (2 fish m^{-2}) with a sex ratio of 3 females: 1 male during the spawning period. Subsequently, juveniles of F_1 generation were selected randomly and stocked into 10 x 5 x 1 m fertilized ponds to produce F_2 generations, which were eventually used in the growth experiment.

2.4. Experimental design and data analysis

A cage–based growth performance experiment on the two indigenous strains was conducted between July–January 2012/2013. Six cages (three cages per strain) were installed in the lake about 200 m away from the shoreline on a floating pier built at the lake. Cages were made of PVC pipes and 20 mm mesh nets (size = 1.8 m x 1.4 m x 1 m = 2.52 m^3). A mixed–sex population of 50 juveniles of F_2 generation from the respective strains were held per cage (stocking density 20 Ind m^{-3}; weighing 2.5 to 3 g). Total length (TL) and total weight (TW) of 50% of the stocked fish were measured from each experimental cage every month throughout the culture period to the nearest 0.5 cm and 0.1 g, respectively. Fish were fed twice a day by hand casting between 10:00 and 16:00 h at a daily feeding rate of 5% of their body weight. The composition of the ingredients used to formulate the diet (containing 28% crude protein) were brewery waste (40%), wheat bran (13%) and Noug cake (47%). Dead fish were removed and recorded to evaluate the survival rate of the stocks. Growth performances of the strains were evaluated in terms of daily growth rate (DGR), final individual weight gain (g), specific growth rate (SGR) and rates of survival. The growth parameters were computed following the standard formulae given by Adebayo *et al*. (2004) and Ridha (2006): DGR (g d^{-1}) = [Wf (g) – Wi (g)] d^{-1}, where Wf and Wi are the final and initial body weight, respectively; d is the culture period of the experiment in days. Weight gain (g) = Wf (g) – Wi (g); survival rate (%) = (Number of fish harvested / Number of fish stocked^{-1}) x100; (SGR % day $^{-1}$) = ln (Wf) – ln (Wi) d^{-1}. Fulton's condition factor (k) was computed following the formula provided by Lagler (1956): K = (Weight Length^{-3}) x 100.

Differences in growth performance between the two strains were compared by using T-test statistics. One–way analysis of variance (ANOVA) was used to test the differences between all the environmental variables during the sampling period followed by the Tukey–Kramer *post hoc* multiple comparisons test. SPSS 16.0 software was used in the statistical analysis and variables differences were considered significant at $P < 0.05$. Graphs were constructed using Sigmaplot version 12.

3. Results

3.1. physico–chemical parameters

Data on the physico-chemical characteristics of Lake Wonchi can be obtained from Degefu *et al.* (2014a). Briefly, the maximum and minimum surface water temperatures during the culture period were 17.3 and 16.2 ^{O}C, respectively. The mean surface DO concentration was 6.9 ± 0.8 mg L^{-1} (SD) (Fig. 1), with the highest vertical mean value of 5.8 mg L^{-1} recorded in January and the lowest mean value 4.4 mg L^{-1} in July 2012.

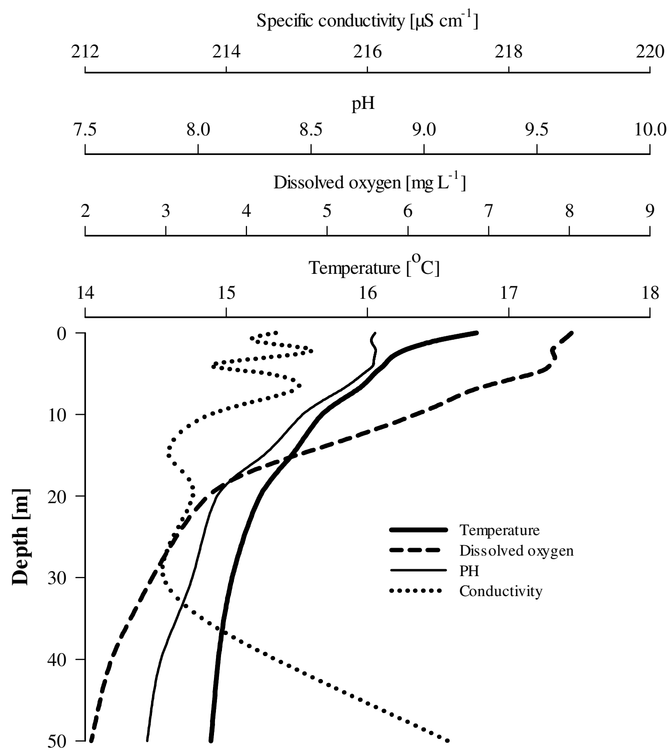

Fig. 1. Mean vertical profiles of temperature, dissolved oxygen, pH and specific conductivity in Lake Wonchi during the culture period (July 2012 – January 2013).

The lake was characterised by high water transparency and low algal biomass, with mean (± SD) secchi depth and chlorophyll *a* concentration of 3.8 ± 0.5 m and 3.1 ± 1.6 mg m^{-3}, respectively. Generally, the lake is fairly basic (pH 7.9 – 8.9), dilute (electric conductivity 185 – 245 µS cm^{-1}) and is categorized as a cold–water tropical lake with mean annual temperatures < 18 ^{O}C.

