Dissertation

Plankton Communities and Ecology of Tropical Lakes Hayq and Awasa, Ethiopia

angestrebter akademischer Grad

Doktor der Naturwissenschaften (Dr. rer. nat.)

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Dissertationsgebiet (lt. Studienblatt)**:** Őkologie

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Vienna, June 2010

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Contents

Dedication

EMAHOY ABEBECH ASFAW, mom, represents all mothers in particular Ethiopian mothers who devoted themselves to the best of their children. Her belief in education reached me here: when I complained the difficulty of learning during childhood, she always kindly responded "you are not requested to carry tons of grain; you are requested to read – just read". That is how I learn 'reading is a secret of knowledge'. Thanks mom and long live to you!

Wonderful Mother

GOD made a wonderful mother,
A mother who never grows old;
HE made her smile of the sunshine,
And HE moulded her heart of pure gold;
In her eyes HE placed bright shining stars,
In her cheeks fair roses you see;
The values you've taught,
the care you've given,
and the never-ending love you've shown,
have enriched my life
in more ways than I can count.
God made a wonderful mother,
And HE gave that dear mother to me.
Pat O'Reilly

Acknowledgments

Several people and institutions have contributed a lot to the completion of this PhD program, and I earnestly thank all of them very much for their understanding and timely support, including those inadvertently oversight.

General Introduction and Thesis Outline

Ethiopia, situated in Eastern Africa, has become a land locked country since 1993 but is still endowed with various inland water resources covering an estimated surface area of 18587 km^2 (Ethiopian Environmental Protection Authority, 2010). Because of their location and opportunity for comparative study, the rift-valley and Bishoftu crater lakes have been relatively better studied (Tudorancea and Taylor, 2002). Phytoplankton community, biomass and primary production has been studied primarily in these lakes (Kebede and Belay 1994; Belay and Wood 1984; Kifle and Belay; Talling et al. 1973). The investigations of physico-chemical environmental variables, zooplankton and fishery were also concentrated on the same lakes (Kebede et al., 1994; Talling and Talling, 1965; Mengistou and Fernando, 1991; Mengistou et al., 1991; Dadebo 2000). These studies were able to compare within themselves to understand similarities and differences along ecosystem gradients, and represent Ethiopian inland water-bodies when compared with other tropical and/or temperate lakes (Talling and Lemoalle, 1998). However, highland lakes have been marginally investigated predominantly due to their remote location and associated logistic constraints. They are located at relatively high altitude (>1800 m), have intense solar radiation around noon, relatively mean lower water temperature (for tropical lakes), some are comparatively deep lakes, have high primary production, and high zooplankton numerical abundance and biomass. The study of these lakes will increase local and global understanding and comparison of aquatic ecosystems. Furthermore, it is important for designing inland water management and sustainable utilization of the resources. Ironically, these highland areas are densely populated in Ethiopia (i.e. about 70% of the population lives in highland area); consequently demographic pressure and anthropogenic effect on natural resources could be high. The highland of northern Ethiopia, where the present study Lake Hayq is located, exhibits severe land degradation, erosion and is periodically prone to drought and famine caused by deforestation (Darbyshire et al., 2003).

Lake Hayq provides a habitat to different fish species, water birds and aquatic organisms. It also plays an economical role via tourism and fishery, and most importantly it provides drinking water to the local inhabitants. The lake has been described as oligotrophic by different visitors. Zanon (1941), for example, described the lake as *'limpida e verdastra',* which means 'crystal clear water'. Some 30 years later, Baxter and Golobitsch (1970) also described the lake as 'an unusual clear-water lake' with a Secchi depth of 9 m, very low algal biomass (< 1 µg L^{-1} Chlorophyll *a*) and oxic conditions down to 40 m depth. Indeed, this lake was a clear-water lake when compared with other Ethiopian rift-valley lakes (Tudorancea and Taylor, 2002). In the meantime, the lake was stocked with Tilapia fish (*Oreochromis niloticus*) in the late 1970-ies to fill an empty pelagic niche of planktivorous fish and to provide cheap protein to the local people (Kebede *et al.,* 1992). This lake was without piscivororous fish species and the stocked Tilapia fish dominated the ecosystem. In the 1990s an annual harvest of 200 ton Tilapia was recorded (Kebede *et al.,* 1992) and a biomass of 298 ton was calculated in the present study. Approximately 10 years later after the introduction of Tilapia, the lake had undergone eutrophication and many Tilapia fish died (Kebede *et al.,* 1992).

Eutrophication, although reversible, is a real and major environmental problem throughout the world (Bronmark and Hansson, 2005). Until the 1980s, limnologists have focused on bottom-up control as the primary determinant of phytoplankton growth and biomass, and phosphorous was a major responsible factor in the process of eutrophication (Schindler 1977; Bronmark and Hansson, 2005). However, in the 1980-ies it became clear that the functioning of ecosystems was not a simple

one-way up the food chain but a more complex web of interactions leading to the top-down control hypothesis. Earlier in the 1960-ies, it was known that planktivorous fish affect the zooplankton assemblage and indirectly influence the phytoplankton community (Brooks & Dodson 1965). There has been considerable debate over the relative importance of top-down versus bottom-up control of lake ecosystems. In bottom-up/top-down hypothesis (McQueen et al., 1986), top-down effects are strong at the top of the food web and weaken towards the bottom, because phytoplankton biomass is thought to be more strongly controlled by resources (bottom-up) than by grazing (top-down). However, trophic cascade hypothesis, which is typically strong in aquatic ecosystem, discusses the importance of top-down effect on lower trophic level (Carpenter and Kitchell 1992). The potential biomass and production of organisms at a given trophic level is determined by bottom-up availability of nutrients (for autotrophs) and food (for heterotrophs), whereas the realized biomass at each trophic level is regulated by the trophic level above through top-down control (Carpenter and Kitchell, 1993; Chase, 2000). For instance, in a three trophic-level food chain, predators can reduce herbivore zooplankton indirectly benefiting the primary producer phytoplankton to grow very well. Trophic cascade hypothesis was supported through a whole lake experiments (Carpenter and Kitchell, 1993). Most planktivorous fish are size-selective predators and feed preferentially on large zooplankton (Hall et al., 1976). An increase in planktivorous fish biomass leads to a correspondence change in zooplankton size structure towards smaller-sized species (Spaak and Hoekstra, 1997). Small zooplankters are less efficient in grazing down phytoplankton than large ones ('*Size Efficiency Hypothesis*'; Brooks and Dodson, 1965) and the dominance of small zooplankton species often results in an increased phytoplankton biomass (Shapiro and Wright, 1984). In some cases, increased algal growth can be absorbed by the food chain resulting in increased fish catches, but in many surface waters, algal blooms can have considerable detrimental impacts on tourism, drinking water supply, resulting in fish-kill and other organisms (due to oxygen depletion). Eutrophication can lead to decreases in species richness and diversity, which may have negative consequences for the food web structure and functioning (Proulx et al. 1996).

In 1989 after a massive fish kill in Lake Hayq, researchers were invited to study the cause behind this adverse phenomenon. Based on their snap-shot survey, Kebede et al. (1992) reported the remarkable changes of Lake Hayq into a stable eutrophic status, with water transparency of only around 1.2 m, Chl a concentrations between 13 and 23 µg L^{-1} and the absence of oxygen below 15 m. Furthermore, the authors proposed two hypotheses for the trophic change of the lake: (i) an increased nutrient to volume ratio and (ii) the introduction of Tilapia (*Oreochromis niloticus* Linnaeus 1758*)* in the late 1970-ies. The former could not be fully substantiated due to scarcity of chronological data. However, nutrient concentration might have been elevated as a result of catchment drain off. In the last three centuries, deforestation and soil erosion has been intensified around Lake Hayq possibly due to human impact (Darbyshire et al. 2003), which could be a signal for nutrient increment in the lake. Moreover, the land uses in the catchments include agriculture on steep land that uses inorganic fertilizer, and livestock grazing.

Additionally, the water level has dropped as St. Estifanos Monastery, which was once on an island, is now connected to the shore via peninsula (Baxter and Golobitsch, 1970; Pankhurst 1967; Ashebir Abebe, personal communication), suggesting nutrient increase to volume ratio. On the other hand, since adult and juvenile Tilapia regularly consumes zooplankton (Getachew 1993; Tadesse 1988), the grazing pressure of introduced Tilapia on zooplankton might have relieved phytoplankton to grow better; consequently higher phytoplankton biomass could develop. For instance, it was shown that the

introduction of fish to previously fishless high-mountain lakes is accompanied by a change in the zooplankton community: the calanoid copepod, *Hesperodiaptomus,* the cladoceran *Daphnia,* and other large zooplankton were eliminated and replaced by smaller copepods and rotifers (Anderson 1972; Gliwicz, 1985; Knapp et al., 2001), which are less efficient filter feeders and eutrophication could result.

Temporal, spatial and seasonal studies on phytoplankton and its ecology with limnological variables have been documented for tropical lakes including Ethiopian rift-valley lakes. It is well known that primary production is the driving force and the base for energy-flow studies within aquatic ecosystems. Based on stable isotope analysis, recent studies reinforced the importance of algal productivity as the primary carbon source for pelagic food web (Zohary et al. 1994, for Lake Kinneret; Yoshii et al.1999, for Lake Baikal). The study of phytoplankton and its ecology in Lake Hayq is important as the commercially important fish species Tilapia feeds on it. Phytoplankton production is considered as a good predictor of fish yield, and seasonal measurements of the former are a prerequisite (Melack, 1976; Tilahun & Ahlgren, 2009), but none were documented for Lake Hayq. Zooplankton, which is an important link in the trophic hierarchy, has been studied sparsely in Ethiopia (Mengistou, 1989; Wondie and Mengistou, 2006). Lake Hayq was visited as early as 1930-ies and large cladocerans such as *Diaphanosoma* and *Daphnia magna* were abundant until 1970 (Cannicci and Almagia, 1947; Baxter and Golobitsch, 1970); whereas cladocerans were completely absent in a 1989 survey instead copepods being dominant in the system (Kebede *et al.,* 1992). It was suggested by Kebede *et al.* (1992) that the stocked Tilapia fish was the cause for the disappearance of cladocerans. Even though the stocked planktivorous fish is a major success in the economy of the local people (Kebede et al. 1992), its effect on the food web structure and lake ecosystem has not been studied in detail until now, particularly in relation to phytoplankton and zooplankton. The trophic status change and cladocerans disappearance has been ascribed to the stocked Tilapia fish, which could alter the food web structure and functioning of the ecosystem. Food webs provide a framework for integrating population dynamics, community structure and ecosystem processes (Kaunzinger and Morin, 1998), and is a central idea in ecology (Wilbur, 1997). The predator-prey interactions provide a means to examine the species' roles in ecological processes, and to understand community and ecosystem functioning (Thapanand et al., 2009). We therefore, constructed mass-balance model to generate the food web structure and trophic interactions within the major functional groups of Lake Hayq, Ethiopia.

Of the Ethiopian rift-valley lakes, I chose a comparatively well-studied Lake Awasa to assess the long-term effect of anthropogenic and natural impacts on plankton communities. Long-term study reveals changes and provides baseline information for the sustainable management of the lake. Unlike temperate lakes, however, long-term plankton variability in tropical lakes has been documented only sporadically. Lake Awasa is located in the vicinity of the growing city receiving many potentially adverse effluents from the Textile Factory, Ceramics Factory, Referral Hospital and municipal sewage apparently with little treatment. Moreover, there are high levels of recreational activity and poor land-use management around the lake and is thus exposed to intense human-induced pollution. Therefore, we studied phyto- and zooplankton communities between November 2003 to August 2004, and compared our data with historical data since the 1980-ies to assess potential inter-decadal changes.

Study Objectives

The present study focused on the food web structure and energy flows of Lake Hayq with due emphasis on lower trophic levels - phytoplankton and zooplankton. Phytoplankton composition, biomass and primary production have been investigated in relation to environmental variables. Similarly, zooplankton abundance and biomass were also studied in detail and associated with limnological variables. The long-term effect on plankton community and abundance in Lake Awasa was investigated and compared with the available literature data. The major specific objectives include:

- ❖ To assess temporal and spatial physical and chemical environmental variables including the major algal nutrients
- ❖ To investigate changes in the phytoplankton species composition and community structure
- ❖ To determine phytoplankton biomass and primary production associating with the major driving factors
- ❖ To determine zooplankton species composition and community structure
- ❖ To investigate zooplankton numerical abundance and biomass and the regulating factors
- ❖ To describe the food web structure, trophic interactions and energy flow of Lake Hayq
- ❖ To assess the long-term effect of lower trophic level of phytoplankton and zooplankton of Lake Awasa

Research questions:

- ➢ Do physico-chemical and algal growth limiting nutrients vary temporally, spatially and vertically in Lake Hayq?
- ➢ Compared to historical taxa, what is the phytoplankton composition of Lake Hayq?
- ➢ Do the patterns of phytoplankton composition, biomass and primary production change temporally?
- ➢ What are the major driving forces of phytoplankton composition, biomass and primary production in Lake Hayq?
- ➢ Is Lake Hayq eutrophic?
- ➢ What could be the major cause in the trophic change of the lake?
- ➢ What is the zooplankton composition of Lake Hayq?
- ➢ Does zooplankton numerical abundance and biomass vary temporally and spatially?
- ➢ What is the possible reason for the success story of *Thermocyclops* in Lake Hayq?
- ➢ How looks like the food web structure of Lake Hayq?
- ➢ What is the transfer efficiency of the ecosystem?
- ➢ Is Lake Hayq a mature ecosystem?
- ➢ Is there a long-term change on plankton in Lake Awasa?

Study Justification

The total surface area of the inland water-bodies of Ethiopia is estimated to be about 18587 km^2 (Ethiopian Environmental Protection Authority, 2010). As a result of their location and opportunity for comparative study, the rift-valley lakes have been relatively better studied (Tudorancea and Taylor, 2002). However, highland lakes have been marginally studied predominantly due to their remote location. One of these lakes is Lake Hayq, which is located in the highland of Ethiopia providing a habitat to different fishes, water birds and aquatic organisms. It also plays economical role via tourism and fishery and most importantly provide drinking water to the local inhabitants. The lake has been described as oligotrophic by different visitors. In the meantime, some 30 years ago, the lake was stocked with Tilapia fish (*Oreochromis niloticus*) to fill an empty pelagic niche of planktivorous fish. Some 10 years later after the introduction of Tilapia, the lake had undergone eutrophication and many planktivorous fish died. Consequently, researchers made a snap-shot survey and proposed two hypotheses for the trophic change of the lake: (i) an increased nutrient to volume ratio, and (ii) the introduced tilapia fish. Furthermore, the researchers also documented the disappearance of cladocerans from the ecosystem; hypothesizing the stocked Tilapia fish could also be the cause. The lake was one of the earlier visited lakes in Africa but this study is the first to discuss about these hypotheses through investigating the temporal, spatial and seasonal phytoplankton and zooplankton along with their environmental variables. Moreover, the food web structure and trophic interaction of Lake Hayq was constructed for the first time, which could clarify the trophic position of Tilapia and also demonstrate its impact to plankton offering to discuss some of the hypothesis (shift of ecosystem structure due to human impact such as stocking) from holistic point of view. Additionally, of Ethiopian rift-valley lakes, Lake Awasa was chosen to assess the long-term man-made or natural impact on the ecology of plankton. Lake Awasa is located in the vicinity of the growing city receiving many potentially adverse effluents from the Textile Factory, Ceramics Factory, Referral Hospital and municipal sewage apparently with little treatment. Moreover, there are high levels of recreational activity and poor land-use management around the lake, and it is thus exposed to intense human-induced pollution. Hence, the long-term effect of natural and anthropogenic effect on the biology of Lake Awasa was investigated with more emphasis on phytoplankton and zooplankton.