Dissolved inorganic nutrient concentrations were very low during the culture period: NH_4–N ranged from 53 to 79 µg L^{-1} with a mean value of 68 ± 61 µg L^{-1} (SD), while NO_3–N ranged from 0.7 to 10.9 µg L^{-1} with a mean value of 4.3 ± 3.8 µg L^{-1} (SD). Similarly, the average concentration of SRP and P_{tot} were < 5 µg L^{-1} with mean values of 2.2 and 4.6 µg L^{-1}, respectively (Table 2).

Table 2
Limnological characteristics of Lake Wonchi (mean ± SD) (from Degefu *et al*., 2014a)

Parameter	Wonchi
Secchi (m)	5.0
Ɛ (m^{-1})	0.34
Z_{eu} (m)	14.0
Conductivity (µS cm^{-1})	201 ±3
pH	8.10 ± 0.31
Chlorophyll-*a* (µg l^{-1})	3.2 ± 2.5
Zooplankton density (Ind m^{-3})	35,600
NO_2-N (µg l^{-1})	0.3 ± 0.2
NO_3-N (µg l^{-1})	1 ± 1
NH_4-N (µg l^{-1})	79 ± 68
SRP (µg l^{-1})	3.4 ± 2.3
P_{tot} (µg l^{-1})	8.4 ± 2.4
Alkalinity (meq l^{-1})	2.32 ± 0.03
Hardness (meq l^{-1})	0.53 ± 0.09
Na (mg l^{-1})	42.5±0.3
K (mg l^{-1})	6.8±0.7
Ca (mg l^{-1})	8.4±0.1
Mg (mg l^{-1})	1.4±0.03

3.2. Natural food availability (phyto– and zooplankton community)

Recently Degefu *et al*. (2014a) identified five phytoplankton groups in Lake Wonchi: Bacillariophyceae, Chlorophyta, Cryptophyta, Cyanobacteria and Dinophyta. The highest taxa number was recorded in the chlorophytes (33 taxa), followed by Bacillariophyceae (11 taxa), cyanobacteria (4 taxa), and Dinophytes (2 taxa), whereas Cryptophyta was represented by only one taxon. Zooplankton included a total of fourteen taxa: six cladocerans, one copepod and seven rotifers. Copepods were the most abundant group and contributed about 50% to the total zooplankton abundance followed by cladocerans (38%) and rotifers (12%). The overall mean (±SD) standing biomass of zooplankton for Lake Wonchi was 62.02 ± 25.76 mg DM m^{-3}.

Cladocerans contributed 53% to the total zooplankton biomass, whereas copepods and rotifers contributed 39% and 8%, respectively.

3.3. Growth of cultured fish

Data on the growth performance and survival rate of juvenile *O. niloticus* strains under cage culture condition are shown in Table 3. The growth of fish showed no significant differences among the strains (t-test, $P > 0.05$), although HS-strain had the highest mean (± SD) final individual size (25.64 ± 1.10 g) than DZ-strain (20.52 ± 1, 06 g). The net weight gain and daily growth rate per fish were 23.20 g and 0.23 g d^{-1} for HS-strain, and 18.49 g and 0.14 g d^{-1} for DZ-strain, respectively.

Table 3
Growth performance of two strains of Nile tilapia juveniles raised under cage culture condition for 150 days

Growth parameters	Strains	
	HS	DZ
Initial mean weight (g)	2.44 ± 0.68	2.03 ± 0.54
Final mean weight (g)	25.64 ± 1.10	20.52 ± 1.06
Initial mean length (cm)	4.68 ± 0.34	4.55 ± 0.43
Final mean length (cm)	12.01 ± 0.90	11.14 ± 0.89
weight gain (g)	23.20	18.49
Daily growth rate (g d^{-1})	0.23	0.14
Fulton's Condition Factor	1.48	1.42
Survival rate (%)	76	71

Growth trends in body weight and length of juvenile *O. niloticus* strains are presented in Fig. 2. Exponential growth was noted between July and October 2012, however fish grew nearly in a linear fashion during the remaining periods of the culture (November–January). Correspondingly, a differential growth of fish among the strains appeared during the cold–dry season between November and January 2012/13 (Fig. 2), however this difference was not significant (ANOVA, $P > 0.05$). The Fulton's condition factor of the strains is illustrated in Fig. 5. HS-strain was found to be in better condition than DZ-strains, which is in accordance with the superior growth rate of the former strain. Survival rate of fish in both strains was below 80% and did not differ significantly (ANOVA, $P > 0.05$) among the experimental strains throughout the culture period (Table 3).