Thesis Outline

This thesis summarizes the results of a doctoral study conducted in Ethiopian lakes: a highland Lake Hayq and a rift-valley Lake Awasa. The overall purpose of the research was to generate baseline information and understand the current condition of Lake Hayq, which is poorly represented in the literature and to give long-term information of Lake Awasa. The first chapter (this chapter) presents the background information of the study, describes the specific objectives and poses the research questions. Chapter 2 – 4 describe the detail research carried out between October 2007 and January 2009 on Lake Hay and presents its original outcomes. The 5th chapter is dedicated to long-term investigation of Lake Awasa. Chapters 2 - 4 in which detailed research finding are reported are written in a form of papers submitted for publication in international peer-reviewed journals (Journal of Plankton Research, Hydrobiologia, Ecological Modelling and International Review of Hydrobiology). The last chapter (Chapter 6) is an overall summary of results and discussions, and highlights research gaps and recommendations for future study.

Paper I. **Phytoplankton community, biomass and primary production of the Ethiopian highland Lake Hayq** (Submitted to Hydrobiologia)

This paper discusses about the temporal dynamics of phytoplankton community composition, biomass (as Chl *a* and biovolume), and primary production. I have related the phytoplankton parameters with the physical and chemical environmental variables, and attempted to pinpoint the major driving factors. Canonical Correspondence Analysis (CCA) was employed to describe the association between algal taxa and environmental variables. Principal Component Analysis (PCA) followed by multiple regression analysis indicated that Chl *a* was influenced by rainfall, temperature and light supply, which are associated with the seasonality of the region. The paper also discusses about the current trophic status of Lake Hayq based on various limnological trophic indices. The historical records were also analyzed and compared with actual data.

Paper II. **Zooplankton Community Structure and Ecology of a Tropical-highland Lake, Lake Hayq, Ethiopia** (Submitted to Journal of Plankton Research)

In this paper I discussed about one higher trophic level in the hierarchy of the food chain-zooplankton. I have attempted to investigate about zooplankton composition, numerical abundance and biomass in relation to the environmental variables. CCA was employed to describe the relationship between zooplankton community and environmental variables. I have discussed the possible reasons of the exclusive dominance of *Thermocyclops ethiopiensis*. During the present study, there was periodic disappearance of cladocerans from the sample and the paper discusses this seasonal disappearance in relation to episodic mixing and planktivorous Tilapia fish.

Paper III. **Food web structure and trophic interaction of Lake Hayq, Ethiopia** (Submitted to Ecological Modelling)

Here I have tried to assess the food web structure and trophic interaction of Lake Hayq using ecological software called Ecopath with Ecosim (EwE). Fifteen functional groups including bacteria and fish-eating birds were used in the analysis. Ecotrophic efficiency and energy transfer efficiencies are discussed. The importance of bottom-up and top-down effect were discussed using Mixed Trophic Impact (MTI) analysis. I ran EwE without Tilapia and with low phytoplankton biomass to represent before Tilapia introduction and compared with the current condition. Odum's (1969) maturity indices were used to describe the maturity of Lake Hayq.

Paper IV. **Decadal changes in phyto- and zooplankton communities in Lake Awasa, Ethiopia** (Submitted to International Review of Hydrobiology)

Long-term study for tropical aquatic ecosystem is not well represented in the literature. Hence, I chose a rift-valley lake, Lake Awasa, which is comparatively well studied in Ethiopia, in order to comprehend the long-term changes the lake had undergone. We studied phyto- and zooplankton communities of Lake Awasa between November 2003 to August 2004, and compared with historical data since the 1980-ies to assess potential inter-decadal changes. The available literature on phytoplankton and zooplankton community and abundances were used for the comparison.

11

Phytoplankton community, biomass and primary production of the Ethiopian highland Lake Hayq

If primary producers were not there, aquatic ecosystems will be merely water without life. One of these groups – phytoplankton - is primarily responsible for the life of Lake Hayq.

Phytoplankton community, biomass and primary production of the Ethiopian highland Lake Hayq

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Abstract

The trophic status of Lake Hayq, a crater and highland lake in Ethiopia, changed from oligotrophic condition to a stable eutrophic status some 20 years ago. For this shift, two hypotheses were proposed: (i) an increased nutrient to volume ratio and (ii) planktivorous Tilapia fish, which were introduced in the late 1970-ies. This study is the first to discuss about these hypotheses. To address this question, historical records were analyzed and compared with actual data. Primary production and biomass, zooplankton abundance, nutrients and physico-chemical variables were measured on a monthly basis from October 2007 to October 2008 at two stations. The overall mean concentration of dissolved inorganic nitrogen was 305 µg L^{-1}, with ammonium being the primary form. Similarly, SRP was 22 µg L^{-1}; TP 58 µg L^{-1}; and Si 3.7 mg L^{-1}. In the 1940-ies only diatoms were reported; however, algal groups and taxa numbers in the present study have increased. Out of 40 phytoplankton taxa identified, chlorophytes and diatoms contributed 77%, and CCA indicated that the former is associated with nutrients and rainfall, and the latter with silica and zooplankton. An overall mean phytoplankton fresh biomass of 1.10 $mm^3 L^{-1}$, mean Chlorophyll a (Chl a) of 12.9 mg m^{-3} and gross primary production of 7.12 g O_2 m^{-2} d^{-1} gave Lake Hayq an intermediate position compared to other tropical lakes. Chl a was influenced by rainfall, temperature and light supply. Lake Hayq is categorized as eutrophic, but the nutrient hypothesis is unlikely true since the nutrient concentrations (SRP 96 µg L^{-1} and NH_4-N 300 µg L^{-1}) were very high when the lake was reported as oligotrophic (Baxter & Golobitsch, 1970). Hence, we support the second hypothesis of Kebede et al. (1992) that the planktivorous fish was most probably the major cause for the trophic change of the lake.

Keywords: Lake Hayq; limnology; nutrients; phytoplankton; trophy.

Introduction

Tropical limnology in Africa predominantly began in the second half of the twentieth century largely due to short-term expeditions (Talling & Lemoalle, 1998). Compared to temperate systems, however, African inland waters have been studied only scarcely, with a few exceptions (Ganf, 1975; Hecky & Fee, 1981; Talling, 1957; Talling, 1965; Vareschi, 1982). This is particularly true of Ethiopian highland lakes even though rift valley lakes have been relatively better studied (Kebede & Belay, 1994; Kifle & Belay, 1990; Lemma, 1994).

In this study, we investigated the crater Lake Hayq located in the highlands of Ethiopia, which was one of the earlier visited lakes in Africa (Cannicci & Almagia, 1947; Vatova, 1940; Zanon, 1941). The latter described the lake as *'limpida e verdastra',* which means 'crystal clear water'. Baxter & Golobitsch (1970), after about 30 years, also described it as 'an unusual clear-water lake' with a Secchi depth of 9 m, very low algal biomass (< 1 mg m^{-3} Chlorophyll a = Chl a) and oxic conditions down to 40 m depth. Nevertheless some years later, Kebede et al. (1992) reported the remarkable changes of the lake into a eutrophic status, with water transparency of only around 1.2 m, Chl a concentrations between 13 and 23 µg L^{-1} and the absence of oxygen below 15 m. Based on their snap-shot survey, Kebede et al. (1992) proposed two hypotheses for the trophic change of the lake: (i) an increased nutrient to volume ratio and (ii) the introduction of Tilapia (*Oreochromis niloticus* Linnaeus 1758*)* in the late 1970-ies. The former could not be fully substantiated due to scarcity of chronological data. It is assumed however, that nutrient concentration might have been elevated as a result of catchment drain off and/or a drop of water level. Certainly the water level has dropped as Estifanos Monastery, which was once on an island, is now connected to the shore via peninsula (Baxter & Golobitsch, 1970; Pankhurst, 1967; Ashebir Abebe, personal communication). In the same way, even though the stocked planktivorous fish is a major success in the economy of the local people (Kebede et al., 1992), its effect on the lake ecosystem has not been investigated, particularly in relation to phytoplankton. Adult and juvenile Tilapia regularly consume zooplankton (Getachew, 1993; Tadesse, 1988), and hence the grazing pressure of introduced Tilapia on zooplankton might have relieved phytoplankton to grow better; consequently higher phytoplankton biomass could develop. Phytoplankton growth and biomass can be regulated by availability of resources (Zhang et al., 2007) and/or through top-down control (Spencer & King, 1984), while its relative importance can be determined by the trophic status (Elser & Goldman, 1991). Though the causes were not obvious, the change of Lake Hayq from oligotrophic to eutrophic status was evident.

A change in trophic status could impact not only the phytoplankton biomass (Kebede et al., 1992), but also its food quality, which in turn affects the transfer efficiency (e.g. fatty acids) and alters the food web structure along the trophic levels (Muller-Navarra et al., 2004). The latter authors have documented that the more nutritious ω3-High Unsaturated Fatty Acid (HUFA) were higher in oligotrophic lakes compared to eutrophic ones, which affects the growth and performance of zooplankton. Fish kill and a decrease in species richness and diversity were also associated with eutrophication (Dodds, 2002). In the case of Lake Hayq, Tilapia was found to be superior in lipid quality to other tropical fish species (Zenebe et al., 1998a, b). The authors related their finding to the diet content of the fish, in particular to diatoms. Intriguingly, a later survey revealed that the same fish species of Lake Hayq contained a lower fatty acid quality than the one found in other lake (Tadesse, 2010). These findings suggested that the study of seasonal phytoplankton assemblages and pelagic production is fundamental to understand the energy flux and trophic interactions in a system.

Phytoplankton production is considered as a good predictor of fish yield, and seasonal measurements of the former are a prerequisite (Melack, 1976; Tilahun & Ahlgren, 2009).

Therefore, this study was designed to investigate the current status of the phytoplankton composition, primary production, biomass and water chemistry. This is the first seasonal study for Lake Hayq since no previous planned research was conducted, predominantly due to its remote location. We also discussed the phytoplankton community composition in comparison with historical taxonomic lists. Moreover, we addressed the question of the current trophic state of Lake Hayq and attempted to explain the temporal shift in phytoplankton composition.

Material and methods

Study area
Lake Hayq ($11^o15'$ N, $39^o57'$ E) is located some 440 km north of Addis Ababa, the capital of Ethiopia, at an altitude of 2,030 m a.s.l. (Fig. 1).
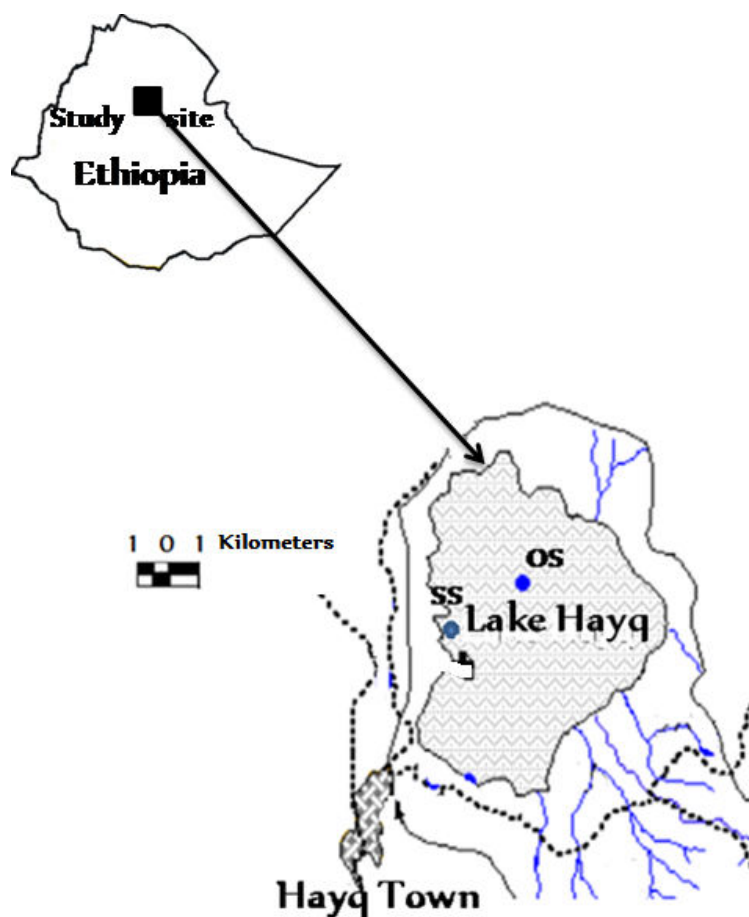
Fig. 1 The map of Lake Hayq together with sampling stations (dots) and drainage basin (redrawn from Demlie 2007)

The study area is categorized as sub-humid tropical with an annual rainfall of 1173 mm and a mean air temperature of 18.2 °C (National Meteorological Service Agency). Based on rainfall data since 1963, the major rainy season is from July to September. During the present study, there was no rainfall from December to March, which is considered as dry season (Fig. 2).
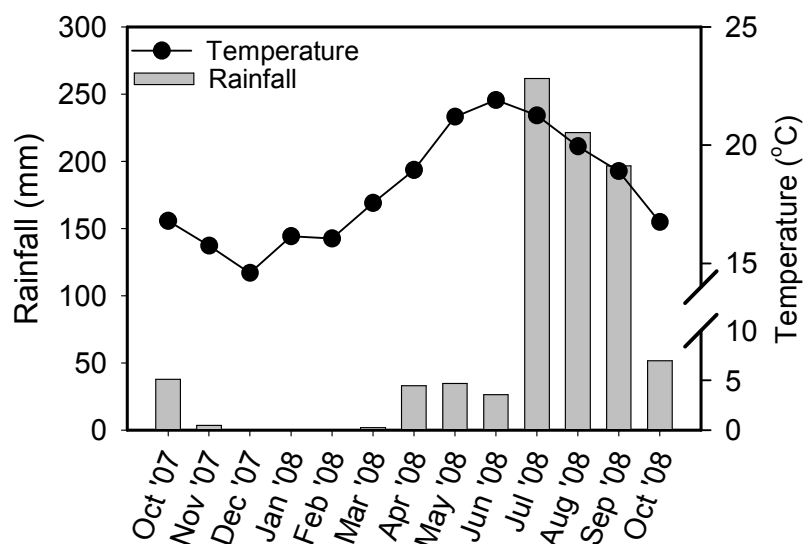
Fig. 2 Air temperature and rainfall data near Lake Hayq during the sampling period from Oct. 2007 to Oct. 2008. Data from National Meteorological Services Agency

Until some 20 years before, Lake Hayq was connected to the nearby Lake Hardibo (11°14'N, 39°46'E; altitude 2150 m a.s.l.) through the Ankwarka River. However, at present these lakes are terminal and there is no known surface outlet due to the irrigation scheme upstream. Lake Hayq is a deep, steeply shelving lake, with a maximum depth of 88 m recorded in 1938 (Table 1). It is a freshwater lake with a salinity of 0.828 g L^{-1} (Zinabu et al., 2002). Predominant cations and anions are magnesium and carbonate/ bicarbonate, respectively (Table 2).

Table 1. Morphometry of Lake Hayq (from Baxter and Golobitsh, 1970)

Variables	Values
Max. Length (north-south)	6.7 km
Max.Width	6.0 km
Shoreline	21.7 km
Surface Area	23.2 km^2
Max. Depth	88.2 m
Mean Depth	37.37 m
Volume	0.867 km^3

The fishes that inhabit Lake Hayq are *Oreochromis niloticus* (Nile Tilapia), *Clarias gariepinus* Burchell 1822 (African catfish), *Cyprinus carpio* (common carp) and *Garra dembecha* Getahun and Stiassny 2007. The last two fish species were introduced in Lake Hardibo most likely in 1980, and eventually reached Lake Hayq due to the connecting river (Tizazu, personal communication). Tilapia is also a stocked fish (Kebede et al., 1992) putting catfish as the only indigenous fish species (Baxter & Golobitsh, 1970). The dominant zooplankton species are *Mesocyclops aequatorialis* Van de Velde 1984, *Thermocyclops ethiopiansis* Kiefer 1934, *Ceriodaphnia reticulata* Jurine, *Daphnia magna* Straus 1820, *Diaphanosoma excisum* Sars and the common rotifers includes *Euchlanis parva* Rousselet 1892, *Keratella tropica* Apstein, *Polyarthra sp.* (Fetahi et al., submitted-b). The land uses in the catchments include agriculture (on steep land) and livestock grazing.

Sampling protocol and analytical methods

Routine sampling and *in situ* measurements were carried out on a monthly basis between October 2007 and October 2008 at shore station (SS) and open-water station (OS) with a mean depth of 18 m and 78 m, respectively. Temperature, conductivity, pH and dissolved oxygen were measured *in situ* using a portable all-in-one meter (Model HQ 40d Multi Hach Lange). Water transparency was estimated using a standard Secchi disc of 30 cm in diameter. Light penetration was measured with a portable light meter (Skye 200, Skye Instrument). The vertical light extinction coefficient (K_d, m^{-1}) was computed using direct light irradiance measurements ($K_d = (lnI_o - lnI_z)/Z)$), where I surface light irradiance, I_z light irradiance at a certain depth and Z depth. Euphotic depth (Z_{eu}), the depth at which 1% incident irradiance available, was determined using $Z_{eu} = 4.6/ K_d$. Water for physico-chemical variables including Chl *a*, organic matter and algal nutrients was sampled at the surface and at 2, 5, 10, and 15 m at SS, and the same measurements were undertaken at OS (surface, 5, 10, 20, 30, 40, 50 and 60 m depth). Samples were transferred and stored under ice until analyses were made at Addis Ababa University, Ethiopia. Total alkalinity was determined from the unfiltered water sample through titration with 0.1 N HCl with bromocresol green/methyl red used as end point indicator (Wetzel & Likens, 1991). Water samples were filtered through Whatman GF/C filter paper and the filtrate was used for the determination of dissolved inorganic nutrients. Soluble reactive phosphorus (SRP) was determined spectrophotometrically using the Ascorbic Acid method, ammonium (NH_4^+-N) was analyzed with the Indo-phenol Blue method and nitrate (NO_3-N) was analyzed using the Sodium-salicylate method (APHA, 1995). Nitrite (NO_2-N) determination was carried out using the reaction between sulfanilamide and N-naphthyl-(1)-ethylendiamin-dihydrochloride. The reactive silica (SiO_2) was measured using Molybdosilicate method (APHA, 1995). To determine total phosphorus (TP), unfiltered water samples were digested using potassium-peroxodisulphate, autoclaved at 120 ^{o}C for 50 minutes and measured following the standard SRP procedure (APHA, 1995).

For Chl *a*, water samples were filtered onto duplicate Whatman GF/C glass-fiber filters and the filters were deep-frozen overnight to facilitate extraction. Then the filters were homogenized and extracted in 90% acetone for 12 h. Chl *a* was determined spectrophotometrically after centrifugation at 665 nm without phaeopigments correction (Talling & Driver, 1963). To determine dry mass (DM), defined volumes of water sample were filtered using combusted- pre-weighed filters (Whatman GF/C) and dried at 95 ^{o}C. Ash mass (AM = inorganic content) was determined by combusting the dry mass in a muffle furnace for 2 hours at a temperature of 450 ± 50 ^{o}C. Organic matter (OM) was calculated by OM = DM - AM. For phytoplankton biovolume analysis, integrated water samples were taken down to

depths of 20 m and immediately fixed with Lugol´s solution. Algal abundance per unit water volume was estimated by the Utermöhl method using an inverted microscope (Nikon Diaphot) equipped with phase contrast device at 400x magnification. The volume of individual taxa was estimated by applying equivalent geometric shapes to cell forms by direct measurement of the cell dimensions (Sun & Liu, 2003; Hillebrand et al., 1999; Wetzel & Likens, 1991). The cell biovolume was converted into biomass by using a conversion factor of 1 (Wetzel & Likens, 1991). In parallel, net samples were collected using 30 µm mesh size from 20 m depth to surface. Phytoplankton taxa were examined under a Zeiss (Imager.A1) microscope and identified using identification keys including Krammer & Lange-Bertalot (2007 a,b; 2008), Komărek & Anagnostidis (1999, 2005), Ettl (1983), Ettl and Gărtner (1988), Popovsky & Pfiester (1990).

Primary productivity was measured at the open water station using light-dark bottle technique (Wetzel & Likens, 1991). The Winkler bottles (125 ml) were filled with integrated water samples and exposed at eight depths: at surface, 0.5 m, 1 m, 2.5 m, 5 m, 10 m, 15 m and 20 m. Dark bottles were kept in lightproof dark-bags and the top of the bottles was wrapped in aluminum foil. After 4-5 hours of incubation, the bottles were retrieved and immediately fixed with Winkler's reagents, then acidified, well-mixed and the whole content titrated with sodium thiosulfate (0.01 N). Gross and net photosynthetic rates and respiration were calculated employing the formula given in Wetzel & Likens (1991). The daily areal gross primary production ($\sum\sum A$, g O_2 m^{-2} d^{-1}) was calculated by multiplying the hourly average by 10 h photoperiod. The trophic status of Lake Hayq was assessed using the trophic status index (TSI) of Carlson (1977), which is calculated based on Secchi disk transparency (TSI (SDT) = 60 – 14.41 ln (SDT)); Chl *a* concentration (TSI (Chl *a*)= 9.81 ln (Chl *a*) + 30.6) and total phosphorus amount (TSI (TP)= 14.42 ln (TP) + 4.15). A TSI < 30 is commonly considered as indicative of oligotrophic condition, between 50 and 70 the water body is eutrophic and values > 70 indicate hypereutrophic condition (Wetzel, 2001). Zooplankton sampling was carried out on monthly basis at SS and OS between October 2007 and October 2008. To determine numerical abundance, samples were vertically hauled from 10 m to the surface at both stations with a 30 µm mesh townet. The samples were immediately preserved with sugar-formalin to a final concentration of approximately 4 %. The concentrated original sample of 250 mL was mixed homogeneously and a 25 mL subsample was taken with a wide mouth pipette (Wetzel & Likens, 2001), then poured into a gridded glass chamber, settled overnight and counted. Bacteria were also enumerated on a monthly basis using DAPI staining and fluorescence microscopy (Wetzel & Likens 1991).

Data analysis

T-test was used to analyze the spatial distribution pattern of limnological variables in Lake Hayq. Regression analyses were employed to model the dependent variable based on the predictors. We also used Kendall's τ correlation to check the variability of phytoplankton community composition over the sampling period. Principal Component Analysis (PCA) with Varimax rotation was run, followed by multiple regression analysis to assess the relationship between Chl *a* and significant environmental variables. SPSS software package version 16 was used in all statistical analyses. Relationships between phytoplankton taxa and significant environmental variables were analysed using a constrained Canonical Correspondence Analysis (CCA, CANOCO for Windows 4.5). CCA was chosen since the value of the longest lengths of gradient was 4.3, which signifies unimodal species response (Leps & Smilauer, 2003). The significance of environmental variables to explain the variance of species data in

CCA was tested using Monte Carlo simulations with default unrestricted permutations. Variables were considered to be significant when $P < 0.05$. Graphs were presented using Sigmaplot version 11.

Results

Lake Hayq is a slightly alkaline system with a mean ($\pm$ SE) total alkalinity of 9.88 $\pm$ 0.18 meq L^{-1} and a pH of 9.00 $\pm$ 0.02, with invariably similar patterns at both stations (Table 2). Electrical conductivity also fluctuated little with a mean ($\pm$ SE) value of 910 $\pm$ 3 μS cm^{-1}. The maximum dissolved oxygen (DO) recorded was 8.42 mg L^{-1} (121.7 % saturation) in April 2008 (Fig. 3). On the top 10 m, a minimum DO concentration (< 3 mg L^{-1}) was observed in January 2008, which coincided with mixing time. The DO concentration below 20 m depth was constantly < 1 mg L^{-1} exhibiting that the greater part of the lake column was anoxic. The depth-time temperature of Lake Hayq revealed thermal stratification and mixing periods (Fig. 3). The temperature difference between surface and 60 m depth was 3.3 ^{o}C in October 2007 but only 1.8 ^{o}C in January 2008, the latter was observed after de-stratification as a result of lower ambient temperatures and surface water cooling (Fig. 2).

Table 2. Mean ($\pm$SE) algal nutrients and physicochemical variables of Lake Hayq (*One time sample (June 2008), analyzed in Isotope Hydrology Laboratory, Addis Ababa University, Ethiopia, [a] significant difference at $P<0.05$)

Variable	OS	SS
TP (μg L^{-1})	67.14$\pm$5.31	49.06$\pm$5.99
SRP (μg L^{-1})	29.41$\pm$3.84	14.2$\pm$3.07
NO_3-N (μg L^{-1})	41.83 $\pm$ 7.23	41.32 $\pm$ 8.2
NO_2-N (μg L^{-1})	4.59 $\pm$ 1.31	8.39 $\pm$ 3.51
NH_4-N (μg L^{-1})[a]	342.33 $\pm$ 36.98[a]	172 $\pm$ 29.28
SiO_2 (μg L^{-1})	3.7$\pm$0.36	2.8$\pm$0.33
Alkalinity (meq L^{-1})	9.78$\pm$0.15	9.98$\pm$0.21
Conductivity (μS cm^{-1})	907.9$\pm$2.5	912$\pm$3
Secchi depth (m)	2.8$\pm$0.52	2.7$\pm$0.49
Euphotic depth (m)	4.95$\pm$0.81	
pH	9.06$\pm$0.02	9.07$\pm$0.02
*Na^+ (mgL^{-1})	61.2	
*K^+ (mgL^{-1})	4.2	
*Mg^{2+} (mgL^{-1})	97.8	
*Ca^{2+} (mgL^{-1})	1.02	
*F^- (mgL^{-1})	1	
*Cl^- (mgL^{-1})	35.8	
*SO_4^{2-} (mgL^{-1})	2.8	
*CO_3^{2-} (mgL^{-1})	24	
*HCO_3^- (mgL^{-1})	292.8	
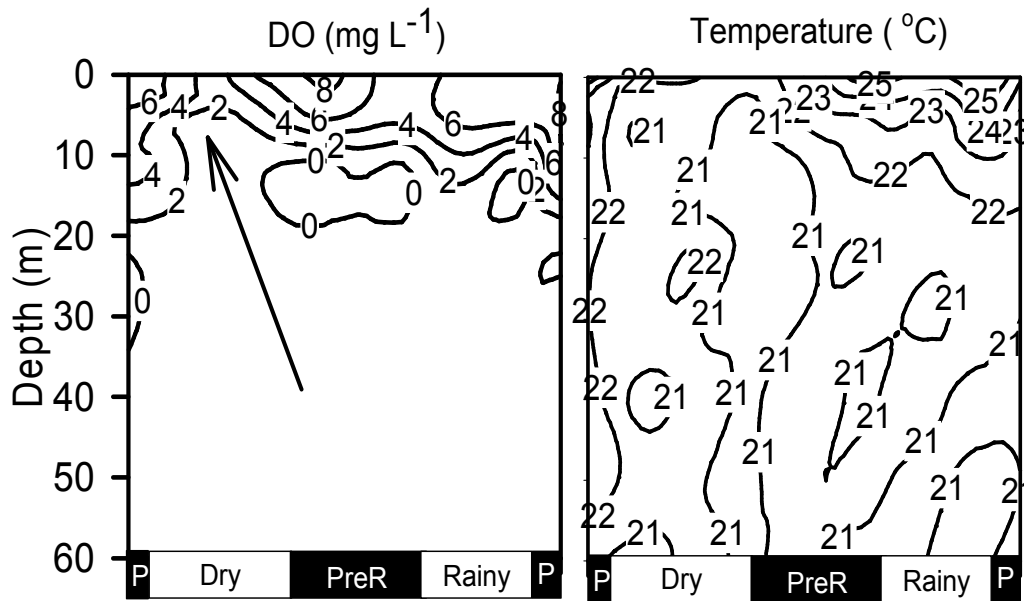
Fig. 3 Depth-time profiles of Dissolved Oxygen (mg L^{-1}) and temperature (^{o}C) at OS station in Lake Hayq between Oct. 2007 and Oct. 2008 (P = post rainy season; Rainy = rainy season; PreR = pre-rainy season; dry = dry season).

The vertical extinction coefficient varied between 0.41-2.28 m^{-1}, Secchi-disc readings were shallow during dry period and coincided with mixing and high Chl *a* concentrations. Average concentration of NO$_3$-N was about 42 µg L^{-1}, NO$_2$-N values never exceeded 10 µg L^{-1} but NH$_4$-N was notably higher than the two nitrogen forms (257.17 µg L^{-}1, Table 2). Following the development of thermal stratification, the concentration of nutrients progressively increased with depth down to the hypolimnion, which was anoxic all year long (Figs. 3, 4). PCA with environmental data as input variables resulted in a significant model including three principal components (PCs), which explained 87% of the total variation in the data set (Table 3). The first PC is strongly correlated with nutrients and grazing pressure referring to 'bottom-up/top-down' effect, whereas the second PC associated with rainfall and temperature indicating the influence of "seasonality". The third PC implied light supply.

Table 3 Principal Component Analysis based on 6 variables; factor loadings > 0.8 are bold. Value in bracket shows the variance of data explained by components.

Parameters	'Bottom-up/top-down (48.2%)'	Seasonality (20%)	Light supply (18.3%)
SRP	**0.818**	0.321	-0.061
NH$_4$-N	**0.911**	0.212	0.191
Zooplankton abundance	**-0.875**	-0.021	0.180
Rainfall	0.245	**0.860**	0.234
Temperature	0.130	**0.915**	-0.207
Extinction coefficient	-0.046	-0.005	**0.977**
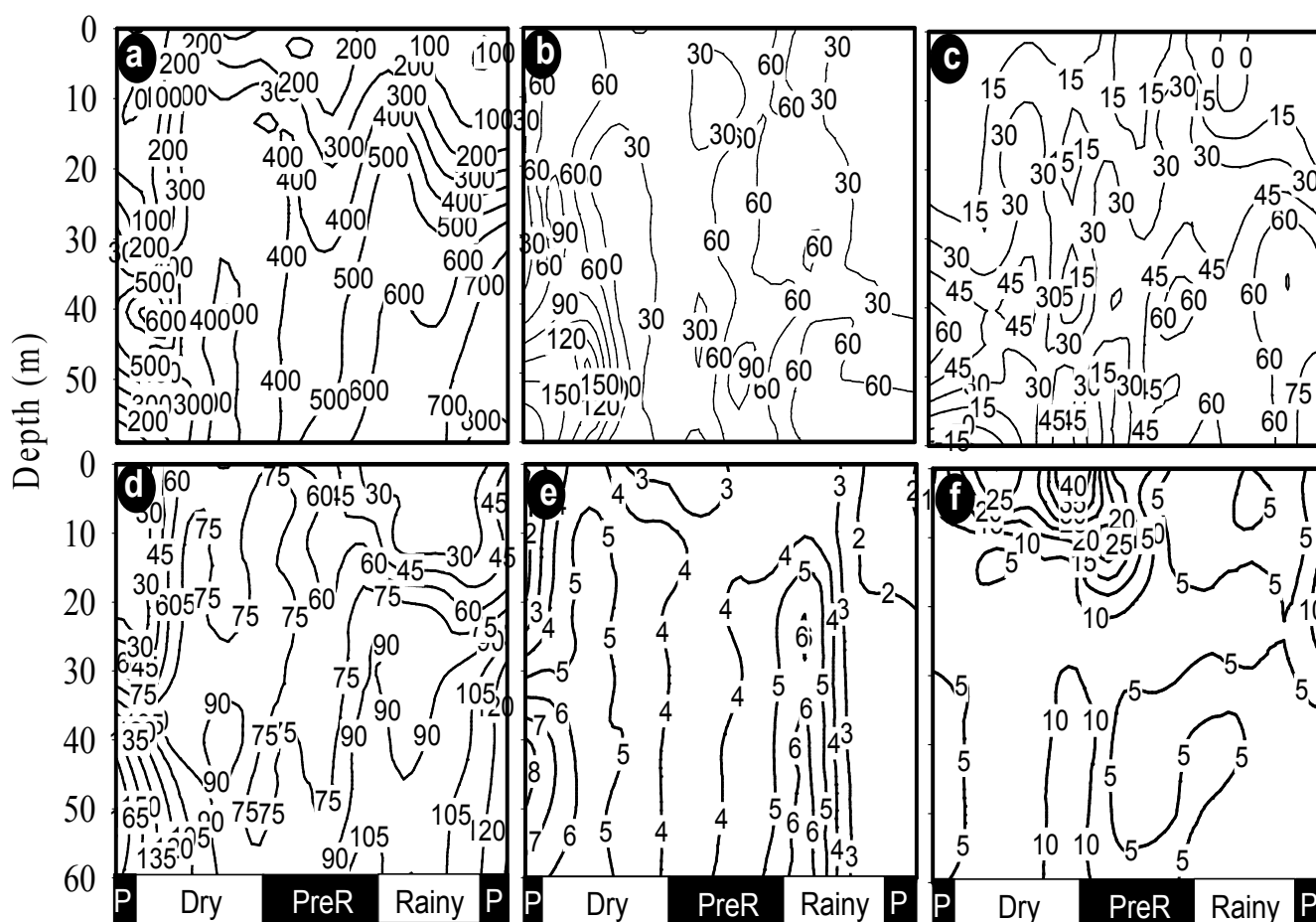
Fig. 4 Depth-time contour plots showing the seasonal and vertical variation of algal nutrients (**a**- NH4-N (μg L^{-1}), **b**- NO3-N (μg L^{-1}), **c**- SRP (μg L^{-1}), **d**- TP (μg L^{-1}), **e**- Silicon (mg L^{-1}), **f**- Chl *a* (mg m^{-3}) at OS station in Lake Hayq (P = post rainy season; Rainy =rainy season; PreR = pre-rainy season; dry = dry season)