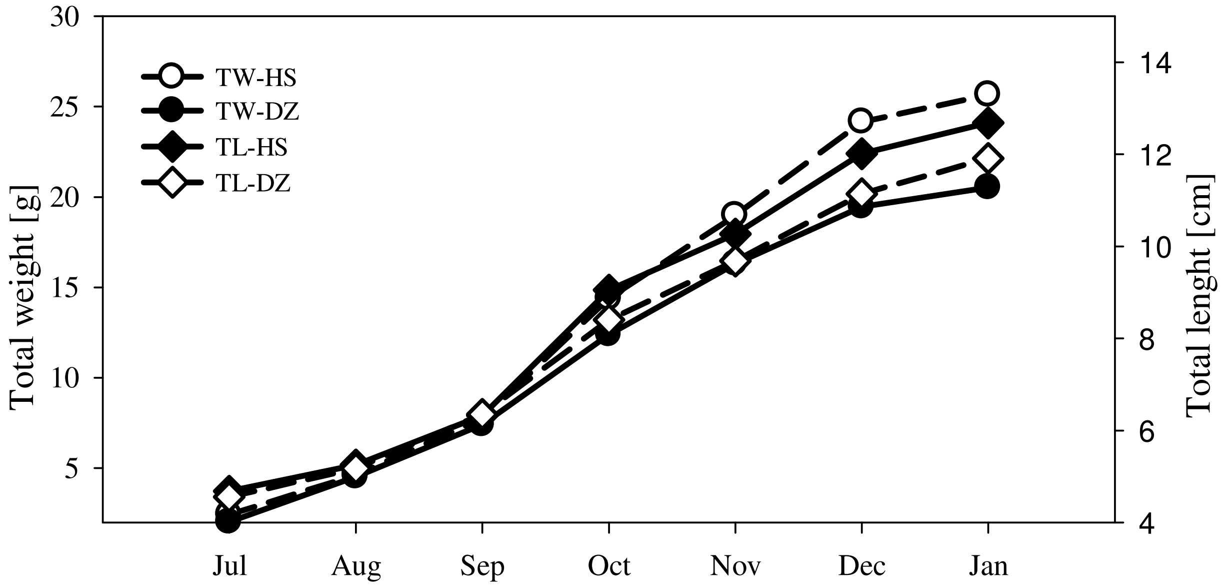

Fig. 2. Changes in body weight (g) and length (cm) of two juvenile strains of Nile tilapia during the culture period. *Note*: HS–Hashengae strain; DZ– Debre–Zeit strain; TW– total weight; TL– total length.

4. Discussion

All the physical and chemical parameters of water were within the favourable range for *O. niloticus* fish growth in Lake Wonchi except for water temperature (annual mean 15.6 ± 0.7 ^{o}C; Degefu *et al.*, 2014a), which was far below the optimum ranged required for tilapia culture (28-30 °C, Boyd, 1990; Beveridge, 1996; El-Sayed, 2006). Apparently, there was no significant difference in all physical and chemical parameters of water except DO concentrations (ANOVA, F (11, 144) = 3.422, P=0.00) during the entire culture period. We also measured only low concentrations of volcanic gases such as CO_2 (< 2 mg l^{-1}) and H_2S (below limit of detection) in the lake (Degefu *et al.*, 2014a). As shown in Table 2, most of the water quality parameters measured during the study period remained within the optimum range for the growth of Nile Tilapia (Boyd, 1990; Beveridge, 1996); however the growth and reproduction rate of tilapia in Lake Wonchi seems to be limited by the apparent low water temperatures. The environmental requirement of *O. niloticus* is well established worldwide as indicated from various studies (Philippart and Ruwet, 1982; Azevedo *et al.*, 1998; Dan and Little, 2000; Pandit and Nakamura, 2010; Noor *et al.*, 2010). Tilapia is classified as eurythermal fish species, however it does not grow and feed at temperature below 17 ^{O}C (Fryer and Iles, 1972; Philippart and Ruwet, 1982; Khater and Smitherman, 1988) and reproduction stops at temperature below 22 ^{O}C (Chervinski, 1982; Dan and Little, 2000). Besides, Degefu *et al*. (2014a) have reported that Lake Wonchi is unusually crystal clear water with a high under water transparency (4 m), and an oligotrophic status (chlorophyll *a* < 3 µg L^{-1}; P_{tot} = 8.4 µg L^{-1}) indicating low plankton biomass, which is the main food source for planktivorous fish like *O. niloticus* (Tudorancea *et al*., 1988; Fernando, 1994; Tadesse, 1999). The natural food of *O. niloticus* in Ethiopian inland water bodies has been reported to be mainly phytoplankton (Tadesse, 1999), but this species can also be omnivorous at some stage in its life cycle (e.g. larva and juvenile) feeding on algae, zooplankton and insect larvae (Tudorancea *et al*., 1988; Tadesse, 1999). Therefore, various factors that influence primary productivity are directly or indirectly linked to the growth rate of tilapia. We however can exclude low food availability as plausible explanation for failure of *O. niloticus* to establish breeding populations in the lake. First, the experimental fish were feed on supplementary diet with crude protein content of 28% and still did not perform well. Second, the quality of the natural food (increased ω3-High Unsaturated Fatty Acid contents, HUFA) in oligotrophic lakes is higher compared to eutrophic ones (Tadesse *et al*., 1998a.; Muller-Navarra *et al*., 2004; Tadesse, 2010); moreover, there are diverse desirable phytoplankton taxa and high biomass of large–bodied cladocerans such as *Daphnia longispina* in the lake (Degefu *et al*., 2014a), suggesting that the natural diet is sufficient to support better fish growth and reproduction of tilapia in Lake Wonchi. Therefore, low water temperature is the overriding factor for the failure of *O. niloticus* to establish breeding populations in the lake.