A total of 40 phytoplankton taxa were identified and some of them are new reports to the lake (Table 4). Chlorophytes contributed about 47% to the total phytoplankton abundance, followed by diatoms contributing around 30%. Cyanoprokaryota and the 'Other group' (those which have fewer numbers of taxa are categorized under "Other group"; Table 4) contributed 11% each. Kendall's τ correlation coefficient indicated that there were major community composition changes during the sampling period (Fig. 5).
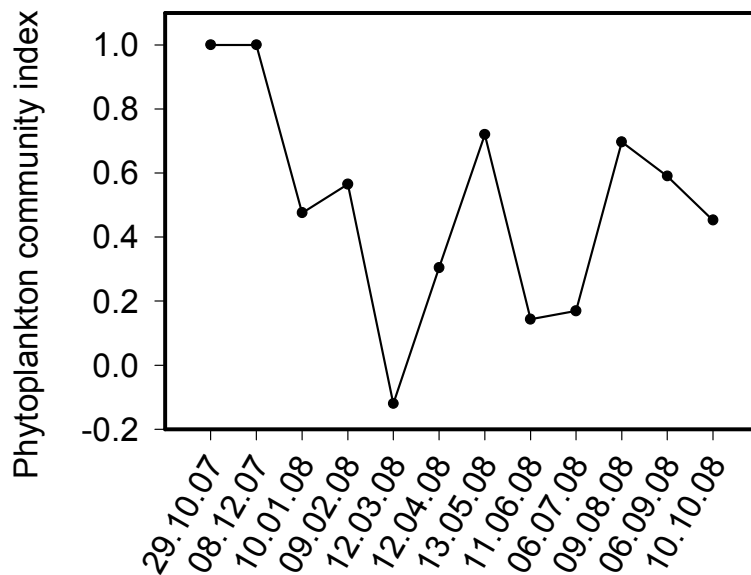
Fig. 5 Phytoplankton community assemblage rank on successive sampling date based on Kendall's τ correlation coefficient

Table 4 Phytoplankton species composition of Lake Hayq

Cyanoprocaryota	Chlorophyta	Bacillariophyceae	'Others group'
Anabena sp.	*Ankistrodesmus*	*Achnanthes**	Cryprophyta
Microcystis flos-aquae	*falcatus**	*Aulacoseira**	*Cryptomonas**
M. aerugenosa	*Botryococcus braunii**	*Cocconeis**	
Merismopedia	*Chodatella cingula*	*Cyclotella comensis**	
Spirulina	*Chodatella subsalsa*	*Cymbella**	Dinophyta (Division
	Coelastrum astroideum	*Epithemia*	Pyrrophyta)
	Cosmarium sp.1*	*Fragilaria*	*Peridinium*
	Cosmarium sp.2*	*Gomphonema*	
	Kirchnerilla*	*Navicula*	Division
	Oocystis	*Nitzschia*	Euglenophyta
	Pediastrum simplex*	*N. elegantula*	*Euglena*
	Pediastrum sturmii*	*Surirella robusta*	*gracilis**
	Scenedesmus sp*	*S. subsalsa*	*Phacus sp. **
	Staurastrum bullardii*	*Synedra ulna*	
	S. quadicuspidatum*		
	S. uplandicum*		
	Synura uvella		
	Tetraedron minimum		

The asterisks* indicate the taxa that were identified for the first time.

The overall mean biomass was 1.1 mm^3 L^{-1}, primarily dominated by *Fragilaria, Navicula* and *Synedra* from December 2007 to June 2008 (Fig. 6). However, the highest value (14.84 mm^{3}L^{-1}) obtained in March 2008 could be related to a bloom of *Euglena gracilis* Lwoff 1932. The biovolume peak in July was mainly caused by the cyanoprokaryote *Merismopedia*, which was replaced by chlorophyte *Oocystis* in August —September, and *Cosmarium* in October 2008. Out of 17 environmental variables considered, manual "forward selection" procedure of CCA resulted in six significant variables (Table 5, Fig. 7). The first two axes accounted for 71% of the variance in the phytoplankton-environment relationship (Table 5).
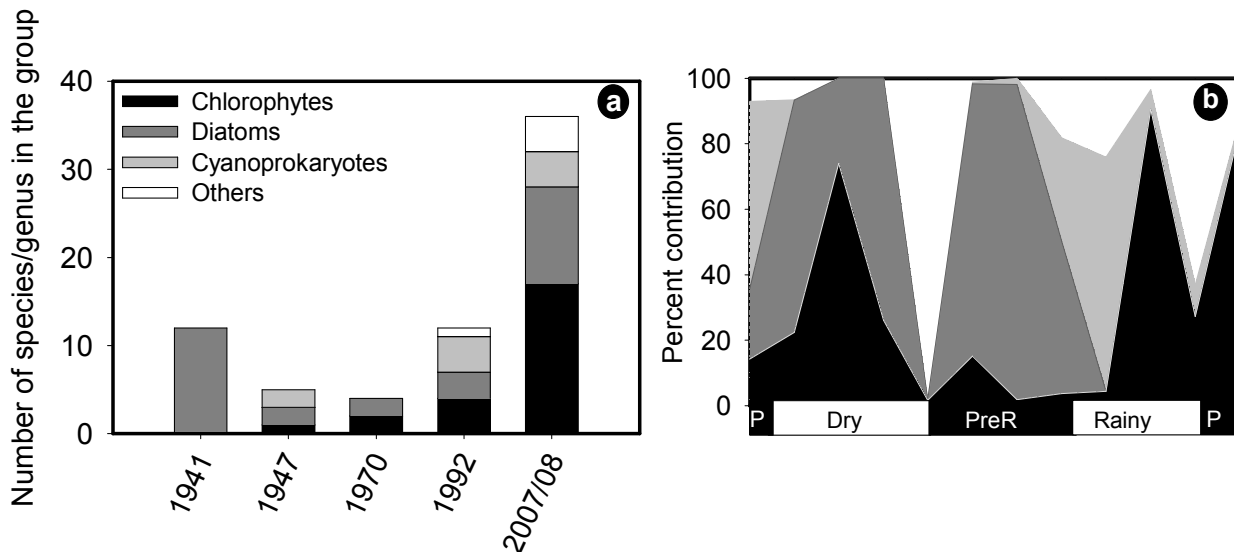
Fig. 6 (a) The contributions of algal groups to the total phytoplankton in chronological order since 1940s (data combined from Baxter and Golobitsch 1970; Kebede et al. 1992), and (b) temporal variations in the biomass of the major phytoplankton groups in Lake Hayq during Oct. 2007 to Oct. 2008

Table 5 Summary statistics of CCA.

Axes	1	2	3	4
Eigenvalues:	0.751	0.425	0.232	0.128
Species-environment correlations	0.996	0.947	0.807	0.904
Cumulative percentage variance				
of species data:	35.9	56.2	67.3	73.4
of species-environ relation:	45.4	71.0	85.1	92.8
Sum of all eigenvalues	2.09			
Sum of all canonical eigenvalues	1.66			

The first axis was correlated with total alkalinity, and the second axis with NH_4-N, SRP, SiO_2, rainfall and zooplankton. *Euglena* occurrence correlated positively and strongly with total alkalinity. *Phacus,* Cryptomonads, and *Merismopedia* coincided positively with rainfall, SRP and NH_4-N. *Synedra, Navicula* and *Fragilaria* were positively related to SiO_2 and zooplankton, and negatively to SRP, NH_4-N and rainfall (Table 5).

Chl *a* is concentrated in the top 10 m depth with mean value of 12.9 mg m^{-3} and a maximum of 45 mg m^{-3} measured in March 2008. Mean Chl *a* concentration of the euphotic zone per unit area was 56 mg m^{-2}. A multiple regression analysis explained 87.7% of the Chl *a* variations, for which PC-'seasonality' (P=0.00) and PC-light supply (P=0.013) contributed significantly (Fig. 8).
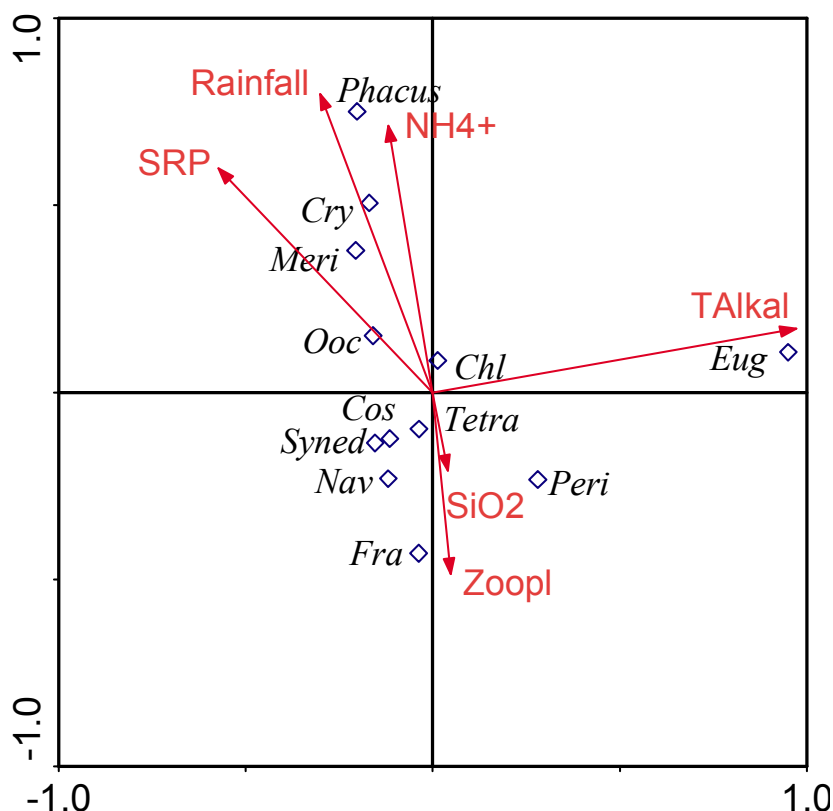
Fig. 7 Bi-plot of the Canonical Correspondence Analysis (CCA) for phytoplankton taxa (diamonds) and environmental variables (arrows; Cry-Cryptomonads, Meri-Merismopodia, Ooc-Oocystis, Chl-Chlorella, Cos-Cosmarium, Tetra-Tetradron, Syned-Synedra, Nav-Navicula, Fra-Fragilaria, Peri-Peridinium, Zoopl- zooplankton, TAlkal- total alkalinity)
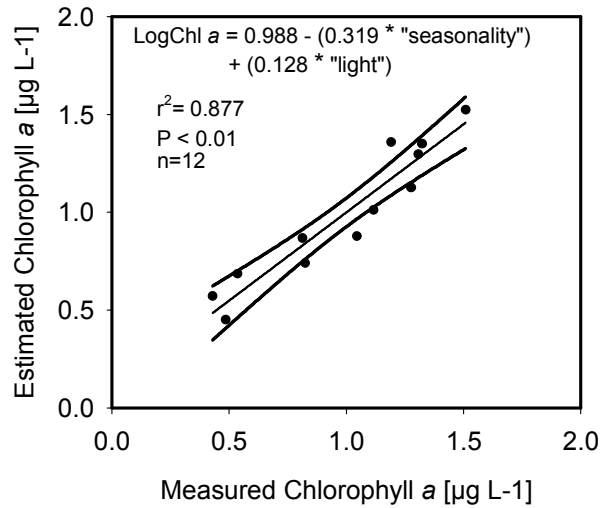
Fig. 8 Regression analysis model of Chl *a*: measured versus estimated and the formula of the model is indicated in the insert

A high and significant linear relationship between Chl *a* and phytoplankton biovolume was calculated (Biovolume $[mm^3 \ L^{-1}]$ = -1.790 + (0.541 * Chl a[$\mu g \ L^{-1}$]. The overall mean gross primary productivity (GPP) was 162.42 mg O_2 m^{-3} h^{-1} (Fig. 9). The maximum GPP at light-saturation (A_{max}, mg O_2 m^{-3} h^{-1}) was 600 mg O_2 m^{-3} h^{-1} recorded in June 2008. The mean ratio between A_{max} and Chl *a*, the specific light saturated rate of primary production or photosynthetic capacity (P_{max}, mgO_2 (mg Chl a^{-1}) h^{-1}), was 21.3. The mean GPP per unit area ($\sum\sum A$) was 7.12 g m^{-2} d^{-1}. Net photosynthetic (NPP) rates ranged from 4.8 to 262 mg O_2 m^{-3} h^{-1} constituting about 60% of the GPP.
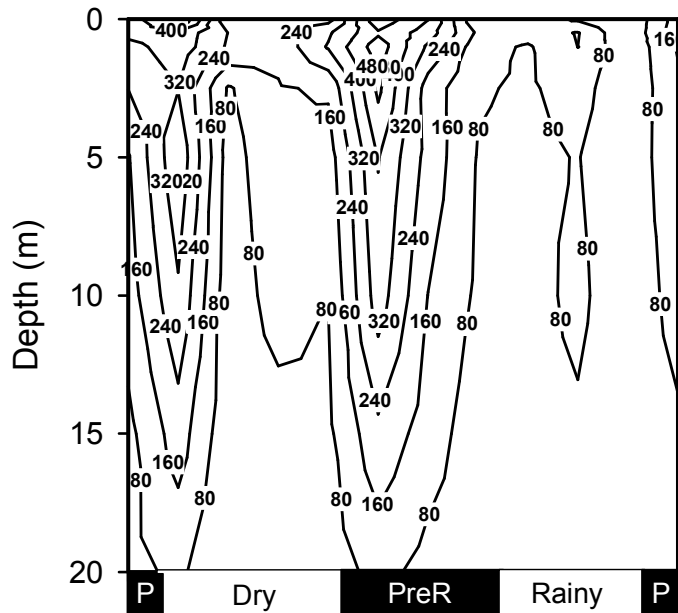
Fig. 9 Isopleth of *in situ* GPP (mg O_2 m^{-3} h^{-1}) for OS of Lake Hayq. Abbreviations are same as Fig. 3

Discussion

Whereas pH and total alkalinity have remained within the same range during the last half a century (c.f. Baxter & Golobitsch, 1970), electrical conductivity has shown a gradual increase over the last 5 decades. In the late 1960-ies, conductivity was reported as 790 µS cm^{-1} (Baxter & Golobitsch, 1970) followed by 869 µS cm^{-1} (Demlie, 2000) and 910 µS cm^{-1} (this study). The concentration of total ions is expected to have increased due to evaporation, biological turn-over and interactions with the sediments (Payne, 1986). However, the lake is still fresh water placed under Tallings' classification II (Talling & Talling, 1965) and has never been saline in its history (Lamb et al., 2007). One justification could be the discharge of the Ankwarka River, which formerly fed the lake with dilute water of about 460 µS cm^{-1} (Baxter & Golobitsh, 1970). However its inflow at present has terminated due to up-stream irrigation. Nevertheless, a recent study revealed a subterranean inflow of freshwater springs and possible solute seepage-out through large faults (Demlie et al., 2007), which would remain a plausible explanation for its freshness. The clinograde oxygen profile typical of eutrophic lakes (Wetzel, 2001) showed constantly <1 mg L^{-1} below 20 m depth (Fig. 3). Minimum DO at surface was observed during January 2008, which was related to a mixing event. In the late 1960-ies, Baxter & Golobitsch (1970) measured good oxygen supply up to 40 m depth. However, the vertical DO layer has been reduced since at least the last 2 decades (Fig. 3), as Kebede et al. (1992) reported a shallow DO layer of only 15 m depth. Lake Hayq is categorized as eutrophic water body based on total phosphorus (TSI = 63) and Chl a (TSI= 55.7) concentration. The mean Chl a concentration was 12.9 mg m^{-3}, giving Lake Hayq an intermediate position when compared with other tropical lakes (Table 6). Besides, Chl a per unit area within the euphotic depth (56 mg m^{-2}) was also greater than in other Ethiopian rift valley lakes Zway (20.9 mg m^{-2}), Awasa (54.2 mg m^{-2}) and Chamo (31.3 mg m^{-2}), which are considered as eutrophic (Tilahun & Ahlgren, 2009).

Table 6 Comparison of phytoplankton GPP and *Chl a* of Lake Hayq with other tropical lakes

Lake	*Chl a* (mg m^{-3})	A_{max} (mg O$_2$ m^{-3}h^{-1})	A_{max}/Chl a mg O$_2$ (mg Chl a)$^{-1}$ h^{-1}	$\sum\sum$A (g O$_2$ m^{-2} d^{-1})	References
Hayq, Ethiopia	12.9	274.7	21.3	7.12	The present study
George, Uganda	60	1322.6	22	13.9	Ganf 1975
Lanao, Philipppines	3	103.2	34.4	5.5	Lewis 1974
Nakuru, Kenya	160	3193.5	20	1.6	Vareschi 1982
Nakuru, Kenya	646	--	5-10.8	10	Oduor, Schagerl 2007
Tana, Ethiopia	4.5	--	--	2.43	Wondie et al. 2007
Tanganyika, Kenya	1.2	21.9	18.3	2.6	Hecky, Kling 1981
Victoria, Uganda	3	90.3	30.1	9	Talling 1965
Zway, Ethiopia	39.2	977.4	24.9	3.4	Tilahun, Ahlgren 2009

The growth of phytoplankton can be limited by the availability of nutrients when light and temperature are adequate and loss rates are not excessive (Hecky & Kilham, 1988). In many lakes, P and sometimes N depletion limit phytoplankton growth (Dodds, 2002). The mean SRP (22 µg L^{-1}) and TP (58 µg L^{-1}) are in the intermediate range to other tropical lakes (Oduor & Schagerl, 2007; Tilahun

& Ahlgren, 2009) and do not indicate any P limitation. Even though Baxter & Golobitsh (1970) had measured higher SRP concentrations of about 96 μg L^{-1}, they described Lake Hayq as oligotrophic based on Chl *a* amount (< 1 mg m^{-3}), which indicated heavy zooplankton grazing pressure on phytoplankton since Lake Hayq was without pelagic planktivorous fish at that time. During the present study, SRP was low in March 2008 which could be interpreted as high nutrient uptake as high phytoplankton biomass was recorded at the same time (reflected also in the high TP concentrations; Fig. 4). Similarly, the concentration of NH_4-N was remarkably high, but this appears typical to some tropical lakes (Talling & Lemoalle, 1998; Tilahun & Ahlgren, 2009). This can be explained by high year-round temperatures and related microbial activities (in Lake Hayq, we found mean bacteria concentrations of $4*10^6$ cells mL^{-1}). Besides, nutrient remineralization due to zooplankton could be large since we observed high zooplankton densities in Lake Hayq (Fetahi et al., submitted-b). Zooplankton primarily excretes P as dissolved phosphorus and nitrogen as ammonium, which are readily available for photoautotrophs (Lampert & Sommer, 1997).

The number and type of the algal taxa seems to have increased in the last six decades with chlorophytes as the abundant taxa in the present study (Fig. 6). Some of the taxa identified in the present study are new reports for the lake including *Cosmarium,* Cryptomonads, *Cyclotella,* and *Euglena* (Table 4). Even though chlorophytes were high in abundance, the biomass was mainly dominated by diatoms (52.3%) from December 2007 through June 2008 with *Fragilaria, Navicula* and *Synedra ulna* as the most abundant taxa. The dominance of diatoms was also reported by the earlier visitors of the lake (Kebede et al., 1992; Zanon, 1942), where the latter identified exclusively diatoms. In the present study, community shifts were pronounced at two inflection points in March and June 2008 (Fig. 5). The first shift was due to an abrupt change from diatoms to *Euglena gracilis* and the latter was because of compositional replacement from the dominant diatoms to Cyanoprocaryota (primarily *Merismopedia*) which in turn was replaced by Chlorophyta (*Oocystis*). The compositional changes could be related to the grazing pressure on diatoms by herbivorous zooplankton (cladocerans), which were quite abundant during this time (Fetahi et al., submitted-b). Such shifts by grazing pressure already have been documented in enclosures (Weers & Zaret, 1975). Additionally, the development of thermal stratification and reduction of Si in the epilimnion (Fig. 4) might have contributed to the changes, as was also reported elsewhere (Zhang et al., 2007). Chl *a* concentration had a temporal fluctuation with the maximum values recorded in March 2008, when minimal grazing pressure from herbivorous cladocerans and Tilapia was reported (Fetahi et al., submitted-b). However based on PCA analysis, the primary factors that regulate Chl *a* variation was PC-rainfall, PC-temperature and PC-light supply, which are associated with the seasonality of the region (Table 3). In actual fact, relatively high mean Chl *a* (21.7 mg m^{-3}) were recorded during dry season and low (4.3 mg m^{-3}) during major rainy season. CCA analysis indicated that *Euglena* occurrence is strongly correlated with total alkalinity (Fig. 7). Lake Hayq showed a pattern of stratification (Fig. 3), which could influence the compositional shift towards flagellated *Euglena* species as it has the ability of controlling their position in the water column (Clegg et al., 2007). The association of diatoms with silica is indicative of their demand for growth (Lampert & Sommer, 1997). The positive correlation of diatoms with zooplankton could be related to 'beneficial predation' (Christensen, Walters & Pauly, 2005), the direct grazing pressure on prey is outweighed by indirect positive effect such as the high nutrient remineralization in the lake.

The mean volumetric rate of light-saturated GPP (A_{max}) in Lake Hayq was 275 mg O_2 m^{-3} h^{-1}, which was greater than values for large tropical lakes such as Tanganyika and Victoria (Table 6). Mean

areal GPP within the euphotic depth ($\sum\sum A$) was 7.12 g O_2 m^{-2} d^{-1}, which is closer to maximum rates of temperate lakes (9.7 g O_2 m^{-2} d^{-1}) (Talling, 1965). However, it is far below the maximum photosynthetic rates (25-30 g O_2 m^{-2} d^{-1}) observed in some tropical water bodies (Table 6). In Lake Hayq, nutrients particularly nitrogen could be a limiting factor for algal growth as has been shown in several tropical lakes (Lewis, 1996; Talling & Lemoalle, 1998). Downing & McCauley (1992) observed N limitation significantly more frequent in lakes with TP > 30 µg L^{-1}, and Lake Hayq with TP> 60 µg L^{-1} could be N-limited. Furthermore, the nutrient ratio (C **:** N **:** P =100 : 14 : 1) also pointed to N-limitation. A major reason for N-limitation in tropical lakes is high denitrification that reduces nitrate- (or nitrite-) nitrogen to biologically unavailable atmospheric N_2 (Lewis, 2002). The ratio of $\sum\sum A$ to $\sum$Chl *a* of Lake Hayq was 0.13, which was equivalent to several other African freshwater lakes, but higher compared to temperate ones (Lemoalle, 1981).

All studies before the introduction of Tilapia placed Lake Hayq as typical oligotrophic water body (Zanon, 1941; Baxter & Golobitsch, 1970) in terms of algal biomass and productivity. During the current study, Lake Hayq is categorized as a eutrophic system employing various limnological parameters. Interestingly, the nutrient concentrations such as SRP (96 µg L^{-1}) and NH_4-N (300 µg L^{-1}) were very high when the lake was reported as oligotrophic (Baxter & Golobitsch, 1970). We therefore assume that Tilapia primarily caused the trophic change via a cascading effect through the food web interactions. In former times, growth of phytoplankton might have been controlled by zooplankton since the lake was without pelagic planktivorous fish. The stocking of Tilapia probably reduced the number of zooplankton, relieving phytoplankton from grazing pressure, which eventually resulted in eutrophication. In the present study, following a massive planktivorous fish kill, large-sized *Daphnia magna* appeared for the first time since the study was launched, and grazed down phytoplankton biomass (Fetahi et al., submitted-b). This phenomenon indicated that the presence of large-sized cladocerans in the lake is evident in the absence of planktivorous fish. Large-sized cladocerans are important filter feeders and largely responsible for clear water (Scheffer, 1998). Therefore, with this seasonal study, we support the hypothesis of Kebede et al. (1992) that the stocked fish was most probably the major cause for the shift of the trophic status of Lake Hayq from oligotrophic towards eutrophic. Fetahi et al. (submitted-c) also supported the same hypothesis based on their analysis on food web structure and trophic interactions of Lake Hayq (using ecological model called Ecopath with Ecosim).

In conclusion, the phytoplankton biomass was dominated by diatoms followed by chlorophytes, the latter being numerically abundant. The photosynthetic and biomass per euphotic depth values were high indicating phytoplankton primary production was the primary carbon source of the lake. Based on biotic and abiotic limnological variables, Lake Hayq is unambiguously categorized under eutrophic status, which most likely resulted from food web interactions as a result of the stocked planktivorous fish species.

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Zooplankton Community Structure and Ecology of a Tropical-highland Lake, Lake Hayq, Ethiopia

In the ladder of food chain, zooplankton is an indispensable link obviously for Lake Hayq.

Zooplankton Community Structure and Ecology of a Tropical-highland Lake, Lake Hayq, Ethiopia

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Abstract

Lake Hayq, Ethiopia, was stocked with planktivorous fish (*Oreochromis niloticus*) in 1978 offering an opportunity to study the effect of fish predation in a natural lake. Since that time, some limnological surveys have been done sporadically documenting a change in zooplankton composition including the disappearance of cladocerans, hypothesizing the stocked Tilapia fish could be a cause. Nevertheless, no detailed research was conducted to identify potential effects of fish stocking. We determined zooplankton composition, abundance and biomass between October 2007 and January 2009 on short-time intervals including the underlying limnological variables in order to assess the temporal and seasonal zooplankton dynamics. The zooplankton community was depauperate comprising two copepods, three cladocerans, and six rotifers taxa. Total mean standing biomass of crustacean zooplankton was 237 mg dry mass m^{-3}, which gives Lake Hayq an intermediate position when compared with other tropical lakes. Of copepods, *Thermocyclops ethiopiensis* was almost an exclusive species, and its temporal variation was influenced by food supply and water temperature. In January 2008, we observed a massive planktivorous fish mortality that triggered high algal biomass, which was later grazed by *Daphnia magna* demonstrating the cascading trophic interactions hypothesis in a natural system. We refute the hypothesis that Tilapia was the cause for the seasonal disappearance of cladocerans, and attribute it to the adverse effect of episodic mixing.

Keywords: Lake Hayq, mixing, *Thermocyclops*, tropical highland lake, zooplankton ecology.

Introduction

Zooplankton plays a pivotal role in mediating the transfer of energy from lower to higher trophic levels in aquatic systems (Lampert and Sommer, 1997). Its community composition, biomass and production determine the strength of the energy transfer. Even though limnological research started around 110 years ago (Le Cren and Lowe-McConnell, 1980), until the early 1960's these studies were predominantly carried out in temperate lakes. This trend, however, changed when the concerted efforts of International Biological Programme (IBP) produced comprehensive information on zooplankton biomass and production that enabled a global comparison (Le Cren and Lowe-McConnell, 1980). To date, zooplankton community composition and biomass have been studied in several tropical inland water bodies, but for Africa there is still scarce information available (Green, 1967; Burgis, 1970; Mengistou and Fernando, 1991; Mavuti, 1994; Irvine and Waya, 1999; Kurki *et al.,* 1999). Zooplankton abundance and composition can be structured by resources, competition and/or predation pressure (top-down control) (Lampert and Sommer, 1997). Large zooplankton species filter more efficiently (Brooks and Dodson, 1965), and they commonly dominate when there is little predation pressure. However, fish selectively feed on larger zooplankton, and the presence of planktivorous fish causes a shift in the zooplankton community towards small-bodied animals, which are relatively inefficient grazers (Brooks and Dodson, 1965; Shapiro and Wright, 1984). Furthermore, low zooplankton types and abundances are documented at lower dissolved oxygen concentration (Vinogradov and Voronina 1961; Longhurst 1967) and anoxic condition could also structure zooplankton community and abundances (Judkins 1980; Alldredge et al. 1984). Thus, the overall consequences could influence population dynamics, predator-prey relationships and energy transfer efficiency in an ecosystem (Baird *et al.,* 2004).

In 1978, Tilapia was stocked in Lake Hayq so as to fill an empty niche of the planktivorous fish and to provide cheap protein to the local people (Kebede *et al.,* 1992). The lake is without strict piscivores, consequently the planktivorous fish dominated the ecosystem offering an opportunity to study the effect of fish predation on plankton in this natural highland lake. Even though stocking of fish to a natural lake is controversial from an ecological point of view (Ribbink, 1987), the stocked planktivorous Tilapia (*Oreochromis niloticus* Linnaeus 1758) is a major success in the economy and nutrition of the local people (Kebede *et al.,* 1992). Fish yield partly depends on the available nutrition, and zooplankton is an important diet of Tilapia at some stage in their life cycle (Fernando, 1994), and food to other larval and juvenile fishes (Post and Kitchell, 1997). Hence, the dynamics of zooplankton population has a critical influence on fish recruitment and yield in a system because of their decisive role as a food source.

Even though economically important, the effects of Tilapia on the food web structure and ecosystem for Lake Hayq have not been studied in detail until now. There are, however, some clues that the zooplankton composition of Lake Hayq has changed through time. The lake was visited as early as 1930s by the Italian expedition (Vatova, 1940; Zanon, 1941; Cannicci and Almagia, 1947) who documented the presence of cladocerans, cyclopoids and catfish. Until 1970, large cladocerans such as *Diaphanosoma* and *Daphnia magna* were abundant (Cannicci and Almagia, 1947; Baxter and Golobitsch, 1970); whereas cladocerans were completely absent in a 1989 survey instead copepods being dominant in the system (Kebede *et al.,* 1992). It was suggested by Kebede *et al.* (1992) that the stocked Tilapia fish was the cause for the disappearance of cladocerans. Despite Lake Hayq was one of the earlier visited lakes in Africa, no previous planned research work was conducted except for archiving the presence/absence of zooplankton taxa by different visitors at different times,

predominantly due to its remote location. It was therefore imperative to study the ecology of zooplankton to assess the seasonal succession, carrying capacity, and to scrutinize the hypothesis of Kebede *et al.* (1992) about the cause of the zooplankton changes. We studied the zooplankton community of Lake Hayq, its numerical abundance and biomass on weekly to fortnightly sampling intervals. The temporal and spatial variations in relation to the underlying environmental variables have also been considered. Furthermore, we discussed potential causes for the exclusive dominance of *Thermocyclops* in recent lake surveys.