The experimental fish used in the present strain comparison were collected from geographically isolated regions, about 677 km apart and differing in climate. The results indicated that the between-strain difference in growth performance was insignificant, however HS-strain had superior final body weight (25.64 ± 1.10 g) at harvest than DZ-strain (20.52 ± 1.16 g). We attribute this result to strain-specific effects of temperature on growth. Nevertheless, the data collected indicate that both strains had a comparable low survival rate (< 80%) during the entire culture period (Table 3). Also the DGR per fish (0.23 and 0.14 g d^{-1} for HS- and DZ-strain, respectively) observed in the present study was very low compared to growth rates of tilapia fingerlings reported from natural lakes and reservoirs in Ethiopia (0.82 g d^{-1}, Ashagrie *et al*., 2008; 0.78 g d^{-1}, Workagegn and Gjoen, 2012; 0.55 g d^{-1}, Dagne *et al*., 2013). We attributed this low DGR to differences in temperature which also affects feeding rates, as has been reported elsewhere (Admassu and Ahlgren, 2000; Tadesse *et al*., 2003). Growth trends in body weight and length varied between months in both strains. Fish exhibited an exponential growth between July and October; however fish gained weight almost linearly during November–January (cold–dry period). The decrease in growth rate of fish during the cold-dry season could be attributed to the relatively low water temperatures between November-January, which subsequently affects the feed intake and metabolic activities of the fish (Philippart and Ruwet, 1982; Khater and Smitherman, 1988) .The Fulton's condition factor of the fish among the strains showed that HS-strain was found to be relatively in better condition than DZ-strains, which is in accordance with the superior growth rate of the former strain (Fig. 3).

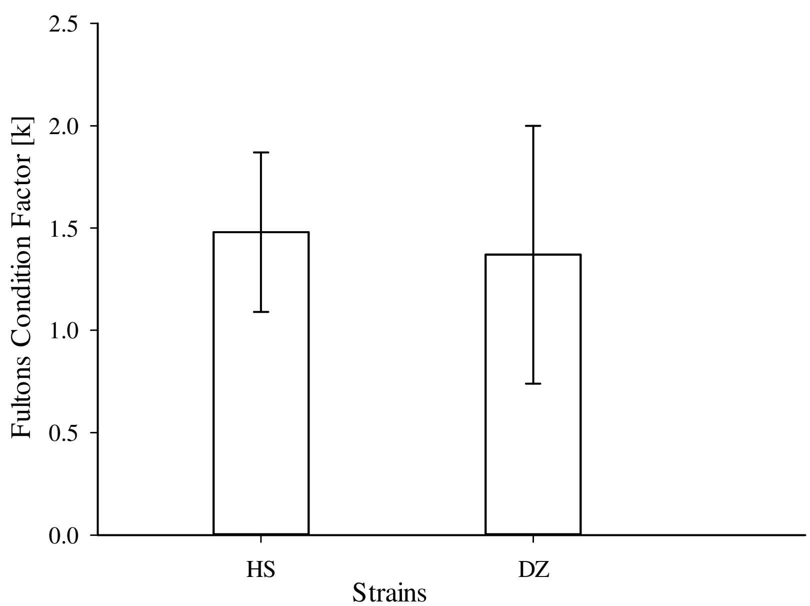

Fig. 3. Fulton's condition factor (K ± SD) of the strains (HS–Hashengae; DZ– Debre–Zeit) during the culture period July–January 2012/13.

5. Conclusion

The results of this study indicate that all the key water quality parameters were within the optimum range for tilapia fish farming except the low water temperature for a tropical lake. Hence, Lake Wonchi can be classified as a cold water tropical high–mountain lake with an annual mean water temperature below18 ^{O}C; as a result the eurythermal planktivorous fish species, *O. niloticus* (optimum range for recruitment: 22–28 ^{O}C) was not able to establish breeding populations irrespective of the apparent diverse desirable phytoplankton taxa and high biomass of large–bodied cladocerans in the lake, which are the main food source for planktivorous fish like *O. niloticus*.

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References

Admasu, D., Ahlgren, I., 2000. Growth of juvenile tilapia, *Oreochromis niloticus* L. from Lakes Ziwai, Langeno and Chamo (Ethiopian rift valley) based on otolith microincrement analysis. Ecol. Freshwat. Fish 9, 127-137.

Adebayo, O.T., Fagbenro, O.A., Jegede, T., 2004. Evaluation of *Cassia fistula* meal as a replacement of soyabean meal in practical diets of *Oreochromis niloticus* fingerlings. Aquacult. Nutr. 9, 99-104.

APHA– American Public Health Association, 1998. Standard Methods for the Examination of Water and Wastewater, 20th edn. American Public Health Association, Washington DC.

Ashagrie, G., Getahun, A., Mengistou, S., 2008. Effect of stocking density on the growth performance and yield of Nile tilapia [*Oreochromis niloticus* (L., 1758)] in a cage culture system in Lake Kuriftu, Ethiopia, Aquaculture Research, 39, 1450-1460

Azevedo, P.A., Cho C.Y., Leeson, s., Bureau, D.P., 1998. Effects of feeding level and water temperature on growth, nutrient and energy utilization and waste outputs of rainbow trout (*Oncorhynchus mykiss*). Aquat. Living Resour. 11, 227-238.