METHODS

Study site
Lake Hayq (11° 15'N, 39° 57'E) is located some 440 km north of Addis Ababa, the capital of Ethiopia, at an altitude of 2,030 m a.s.l. (Baxter and Golobitsch, 1970). Lake Hayq, its catchment area and sampling stations are indicated in Fig. 1.
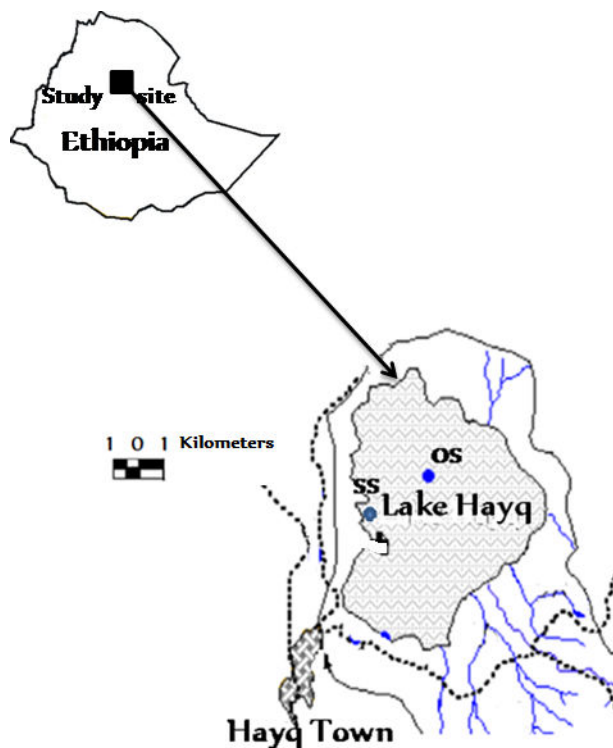
Fig. 1. The map of Lake Hayq together with sampling stations (dots) and drainage basin (redrawn from Demlie, 2007).

The study area is categorized as sub-humid tropical with an annual rainfall of 1173 mm and a mean air temperature of 18.2 ^{o}C (National Meteorological Service Agency). Based on rainfall data since 1963,

the major rainy season is identified from July to September (Fig. 2). During our sampling period, there was no rainfall from December to March, which is considered as dry season.
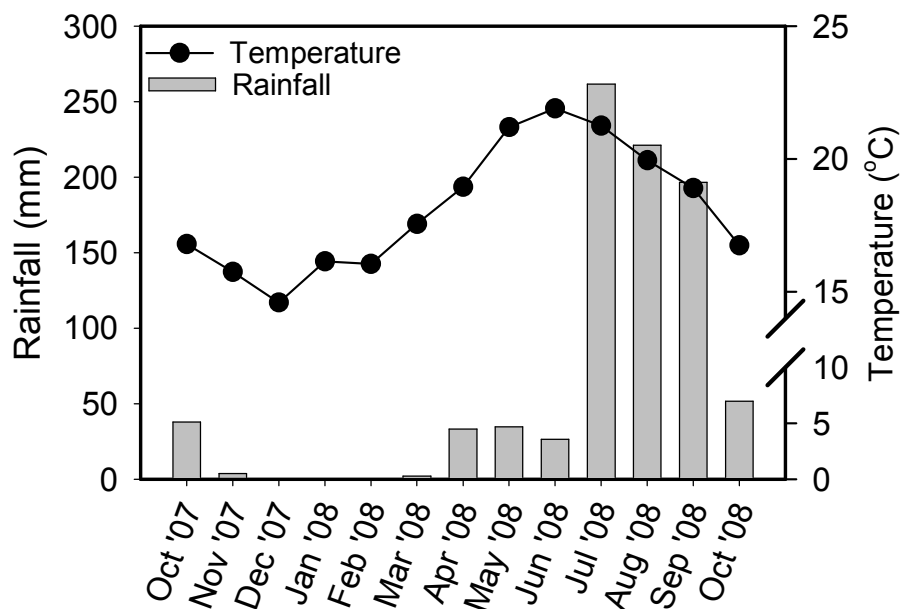
Fig. 2. Air temperature and rainfall data of Lake Hayq during sampling period from October 2007 to October 2008. Data provided from the National Meteorological Services Agency.

Previously, Lake Hayq was connected to the nearby Lake Hardibo (11° 14'N, 39° 46'E; altitude 2150 m a.s.l.) through Ankwarka River. However, at present these lakes are terminal and there is no known surface outlet due to the irrigation scheme upstream. Lake Hayq is a deep, steeply shelving lake, with a maximum depth of 88 m recorded in 1938 (Table I). The lake is fresh water, with a salinity of 0.83 g L^{-1} (Zinabu *et al*., 2002) and never has been saline (Lamb *et al.,* 2007). Predominant cations and anions are magnesium and carbonate/ bicarbonate, respectively.

Table I: Morphometric data of Lake Hayq according to Baxter and Golobitsh (1970)

Variables	Values
Max. Length (north-south)	6.7 km
Max.Width	6.0 km
Shoreline	21.7 km
Surface Area	23.2 km^2
Max. Depth	88.2 m
Mean Depth	37.37 m
Volume	0.867 km^3

Fishes that inhabit Lake Hayq are *Oreochromis niloticus* (Nile Tilapia), *Clarias garapienus* Burchell 1822 (African catfish), *Cyprinus carpio* (common carp) and *Garra dembecha* Getahun and Stiassny 2007. The latter two species were introduced in Lake Hardibo most likely in 1980, and

36

eventually reached Lake Hayq due to the connecting river (Tizazu, personal communication). Tilapia also has been stocked (Kebede *et al.*, 1992) putting catfish as the only indigenous fish species (Baxter and Golobitsh, 1970). According to Kebede *et al.* (1992), phytoplankton biomass is dominated by a diatom, *Navicula* sp. and the cyanobacteria *Microcystis delicatissima* (W. & G.S. West) Starmach and *M. elachista* (W. West & G.S. West) Compère, which comprise about 90 % of the biomass.

Field sampling and measuring protocol

Spatial and vertical profiles of water temperature, conductivity, pH and dissolved oxygen were measured using a portable multiprobe (Model HQ 40d Multi Hach Lange). Chlorophyll *a* (Chl *a*) concentration was determined spectrophotometrically at 665 nm without phaeopigments correction (Talling and Driver, 1963).

Zooplankton sampling was carried out on weekly to fortnightly intervals from the open-water station (OS) between October 2007 and January 2009 (Fig. 1). Additionally, a shore station (SS) was sampled on a monthly basis between October 2007 and October 2008. OS is located some 2 km offshore in the open water and had a mean depth of 78 m. SS with a mean depth of 18 m, is located about 100 m offshore. Three replicates were taken at each station on each sampling date. Samples were collected with 100 μm mesh townet for the first two sampling dates and then 30 μm was used until the end of the sampling period. The mesh-size was changed to improve sampling efficiency for copepod nauplii and rotifers. To determine numerical abundance, samples were vertically hauled from 10 m to the surface at both stations. The volume of water filtered (V) was calculated from $V = \pi r^2 h$, where r = radius of net ring (0.15 m) and h the distance towed (10 m). The samples were immediately preserved with sugar-formalin to a final concentration of approximately 4 %. The concentrated original sample of 250 mL was mixed homogeneously and a 25 mL subsample was taken with a wide mouth pipette (Wetzel and Likens, 2001), then poured into a gridded glass chamber where three pre-selected grids/strips were counted and hand-tallied. The species were examined under a Wild binocular Microscope (50x magnification). Cladocerans were identified using the identification keys of Korinek (1999). For copepods, the identification guide of Defaye (1988), Van de Velde (1984) and Fernando (2002) were used. Rotifers were identified almost exclusively using Koste (1978).

Copepod total body length was measured from the apex of the head to the base of the spine and to the tip of the furcal rami whereas nauplii were scaled from head to bottom (Culver *et al.,* 1985). Cladocerans were measured from the top of the head to the tip of the abdomen, excluding spines and projections (Downing and Rigler, 1984). For dry mass determinations, nauplii, post-nauplii, and cladocerans were isolated using a wide-mouth pipette and a needle. The isolated animals were rinsed several times with distilled water to remove detritus, and were placed on pre-weighed aluminum boats and dried at 60 ^{O}C in an oven for 30 ± 6 h. The number of individuals in each boat varied from 30 to 110. After drying, the samples were cooled in a desiccator then measured on a PerkinElmer AD6 Autobalance (sensitivity 10 μg). Replicates were made for each monthly sample. The biomass on each sampling date was calculated as the product of the mean individual dry mass and abundance. A brief study was conducted on the surviving ability of *Thermocyclops* by changing the oxic to anoxic condition abruptly. In containers filled with aged water (mixed with organic matter), oxygen concentration was lowered down to 1.2 mg O_2 L^{-1} by bubbling with compressed N_2 (Landman and van den Heuvel, 2003) and then zooplankton was added into the container.

Data Analysis

T-test was used to analyze the spatial distribution pattern of zooplankton in Lake Hayq. Pearson correlation and regression analyses were used to assess pair wise association of variables and their strength, and to model the dependent variable based on the predictor. We also used Kendall's tau correlation to check the variability of zooplankton community over the sampling period. SPSS software package version 16 was used in all statistical analysis. Relationships between taxa and significant environmental variables were analysed using a constrained Redundancy Analyses (RDA, CANOCO for Windows 4) (ter Braak and Smilauer, 1998). RDA was chosen because lengths of gradient determined by DCA were 1.7 standard deviation units that indicated a linear species response (ter Braak and Prentice, 1988). Environmental variables were selected by means of the manual "forward selection" procedure. Monte Carlo analysis with 499 permutations was used to test the significance of the first four axes. Inter-set correlations of environmental variables with axes were examined to determine the environmental variables which correlate significantly with axes (ter Braak, 1995). Statistical significance was set at P = 0.05. Graphs were presented using Sigmaplot version 11.

Results

Environmental variables

Based on the amount of rainfall received, four seasons around the lake can be distinguished: major rainy season (July-September), post rainy season (October-November), dry season (December – March), and pre-rainy season (April – June; Fig. 2). Vertical and temporal water temperature differences during the study period were low with a maximum of ca. 26 $^{\circ}$C and minimum of ca. 21 $^{\circ}$C (Fig. 3). The concentration of dissolved oxygen (DO) showed some temporal variation with a maximum of 8.42 mg O_2 L^{-1} (122 % of saturation) recorded in October 2008 and a minimum of 2.60 mg O_2 L^{-1} (37 %) in January 2008 (Fig. 3, indicated by an arrow).
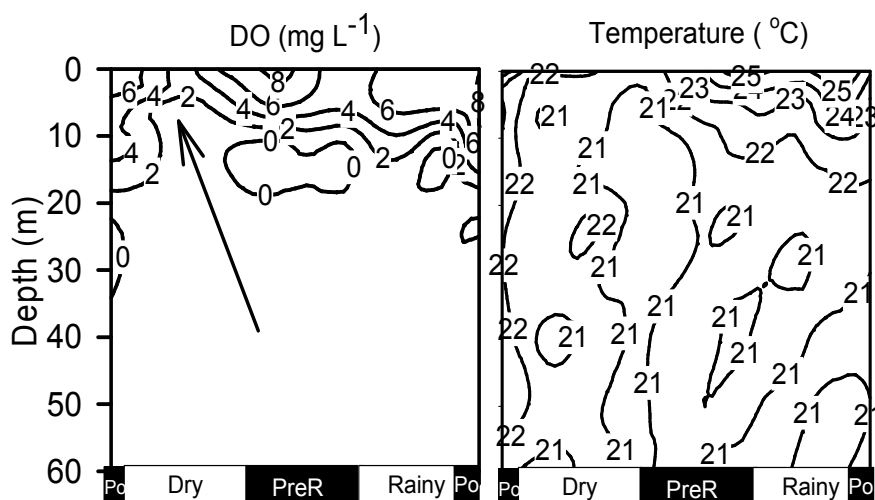
Fig. 3. Depth-time profile of dissolved oxygen (DO) and water temperature of Lake Hayq over the sampling period (PO = post rainy season; Rainy = rainy season; PreR = pre-rainy season; dry = dry season).

Both conductivity and pH showed invariably constant values during the sampling period with mean 910 µS cm^{-1} and 9.0, respectively. Chl *a* concentration in the top 10 m varied temporally and seasonally with highest amounts (45 µg L^{-1}) measured in March and lowest (3 µg L^{-1}) in June 2008. There was no spatial variation in Chl *a* concentration (t-test, P=0.586; Fig. 4).
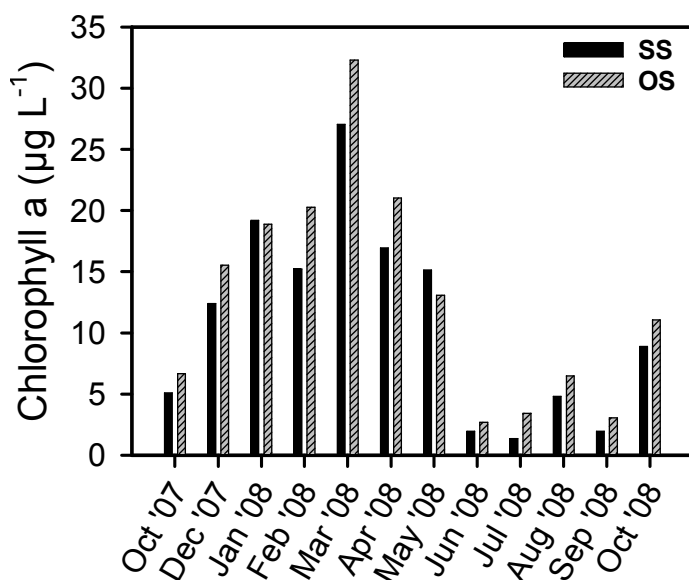
Fig. 4. Spatial and temporal mean chlorophyll *a* concentration on the top 10 m depth of Lake Hayq of the open water (OS) and inshore station (SS).

Zooplankton community and numerical abundance

Cyclopoid copepods contributed 64 % to the total zooplankton density, whereas cladocerans and rotifers contributed 23 % and 13 %, respectively (Table II). The latter two groups were encountered only during the first two sampling dates and disappeared for the next 5 and 8 consecutive months (Fig. 5, top panel). *Thermocyclops ethiopiensis* Kiefer 1934 dominated zooplankton abundance throughout the year. Within the cladocerans, *Ceriodaphnia reticulata* Jurine peaked in December 2007, *Daphnia magna* Straus 1820 was abundant in June and July 2008 and *Diaphanosoma excisum* Sars was dominant in August and September 2008. *Daphnia magna* and *Ceriodaphnia reticulata* never co-existed during any of the sampling dates.

Of rotifers, *Euchlanis, Polyarthra* and *Keratella* were alternatively common on different sampling dates in August, November and December 2008, respectively. Zooplankton community analysis based on Kendall's tau indicated that there were changes in the structure of the community particularly at one point during the dry season (Fig. 6).
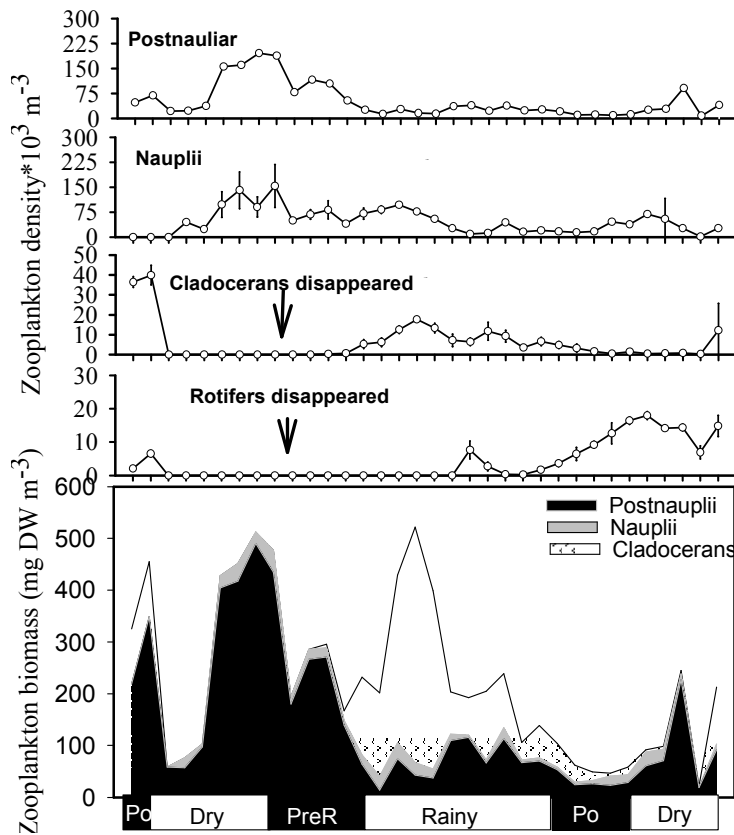
Fig. 5. Temporal variations of mean zooplankton abundance (Indl m^{-3}) (top) and standing biomass (mg DW m^{-3}) (lower) of Lake Hayq in open-water station sampled from Oct. 2007 to Jan. 2009. The bar represents ±1 SD (PO = post rainy season; Rainy = rainy season; PreR = pre-rainy season; dry = dry season).
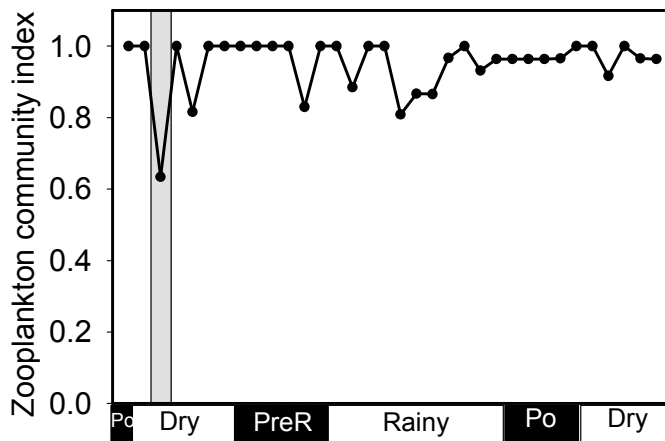
Fig. 6. Zooplankton species ranks on successive sampling date based on Kendall's tau correlation coefficient. The zooplankton species used for the analysis is found in Table II. The gray column indicates the mixing period (PO = post rainy season; Rainy = rainy season; PreR = pre-rainy season; dry = dry season).

40

Post-nauplii (ca. 60 %) contributed more than nauplii (ca. 40 %) to the total copepod density (Table III). Monthly mean densities of copepods, cladoceran and rotifers did not show any significant differences between the stations (t-test, P=0.443, 0.424, 0.227, respectively; Table III). Cladoceran and rotifer densities were generally low with an annual mean of around 5000 and 3100 Indl m^{-3}. At the first three sampling dates, nauplii could not be observed (Fig. 5). Cyclopoid copepods peaked during March and April 2008, and densities were lowest during January and October 2008. High copepod densities were recorded during pre-rainy season and relatively low abundances during the rainy season.

RDA was performed to detect taxa occurrences along gradients and resulted in a significant model with four axes (Monte Carlo test, P = 0.002). The first two axes accounted for 94.3 % of the variance in the zooplankton-environment relationship (Table IV). The first axis was correlated with NH_4-N and pH, and the second axis with Chl *a* and temperature (Fig. 7). Taxa scores represent centroids of the abundance curves for each taxon along the axes. *Ceriodaphnia* and *Mesocyclops* were mainly negatively related to NH_4-N and showed a positive relation to pH (Table V). *Diaphanosoma* and *Daphnia* coincided with water temperature and were negatively related to Chl *a*. *Thermocyclops* showed low relationships to significant variables.

Table II: Species list and mean abundance (Indl m^{-3} ± SE) of major zooplankton community in Lake Hayq, Ethiopia

Zooplankton groups	Numerical abundance (Indl m^{-3})
Copepoda	
Mesocyclops aequatorialis Van de Velde 1984	10716 ± 1080
Thermocyclops ethiopiansis Kiefer 1934	92393 ± 6020
Cladocera	
Ceriodaphnia reticulata Jurine	1533 ± 612
Daphnia magna Straus 1820	1950 ± 330
Diaphanosoma excisum Sars	2811 ± 419
Rotifera	
Brachionius angularis Gosse	300 ± 68
B. quadridentatus Herman	260 ± 54
Euchlanis parva Rousselet 1892	627 ± 110
Keratella tropica Apstein	760 ± 184
Polyarthra	957 ± 242
Trichocerca smilis	457 ± 74
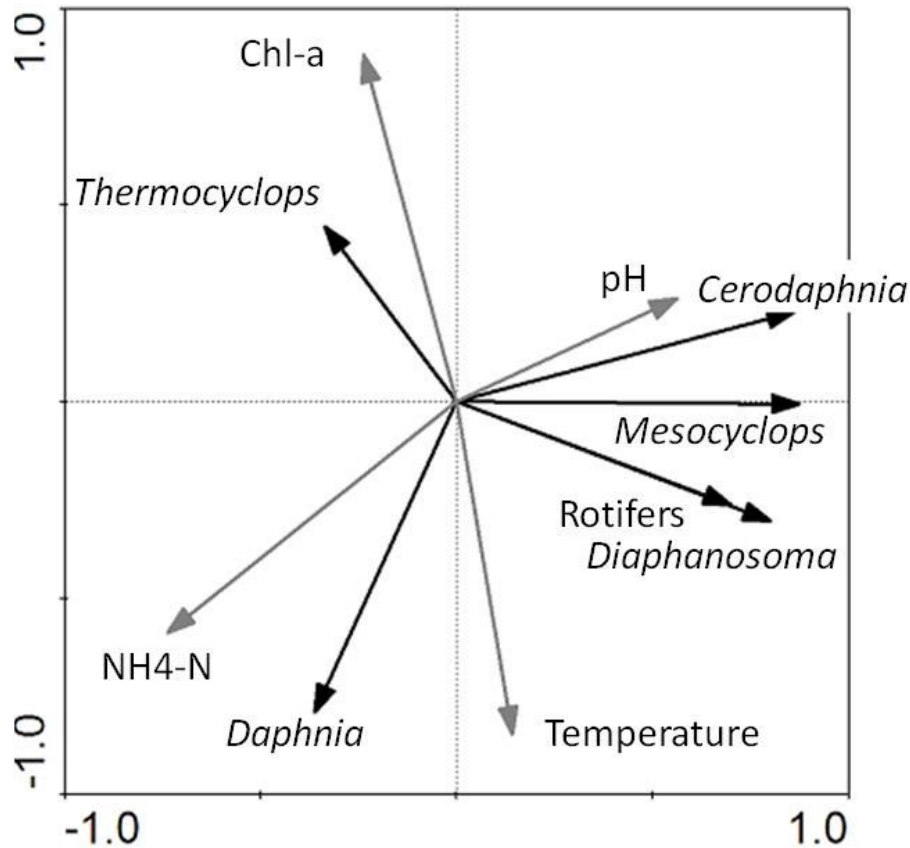
Fig. 7. Bi-plot of the Redundancy Analysis for zooplankton species and environmental variables. Bold arrows represent species and gray the environmental variables.

Zooplankton standing biomass of Lake Hayq was estimated for OS (Table VI, Fig. 5, lower panel): the overall mean standing biomass of crustaceans was 237 ± 28 mg DW m^{-3}. The mean standing biomass (mg DW m^{-3} $\pm$ SE) for post-naupliar was 147 ± 15, 15 ± 1 for nauplii and 75 ± 12 for cladocerans. Post-naupliar stages showed high variations with maximum and minimum values of 624 and 13 mg DW m^{-3} for March 2008 and July 2008, respectively (Fig. 5). Highest biomass for copepods was recorded during the dry and pre-rainy seasons, but amounts decreased to a minimum during the rainy season. Because of their size, cladocerans contributed more to total zooplankton biomass (32 %) than to numerical abundance (23 %). The maximum cladoceran biomass recorded was 469 mg DW m^{-3} in July 2008 when the post-naupliar biomass was significantly low (Fig. 5). During this time, the large-sized *Daphnia magna* was the dominant cladoceran. Phytoplankton (Chl a) and zooplankton biomass showed a positive relationship (r = 0.962, P = 0.176) from January to March 2008 (Fig. 8). However, there were a negative and statistically significant correlation between phytoplankton and cladocerans biomass (r = -0.78, P = 0.003).
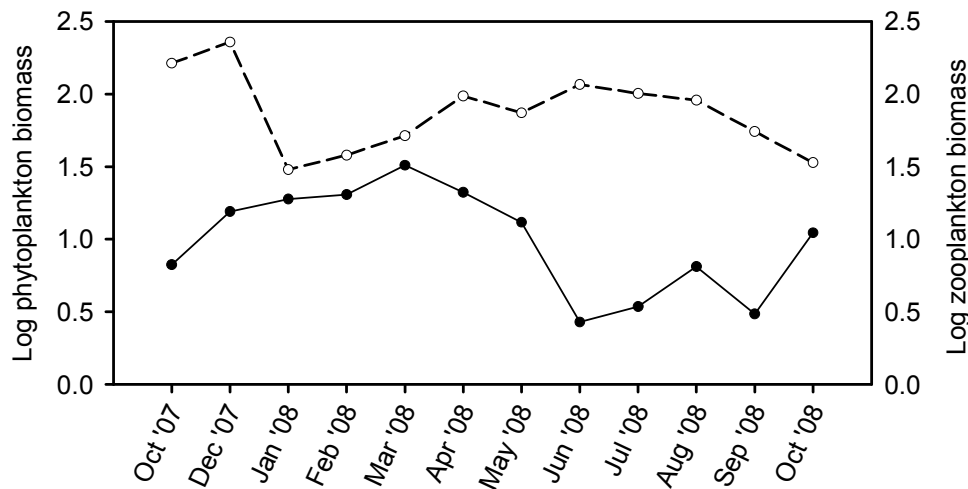
Fig. 8. Temporal variation of log zooplankton standing biomass (broken line) and log phytoplankton biomass (bold line) during the sampling period between October 2007 and October 2008. Note that the graph shows monthly values so as to fit the monthly measurements of Chl *a*.

Discussion

Structure and numerical abundance of zooplankton

The zooplankton community composition of Lake Hayq is generally depauperate comprising three cladocerans species, two cyclopoid copepods, and six rotifer taxa. Such low taxa numbers, however, appears to be a typical feature of tropical water bodies (Mengistou and Fernando, 1991; Irvine and Waya, 1999; Kurki *et al.,* 1999). Cyclopoid copepods, in particular *Thermocyclops ethiopiensis,* dominated the zooplankton community of Lake Hayq. This is in accordance with several other authors, who reported the dominance of copepods in tropical and subtropical lakes and reservoirs (Bergis, 1974; Lewis, 1979; Mengistou and Fernando, 1991; Amarasinghe *et al.,* 1997; Irvine and Waya, 1999; Dejen *et al.,* 2004; Wondie and Mengistou, 2006). Interestingly, the mean annual numerical abundance of copepods was above that of several other tropical lakes (Table VI), and persisted over the whole sampling period even during the hypoxia condition. We hypothesize that special physiological features accounted for their success. After a dramatic mixing event (Fig. 3), Lake Hayq changed from oxic to anoxic conditions even near the surface resulting in massive Tilapia fish kill. The threshold oxygen concentration for cichlid fish and cladocerans is reported with about 2 mg O_2 L^{-1} (Hanazato *et al.,* 1989; Magadza, 1997; Mhlanga *et al.*, 2006), and we assume that the sudden anoxia have killed cladocerans as well. Moreover, *Mesocyclops* might have been adversely affected by the mixing as it brought shortage of food as an additional detrimental condition (its prey cladoceran and rotifers disappeared), giving its competitor *Thermocyclops* an upper hand. The question remains how *Thermocyclops* might have survived these adverse conditions. We did a brief survey on the animal's ability to survive during shifts to anoxia and found several of the cladocerans dying off when the oxygen gradient sharply dropped from 7.75 to 1.2 mg O_2 L^{-1}. A few survivor cladocerans remained on

43

the top of the container enhancing oxygen supply, while the red pigmented cyclopoids were not much affected. Actually, Williamson (1991) reported the tolerance of copepods to hypoxic conditions, but the mechanism was not discovered. Generally, zooplankton is known to tolerate low oxygen concentrations down to 3 mg O_2 L^{-1} (Taleb *et al.,* 1993; Chang and Hanazato, 2004), then a heavy decline of respiration and filtering rates in *Daphnia* can be observed (Sell, 1998). Research results have shown that the survivorship of *Daphnia* is significantly related to the presence of hemoglobin. Sell (1998) demonstrated that oxygen concentration below 3.5 mg O_2 L^{-1} can be lethal for hemoglobin-deficient daphnids, but specimens rich in hemoglobin survived even at 0.5 mg O_2 L^{-1}. An increase in hemoglobin concentration improves the physiological performance of red animals exposed to hypoxia (Fox *et al.,* 1951; Kobayashi and Gonoi, 1985; Pirow *et al.,* 2001). Nevertheless, in well-oxygenated water, cladocerans do not synthesize hemoglobin since it incurs energy cost, plus red pigmentation would increase the likelihood of visual predation (Brooks and Dodson, 1965; Engle, 1985; Nebcker *et al.,* 1992). Furthermore, hemoglobin synthesis demands time (Zeis *et al.,* 2002) and in Lake Hayq pale cladocerans probably have failed to synthesize hemoglobin swiftly. Of copepods, its pigmentation is primarily coiled with protective mechanism against harmful ultraviolet radiation (Hansson, 2000). Hemoglobin was already detected in marine benthic copepods (Fox, 1957; Terwilliger, 1992; Hourdez *et al.,* 2000) and possibly *Thermocyclops* is also able to synthesize this pigment. The acquisition of oxygen by red copepods, especially *Thermocyclops* in Lake Hayq, calls further investigation; as the fruit fly *Drosophila melanogaster* recently reported to have hemoglobin in contrast to previous assumptions (Hankeln *et al.,* 2002).

In Lake Hayq, *Ceriodaphnia reticulata* and *Diaphanosoma excisum,* were observed during October and December 2007, but vanished thereafter. The disappearance coincided with a mixing event after the air temperature decreased causing isothermal conditions (Figs. 2, 3). Such crashes have already been observed elsewhere: Saunders and Lewis (1988) reported large mortalities of zooplankton in Lake Valencia, Venezuela, following annual overturn. For Lake Hayq, Kebede *et al.* (1992) also reported the absence of cladocerans from 1989 samples, suggesting that the introduction of planktivorous fish could be the cause. Nevertheless, with a seasonal study we refute this hypothesis since cladocerans existed in the beginning of the sample but disappeared following mixing and massive fish-kills. Interestingly, the cladocerans reappeared after about 5 months when the oxygen concentration stabilized again (Fig. 3). *Daphnia magna* appeared in May 2008 for the first time since the study was launched. We assume that the strong reduction of planktivorous fish could have been the reason for the appearance of this large-sized zooplankton (Van Donk *et al.,* 1990; Meijer *et al.,* 1994; Scheffer, 1998). After the disturbance, high algal biomass was recorded (Fig. 4), which was later grazed by *Daphnia magna* demonstrating the cascading trophic interactions hypothesis in a natural system. As resource availability, such as nutrient and light (Tadesse *et al.,* submitted), were not much affected after the fish kill, the phytoplankton response was probably due to trophic interactions (Bronmark and Hansson, 2005) and not bottom-up controlled.