Balarin, J.D., Hatton, J.P., 1979. Tilapia. A guide to their biology and culture in Africa. University of Stirling, Stirling, Scotland.

Balarin, J.D., 1986. National review of aquaculture development in Africa. FAO Fish.Circ.770. pp. 8- 128, FAO, Rome.

Bentsen, H.B., Eknath, A.E., Palada-De Vera, M.S., Danting, J.C., Bolivar, H.L., Reyes, R.A., Dionisio, E.E., Longalong, F.M., Circa, A.V., Tayamen, M.M., Gjerde, B., 1998. Genetic improvement of farmed tilapias: growth performance in a complete diallel crosses experiment with eight strains of *Oreochromis niloticus*. Aquaculture 160, 145-173.

Beveridge, M., 1996. Cage Aquaculture, 2nd ed. Fishing News Book, Blackwell Science Ltd., Oxford.

Boyd, C., 1990. Water Quality in Ponds for Aquaculture. Alabama Agriculture Experiment Station, Auburn University, Alabama, USA.

Carlson, RE., 1977. A trophic state index for lakes. Limnol. Oceanogr. 22, 361-369.

Caulton, M.S., Hill, B.J., 1973. The ability of Tilapia mossambicus to enter deep water. Journal of Fish Biology 5, 783-788.

Chervinski, J., 1982. Environmental physiology of tilapias. In: Pullin, R.S.V., Low-McConnell, R.H. (Eds). The Biology and Culture of Tilapia. ICLARM, Manila, Philippines, pp. 119-126.

Dan, N.C., Little, D.C., 2000. The culture performance of monosex and mixed-sex new season and overwintered fry in three strains of Nile tilapia (*Oreochromis niloticus*) in northern Vietnam. Aquaculture 184, 221-231.

Degefu, F., Herzig, A., Jirsa, F., Schagerl, M., 2014a. First limnological records of highly threatened tropical high-mountain crater lakes in Ethiopia**.** Aquatic Conservation: Marine and Freshwater Ecosystems, submitted for publication. Tropical Conservation Science. Accepted.

Dagne, A., Degefu, F., Lakew, A., 2013. Comparative Growth Performance of Mono-Sex and Mixed-Sex Nile Tilapia (*Oreochromis niloticus L.*) in Pond Culture System at Sebeta, Ethiopia. International Journal of Aquaculture 3, 30-34.

El-Sayed, A.F.M., 2006. Tilapia culture. CABI Publishing Wallingford Oxfordshire, UK, pp.1-45.

Fernando, C.H., 1994. Zooplankton, fish and fisheries in tropical freshwaters. Hydrobiologia 272, 105-123.

Fryer, G., Iles, T.D., 1972. The Cichlide fishes of the Great Lakes of Africa: their biology and evolution. Oliver and Boyd. Edinburgh, UK.

Gjedrem, T., 2005. Status and scope of aquaculture. In: Gjedrem, T. (Eds). Selection and breeding program in aquaculture. Springer, New York, pp.1-7.

Golubstov, A.S., Mina, M.V., 2003. Fish species diversity in the main drainage system of Ethiopia: current state of knowledge and research perspectives. *Ethiopian Journal of Natural Resources* 5, 281-318.

Ita, E.O., 1978. An analysis of fish distribution in lake Kainji, Nigeria. Hydrobiologia 58, 233-344.

Khater, A.A., Smitherman, R.O., 1988. Cold tolerance and growth of three strains of *Oreochromis niloticus*. In: Pullin, R.S.V., Bhukaswan, T., Tonguthai, K., Maclean, J.L. (Eds.), The Second International Symposium on Tilapia in Aquaculture. ICLARM, Manila, Philippines, pp. 215-218.

Komărek, J., Anagnostidis, K., 2005. Freshwater Flora of Central Europe: Cyanoprokaryota 19/2. Elsevier GmbH, München, 759 pp.

Lagler, K.F., 1956. Freshwater fishery biology, 2nd ed. W.C. Brown publishers, Dubuque, Iowa

Liti, D., Cherop, L., Mungitti, J., Chorn, L., 2005. Growth and economic performance of Nile tilapia (*Oreochromis niloticus*) fed on two formulated diets and two locally available feeds in fertilized ponds. Aquac. Res. 36, 746-752.

Lowe-McConnell, R.H., 1982. Tilapia in fish communities. In: Pullin, R.S.V., Low-McConnell, R.H. (Eds). The Biology and Culture of Tilapia. ICLARM, Manila, Philippines, pp. 83-113.

Melaku, A., Dagne, A., Alemayehu, E., 2013. Observations on the limnological features of Lake Hashengae. In: Assefa, G., Alemayehu, M., Tadesse, Z. (Eds). EIAR, Addis Ababa, Ethiopia, PP. 159-168.

MOFED, 2012. Ethiopia's Progress towards eradicating poverty. Addis Ababa, Ethiopia. Ministry of Finance and Economic Development (MOFED), Federal Democratic Republic of Ethiopia (FDRE), Addis Ababa, Ethiopia.

Muller-Navarra, D.C., Brett, M.T., Park, S., Chandra, S., Ballantyne, A.P., Zorita, E., Goldman, C.R., 2004. Unsaturated fatty acid content in seston and tropho-dynamic coupling in lakes. Nature 427, 69-72.

Noor, E.L., Deen, A.I.E., Mona, S.Z., 2010. Impact of climatic change (oxygen and temperature) on growth and survival rate of Nile tilapia (*Oreochromis niloticus*). Report and Opinion 2, 192-195.

Pandit, N.P., Nakamura, M., 2010. Effects of high temperature on survival, growth and feed conversion ratio of Nile tilapia, *Oreochromis niloticus*. Our Nature 8, 219-224.

Pillay, T.V.R., Kutty, M.N., 2005. Aquaculture principles and practices. 2nd Edn. Blackwell Publishing, Oxford, UK, pp.400-415.

Philippart, J.Cl., Ruwet, J.Cl., 1982. Ecology and distribution of Tilapia. In: Pillin, R.S.V., Lowe-McConnell, R.H. (Eds.), the biology and culture of tilapias. ICLARM conference proceedings, Manila.

Popovsky, J., Pfiester, L.A., 1990. Freshwater Flora of Central Europe: Dinophyceae (Dinoflagellida). Gustav Fischer Verlag, Stuttgart, pp. 272.

Tadesse, Z., Ahlgren, G., Boberg, M., 1998a. Fatty acid content of some freshwater fish of commercial importance from tropical lakes in the Ethiopian Rift Valley. Journal of Fish Biology 53, 987-1005.

Tadesse, Z., 1999. The nutritional status and digestibility of Oreochromis niloticus L. diet in Lake Langano, Ethiopia. Hydrobiologia 417, 97-106.

Tadesse, Z., Boberg, M., Sonesten, L., Ahlgren, G., 2003. Effects of algal diets on the growth and fatty acid content of the cichlid fish *Oreochromis niloticus* L. A laboratory study. *Aquat. Ecol.* 37, 169-182.

Tadesse, Z., 2010. Diet composition impacts the fatty acid contents of Nile Tilapia, *Oreochromis niloticus* L., in Ethiopian highland lakes. Verh Internat Verein Limnol 30, 1363-1368.

Talling, J.F., Driver, D., 1963. Some problems in the estimation of chlorophyll a in phytoplankton. In: proceedings of a Conference on Primary Productivity Measurements, Marine and Freshwater, US Atomic Energy Commission, TID 7633, pp. 142-146.

Talling, J.F., 1987. The phytoplankton of Lake Victoria (East Africa). Arch. Hydrobiol. 25, 229

256.

Tigabu, Y., 2010. Stocking based fishery enhancement programmes in Ethiopia. Ecohydrology and Hydrobiology 10, 241-246.

Tsadik, G.G., Bart, A.N., 2007. Characterization and comparison of variations in reproductive performance of Chitralada strain Nile tilapia, *Oreochromis niloticus* (L.). Aquaculture Research 38, 1066-1073.

Tudorancea, C., Fernando, C.H., Paggi, J.C., 1988. Food and Feeding Ecology of Oreochromis niloticus (LINNAEUS, 1758) juveniles in Lake Awassa, Ethiopia. Arch. Hydrobiol. 79, 267-289.

Wetzel, R.G., Likens, G.E., 2000. Limnological Analyses, 3rd ed. Springer Verlag, New York.

Whitford, L.A., Schumacher, G.J., 1973. A Manual of Freshwater Algae. Sparks Press, Raleigh, NC: 324 pp.

Willen, E., 1991. Planktonic diatoms-an ecological review. Algological Studies 62, 69-106.

Workagegn, K., Gjoen, H.M., 2012. Comparative Studies on the Growth Performance of Four Juvenile *Oreochromis niloticus* L., (1785) Strains in Pond Culture, Ethiopia. International Journal of Aquaculture 7, 40-47.

World Bank, 2006. Repositioning nutrition as central to development: a strategy for large-scale action. World Bank, Washington DC.

World Bank, 2012. World Bank indicators: Ethiopia density and urbanization. World Bank, Washington DC.

World Bank, 2013. World Bank development indicators: World Bank, Washington DC.

Wudneh, T., 1998. Biology and Management of Fish Stocks in Bahir Dar Gulf, Lake Tana, Ethiopia. PhD Thesis, Wageningen Agricultural University, The Netherlands.

Conclusions and Outlook

Lakes Dendi, Wonchi and Ziqualla are among the few remaining patches of undisturbed aquatic ecosystems in Ethiopia, and yet have never been investigated reliably owing to seclusion and lack of infrastructure. This PhD research work provided a first morphometric and limnological description of these fairly pristine tropical high-mountain crater lakes during different sampling campaigns, with the aim of establishing baseline data against which future environmental and biological changes can be monitored and assessed. Besides, the study provided plausible explanations as to why the introduced fish Nile Tilapia (*Oreochromis niloticus*) was unable to inhabit and establish successful breeding populations in Lake Wonchi. Moreover, multivariate statistical tools for result analysis enabled us to determine the significant environmental and biological variables influencing the dynamics of phytoplankton and zooplankton in Lake Wonchi on seasonal scale.

- The first paper in this research compared data from three lakes based on two different sampling campaigns and demonstrated that all the three lakes show low concentrations of solutes, displaying an equal distribution of readily soluble components throughout the water column, but distinct oxygen depletion in greater depths linked to raising concentrations of Fe and Mn, which points at subterraneous springs (Chapter 1).
- Environmental and biological variables revealed that lakes Dendi and Wonchi are classified as oligotrophic and Ziqualla as oligo-mesotrophic (Chapter 1). The phytoplankton community is dominated by coccal green algae, desmids and dinoflagellates in lakes Dendi and Wonchi, as typical for unpolluted freshwater lakes; whereas chlorococcales, in particular *Botryococcus braunii* and benthic diatoms prevail in Ziqualla (Chapter 1).
- The zooplankton fauna is depauperate comprising a total of 11 rotifer taxa and 13 crustaceans. Copepods were the most abundant group and contributed significantly to the total zooplankton abundance in all three lakes, followed by cladocerans and rotifers, however, cladocerans were more important in terms of the total biomass (Chapter 1).
- In Wonchi, the fortnightly sampling periods over an extended period of seventeen months revealed partial–atelomixis to be a fundamental driving force in structuring phytoplankton community composition, which was quite stable and characterized by high diversity of planktonic desmids (N_A codon) followed by diatoms (MP codon). This indeed indicates oligotrophic conditions highly sensitive to nutrient enrichment,

demonstrating the significance of phytoplankton autecology for monitoring the ecological status of tropical aquatic ecosystems as it is in temperate region (Chapter 2).

- The seasonal study on fortnightly sampling basis in Wonchi also revealed that the zooplankton community composition comprises both temperate and tropical species possibly due to the high altitude at which the lake is located and the subsequent low water temperature (Chapter 3).
- The seasonal dynamics of zooplankton biomass in Lake Wonchi was mainly correlated with Chl-*a* concentration, which reflects a bottom-up effect of algal biomass on zooplankton (Chapter 3).
- It can be assumed that intense interspecific competition for limited food sources, rather than fish predation pressure, is the key factor structuring the vertical distribution of zooplankton in Lake Wonchi (Chapter 3).
- Lake Wonchi can be classified as a cold water tropical high–mountain lake with a temperature below18 ^{O}C; as a result the eurythermal planktivorous fish species, *O. niloticus* might not able to establish breeding populations irrespective of the apparent diverse desirable phytoplankton taxa and high biomass of large–bodied cladocerans in the lake (Chapter 4).

Recommendations

Based on the findings of the present study and on field observations, all the three lakes have similar characteristics with no obvious surface inflows and/or out flows and encompasses very small catchment which is indeed the crater itself, this makes them extremely sensitive to anthropogenic impacts. Besides, the lakes offer a pristine environment in a beautiful landscape and are located in the vicinity of the capital city Addis Ababa, and recently are highly threatened by unsustainable tourism, shoreline and crater rim modifications for resort development, water abstraction and land grabbing. Therefore, the following are areas that could be proposed for protecting and/or conserving these sensitive ecosystems before deleterious effects have become evident.

Lake Wonchi- Major problems

- Becoming the main touristic destination in the central highlands due to its proximity to the capital city Addis Ababa.

- Modifications of the crater rim and shoreline for the newly erected resorts and tourist facilities.
- Aggressive land grabbing and encroachments, deforestation and subsequent farming of vegetables and cereal crops along the shoreline.
- Siltation, use of inorganic fertilizers and the subsequent nutrient enrichment.
- Failure *O. niloticus* fish to establish breeding populations.

Lake Wonchi-recommendations

- Raising awareness and educating the public on sustainable ecotourism (e.g. training and developing education media on aquatic biodiversity and disseminating it to schools, district and local administrative, tour guides and riparian communities).
- Adapting integrated catchment management system with due emphasis on the tradition of local people for keeping conservation and sustainable management of natural resources (e.g. practicing agroforestry and bench terraces to reduce siltation and the subsequent eutrophication of the lake).
- Revising the current land ownership police in the country with due emphasis on shorelines and aquatic ecosystems (e.g. by stopping land grabbing and leasing of lakes to investors e.g. Lake Dendi).
- Developing well-designed sewerage system for the newly erected resorts and tourist facilities.
- The introduced fish Nile Tilapia seems to be a wrong species in Lake Wonchi due to the year round very low water temperature; therefore I suggest a training of alternative livelihood for the local communities (e.g. Beekeeping).
- There is a need to develop integrated monitoring programs for sustainable utilization of the products and services of the natural resources around Lake Wonchi (e.g. long term monitoring program on the water quality of the lake).

Lake Dendi- Major problems

- The ongoing mega Dendi lake project (area 26.4 km^2) by ALMOEZ GROUP (www.dendilake.com) in the lake basin and the subsequent deforestation and siltation.

Lake Dendi- recommendations

- Although the project has started in 2011, there is an urgent need for Environmental Impact Assessment (EIA) including the investigations of aquatic biodiversity.
- Raising awareness and educating the local communities about the long term impact of such a mage project for precautions.
- Acknowledging and adopting the tradition of the local people for keeping conservation and sustainable management of natural resources for millennia.
- Endorsing the land ownership of riparian communities (e.g. Problem around lake Dendi will be solved).

Lake Ziqualla- major problems

- Although the lake is believed to be "holy" by the members of Ethiopian Orthodox-church, and highly protected by monks; I observed massive uncontrolled water abstraction (using motor pump) exclusively for baptizing on a daily basis. Consequently, the lake surface area has receded dramatically over the last two decades.
- Increase in population size (both local and incoming religious communities).
- Deforestation for fuelwood.

Lake Ziqualla- recommendations

- Due to the local customs, any recommendations may raise ethical considerations; however, there might be possibilities for sustainable utilization of the lake water.
- Practicing agroforestry can alleviate the critical firewood shortage around the lake and immensely contributes to the sustainable utilization of the natural resources.

Curriculum Vitae

Fasil Degefu ABERA born on the 14th, June 1980 in Southwest Shoa, Ammeya, Ethiopia. Worked as a junior instructor between September 2002 & December 2003 at Bako ATVET College. Moved to Ethiopian Institute of Agricultural Research, National Fisheries and Other Aquatic Life Research Center, and have worked as a Research assistant III since 2004. Attained a Bachelor of Science in Animal and Range Science from Mekelle University, Mekelle Ethiopia in 2002, then a Master of Science in Environmental Science, Specialisation in Limnology and Wetland Ecosystems at UNESCO-IHE Institute for Water Education, (IHE) Delft the Netherlands in 2008.

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Publications

Peer-reviewed Journals

1. **Degefu F.**, Mengistu S. and Schagerl M., 2011.Influence of fish cage farming on water quality and plankton in fish ponds: A case study in the Rift Valley and North Shoa reservoirs, Ethiopia. *Aquaculture* 316:129-135.
2. **Degefu F.**, Teshome K., Tesaye G., Tefera F. and Lakew A., 2011. Some limnological aspects of Koka reservoir, a shallow tropical artificial lake, Ethiopia. *J. Recent Trends Biosci.* 1:94-100.
3. **Degefu F.**, Tigabu Y. and Tadesse Z., 2011. Use of periphyton as an alternative fish feed in pond culture system. *Ethiopian Journal of Agriculture and Development* 2: 105-121.
4. **Degefu F**, Tesfaye G. and Tefera F., 2012. Study on the Adaptability Status and Reproductive Success of Oreochromis niloticus L. (Pisces: Cichlidae) and Carp (Cyprinus carpio L., 1758) in a Tropic Reservoir (Fincha, Ethiopia). *International Journal of Aquaculture* 2(10): 65-71.

5. **Degefu F**., Lakew A., Tigabu Y. and Teshome K., 2013.The water quality degradation of upper awash river, Ethiopia. *Ethiopian Journal of Environmental Studies and Management* 6(1):58-66.
6. Dagne A., **Degefu F**. and Lakew A., 2013. Comparative Growth Performance of Mono-Sex and Mixed-Sex Nile Tilapia (*Oreochromis niloticus* L.) in Pond Culture System at Sebeta, Ethiopian. *International Journal of Aquaculture* 3(7):30-34.
7. Tadesse Z., Wolde-Gebriel A., Jovani M., Tefera F. and **Degefu F**., 2011. Effect of supplementary feeding of Agro-industrial by products on the growth performance of Nile tilapia (*Oreochromis niloticus* L.) in concrete ponds. *Ethiop. J. Biol. Sci.* 11:29-41.
8. **Degefu F**., Herzig A., Jirsa F., and Schagerl M., 2014. First limnological records of highly threatened tropical high-mountain crater lakes in Ethiopia. Tropical Conservation Science. Accepted.

Proceedings

1. Dagne A. and **Degefu F**., 2007. Current status and condition of introduced fish species in small water bodies: case studies at Birati reservoir. Proceedings of the 10th *Ethiopian Society of Animal Production*. 15:173-182. Addis Ababa, Ethiopia.
2. Tigabu Y., **Degefu F**., Lakew A. and Tesfaye G., 2011. Development of small scale fish farming: for livelihood diversification in North Showa zone, Amhara Regional State. Proceedings of the Ethiopian society of fisheries and aquatic sciences: *Impacts of climate change and population on tropical aquatic resources*. 02-04 February, 2011, Haramaya, Ethiopia.

3. **Degefu F**. and Schagerl M., 2009. Influence of small-scale cage fish farming on water quality and biotic communities in small water bodies in Ethiopia. *Proceedings of BOMOSA final conference*. 2nd-4th September, 2009, Machakos, Kenya.

Master Science thesis

1. **Degefu F**. 2008. Potential Influence of Fish Cage Farming on Water Quality, Phytoplankton Biomass and Plankton Species Composition in Fish Ponds: a case study in the Rift valley & North Shoa Reservoirs, Ethiopia. MSc Thesis, UNESCO-IHE Institute for Water Education, Delft, the Netherlands.