Kebede *et al.* (1992) reported an absentee of rotifers during their survey. Similarly, we also observed low rotifers abundance that could be due to food limitation and predation. Large cladocerans are known to reduce phytoplankton biomass significantly, even to the extent that becomes too low to sustain most competitors (Brooks and Dodson, 1965; Pace, 1984; Lampert and Rothhaupt, 1991). Besides, rotifers are fed by copepods (Scheffer, 1998). Their disappearance (Fig. 5), however, coincided with the adverse condition of mixing.

Table VI: Numerical abundance and biomass of Lake Hayq in comparison to other tropical lakes ([a]present study; [b]Mengistou (1989); [c]Mengistou and Fernando (1991); [d]Gras and Saint-Jean (1983); [e]Burgis (1974); [f]Irvine and Waya (1999); [g]Mavuti (1994); [h]Vareschi and Jacobs (1984); [i]Wondie and Mengistou (2006); [j]Kurki et al. (1999).

Lake	Copepod abundance (Indl m^{-3})	Copepod biomass mg DW m^{-3}	Total zooplankton biomass (mg DW m^{-3})
Hayq, Ethiopia	67280[a]	161.46[a]	236.4[a]
Awasa, Ethiopia	59929[b]	36.93[c]	44.9[c]
Chad, Chad	---	---	333[d]
George, Uganda	---	248[e]	368
Malawi, Malawi	31142[f]	---	23[f]
Naivasha, Kenya	---	120.45[g]	---
Nakuru, Kenya	---	---	6438[h]
Tana, Ethiopia	37210[i]	34.43[i]	---
Tanganyika, Tanzania	7000[j]	---	---

The temporal zooplankton community variation showed clear oscillation indicating seasonal fluctuations (Fig. 6). It was particularly significant during the dry season in January 2008, which coincided with the mixing period and low oxygen concentration (Fig. 3). Several studies revealed that temporal variations of tropical zooplankton were associated with turbidity, water level, temperature, zooplanktivorous fishes, stratification and food availability (Burgis, 1974; Rocha *et al.,* 1982; Saint-Jean, 1983; Mengistou, 1989; Irvine and Waya, 1999; Dejen *et al.,* 2004; Melao and Rocha, 2004; Isumbisho *et al.,* 2006; Wondie and Mengistou, 2006). In the present study, the RDA analysis indicated that the temporal variation of *Thermocyclops* is probably influenced by food and temperature (Fig. 7). The association of the species with temperature and food is in accordance with literature, as embryonic and post-embryonic developments are predominantly a function of temperature and food (Vijverberg, 1989; Wondie and Mengistou, 2006). The environmental optima for the zooplankton species indicate that different condition may play an important role for different species (Table V). *Ceriodaphnia* was highly negatively related with nutrient concentrations. In addition to nutrients, *Daphnia* was associated with food (Chl *a*) and climate (water temperature). The negative relationship of *Daphnia* with Chl *a* indicated its high grazing pressure on phytoplankton biomass, which is a well established fact for several lakes (Schiefer 1998). Since zooplankton is an important diet of planktivorous fish (Fernando, 1994), the effect of predation on zooplankton temporal variation cannot be ruled out. In L. Hayq, the breeding season of tilapia is continuous with high peaks during March-May and July-October (Alemu, 1995), playing a role in structuring the zooplankton community.

Zooplankton biomass

Length – weight relationships of taxa generated for Lake Hayq (Table III) are in agreement with other studies (Amarasinghe *et al.*, 1997). The regression equations of Lake Hayq were comparable with the work of Culver *et al*. (1985) except for nauplii, in which the slop of the length-weight relationship (*b* value) was smaller (1.07). This could be due to the inclusion of juveniles of large copepods such as *Diaptomus* in Culver's length-weight relationship. Total mean standing biomass of the dominant crustaceans and copepods was comparable with other tropical lakes (Table VI). The highest total biomass was obtained during the post-rainy season and the lowest during dry season, which could be related to the absence of cladocerans during the dry season (Fig. 5). Lowest nauplii and post-naupliar biomass were recorded during rainy season and could be attributed to intense competition with *Daphnia magna* and predation pressure by juvenile fish species (Alemu, 1995).

The temporal pattern of total log zooplankton standing biomass and log phytoplankton biomass indicated a negative relationship (Fig. 8). Top-down control of zooplankton on phytoplankton is already documented for many lakes (Brooks and Dodson, 1965; Pace, 1984), and the negative correlation in the present study was predominantly due to the grazing pressure of cladocerans (r = -0.78, P = 0.003; Fig. 8). Interestingly, the correlation between post-naupliar and phytoplankton biomass was positive and insignificant (r = 0.43, P = 0.163) indicating that *Thermocyclops* was feeding on other food sources in addition to phytoplankton to supplement its diet. One possible food candidate is detritus as has been shown for other lakes (Wondie and Mengistou, 2006), but further research is needed to understand its feeding switches between herbivore and detritivore more precisely.

In conclusion, Lake Hayq can be categorized under eutrophic status and stands at intermediate position when compared with other tropical water bodies. Cladocerans as herbivores might have nutrition constraints to dominate the system, but its disappearance for several months is due to the adverse effect of mixing that ensued hypoxia. However, *Thermocyclops* persisted to inhabit during the hypoxia condition, an ability that needs further investigation.

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Food web structure and trophic interactions of the tropical highland lake Hayq, Ethiopia

Everything is Connected to Everything Else
(Magnuson et al. 2006)
and
The Whole Is Greater Than The Sum Of It's Parts
(Aristotel)

Food web structure and trophic interactions of the tropical highland lake Hayq, Ethiopia

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Abstract

We generated a mass-balance model to figure out the food web structure and trophic interactions of the major functional groups of the Ethiopian highland Lake Hayq. Moreover, the study lay down a baseline data for future ecosystem-based investigations and management activities. Extensive data collection has been taken place between October 2007 and May 2009. Ecotrophic efficiency (EE) of several functional groups including phytoplankton (0.8) and detritus (0.85) was high indicating the utilization of the groups within the system. However, the EE of *Mesocyclops* (0.03) and *Thermocyclops* (0.30) was very low implying these resources were rather a 'sink' in the trophic hierarchy. Flows based on aggregated trophic level *sensu* Lindeman revealed the importance of both phytoplankton and detritus to higher trophic levels. The computed average transfer efficiency of 11.5% for the first four trophic levels was within the range for highly efficient African lakes. The primary production to respiration (P/R) ratio (1.05) of Lake Hayq indicates the maturity of the ecosystem. We also modeled the food-web by excluding Tilapia and reduced phytoplankton biomass to get insight into the mass balance before Tilapia was introduced. The analysis resulted in a lower system omnivory index (SOI=0.016) and a reduced P/R ratio (0.13) that described the lake as immature ecosystem, suggesting the introduction of Tilapia might have contributed to the maturity of the lake. Tilapia in Lake Hayq filled an ecological empty niche of pelagic planktivores, and contributed for the better transfer efficiency observed from primary production to fish yield.

Keywords: food web; mass balance; trophic efficiency; tropical lake; Ecopath

Introduction

Food webs provide a framework for integrating population dynamics, community structure and ecosystems processes (Kaunzinger and Morin, 1998), and are a central idea in ecology (Wilbur, 1997). Predator-prey interactions provide a means to examine the species' roles in ecological processes, and to understand community and ecosystem functioning (Thapanand et al., 2009). Furthermore, food-web structure also affects primary production through its influence on grazing (Carpenter et al., 1998). For instance, in a three trophic-level food chain, predators can reduce herbivore zooplankton indirectly benefiting the primary producer phytoplankton, which partly explains the variation that otherwise would remain unexplained by the effect of nutrient input experiments (Carpenter et al., 1985; Carpenter and Kitchell, 1993; Bronmark and Hansson, 2005). Moreover, it gives a clue whether the basal trophic groups such as phytoplankton are adequate to sustain the whole ecosystem through estimates of primary production required (Christensen et al., 2005). Experiments and modeling approaches are two ways to study structure and function of an ecosystem, the former being more informative in a whole-lake experiment (Carpenter and Kitchell, 1992). Ecosystem-level experiments, however, are few due to methodological problems, large economic costs and time requirements (Wetzel and Likens, 1991). Among the different hypothesis, trophic cascades are typically strong in aquatic ecosystems particularly in whole-lake experiments (Carpenter and Kitchell, 1992). Nevertheless, trophic interactions in aquatic ecosystems are much more complex and dynamical than thought before (Paine, 1980; Wetzel and Likens, 1991). In biomanipulation research, for example, juvenile predator fish, which are expected to be piscivore, are zooplanktivore and are able to reverse the effect of biomanipulation (Hansson et al., 1998). An alternative to experimental approaches is ecosystem modeling that can be used to describe pathways of organic matter, to predict ecosystem responses of perturbations and to identify higher-level properties of the ecosystem that are not readily measurable, such as the goal functions (Muller and Leupelt, 1998). We used the modeling software Ecopath, which offers a network analysis and provides insights into the structure and dynamics of aquatic ecosystems (Wulff and Ulanowicz, 1989; Christensen et al., 2005). In Ecopath, the trophic levels are represented both as fractions (Christensen et al., 2005) and as integers *sensu* Lindeman (1942) offering more opportunity to describe the trophic interactions. The structure of food webs has important implications for ecosystem stability (De Ruiter et al., 1995; McCann et al., 1998), biogeochemical cycling (Berg et al., 2001), and fishery harvest (Ryther, 1969). Furthermore, food-web interactions may play a key role for understanding the effects of climate change on lakes (Straile, 2005). For instance, the impact of global warming on the food web structure of Lake Tanganyika has been demonstrated accompanied with fishery reduction (O'Reilly et al., 2003; Verburg et al., 2003; Verschuren, 2003). Nonetheless, though ecological management based on food web studies is common practice in temperate lakes, it is generally meager in tropical-African water bodies.

In Ethiopia, food web studies are an emerging field of interest (Fetahi and Mengistou, 2007). Food web studies will increase the optimum utilization of the inland water bodies by pointing out mis-utilization and/or overexploited resources. The present study focuses on Lake Hayq, which is located in the highlands of Ethiopia. The lake provides different purposes for the local inhabitants: fishing, drinking water and source of income via tourism. The lake switched to a eutrophic status some 25 years ago, caused most probably by the introduction of planktivorous Tilapia fish (Kebede et al., 1992; Fetahi et al., submitted-a). It is a deep lake having functional groups at different trophic levels and thus amenable to trophic analysis. We applied the software ecological tool Ecopath with Ecosim (EwE version 5.0 beta; Christensen et al., 2005) to describe the trophic structures, their linkage and mass

balance flows of Lake Hayq. The paper also attempts to explain the trophic interactions before and after Tilapia introduction in the ecosystem.

Material and methods

Study site

Lake Hayq (11° 15'N, 39° 57'E; Fig. 1) is located some 440 km north of Addis Ababa, the capital of Ethiopia, at an altitude of 2,030 m a.s.l. (Baxter and Golobitsch, 1970).
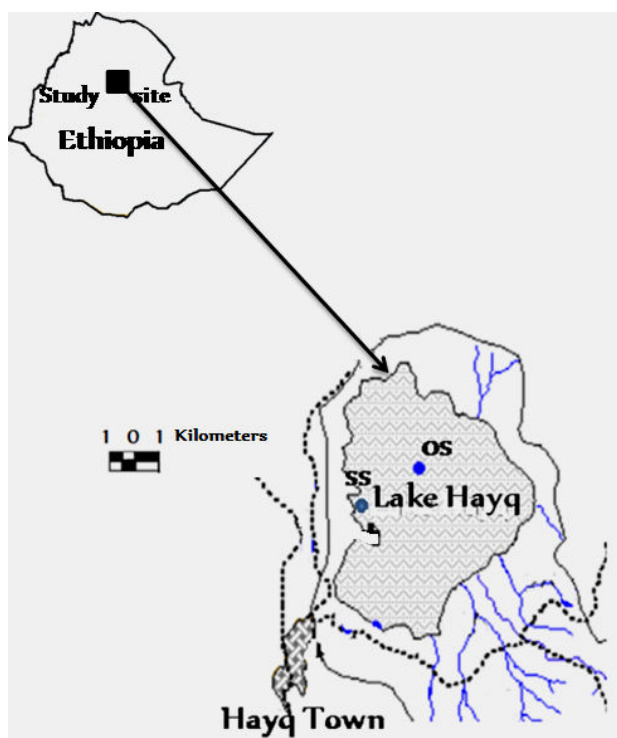
Fig. 1. The map of Lake Hayq together with sampling stations (dots) and drainage basin (redrawn from Demlie 2007).

The study area is categorized as sub-humid tropical with an annual rainfall of 1173 mm and a mean air temperature of 18.2 ^{o}C (National Meteorological Service Agency). Previously, Lake Hayq was connected to the nearby Lake Hardibo (11° 14'N, 39° 46'E; altitude 2150 m a.s.l.) through Ankwarka River. However, at present these lakes are terminal and there is no known surface outlet due to the irrigation scheme upstream. Lake Hayq is a deep, steeply shelving lake, with a maximum depth of 88 m recorded in 1938 (Table 1). The lake is fresh water, with a salinity of 0.83 g L^{-1} (Zinabu et al., 2002) and has never been saline (Lamb et al., 2007). Predominant cations and anions are magnesium and carbonate/ bicarbonate, respectively (Fetahi et al., submitted-a).

Table 1 Morphometery of Lake Hayq (from Baxter and Golobitsh, 1970).

Variables	Values
Max. Length (north-south)	6.7 km
Max.Width	6.0 km
Shoreline	21.7 km
Surface Area	23.2 km^2
Max. Depth	88.2 m
Mean Depth	37.37 m
Volume	0.867 km^3

Fishes that inhabit Lake Hayq are *Oreochromis niloticus* Linnaeus (Nile Tilapia), *Clarias garapienus* Burchell (African catfish), *Cyprinus carpio* Linnaeus (common carp) and *Garra dembecha* Getahun and Stiassny. The latter two species were introduced in Lake Hardibo most likely in 1980 and eventually reached Lake Hayq due to the connecting river (Tizazu, personal communication). Tilapia was also introduced in 1978 (Kebede et al., 1992) putting catfish as the only indigenous fish species (Baxter and Golobitsh, 1970). Phytoplankton biomass is dominated by the diatoms in particular by *Fragilaria, Navicula* and *Synedra,* and several green algae (Fetahi et al., submitted-a). The dominant zooplankton species are *Mesocyclops aequatorialis* Van de Velde, *Thermocyclops ethiopiansis* Kiefer, *Ceriodaphnia reticulata* Jurine, *Daphnia magna* Straus, *Diaphanosoma excisum* Sars and rotifers (Fetahi et al., submitted-b). The benthos in the littoral, sublittoral and profundal is dominated by mollusks (Assefa, 2010).

Ecopath with Ecosim model

A mass-balanced model was constructed using EwE software (Christensen et al., 2005; freely available at www.ecopath.org); basic input parameters were mostly obtained from studies done since October 2007. Growth and other parameters are presented in Table 2. The model comprised of 15 functional groups including detritus, bacteria and fish-eating birds so as to assess a holistic picture of the lake.

Table 2 Fish growth, mean temperature (T) and other parameters.

Growth parameters	Tilapia	Catfish	Carp	*Garra*
L$_{inf}$ (cm)[a]	42	66	55	15.4
W$_{inf}$ (g)[a]	1440	1947	2500	44
T (^{o}C)[a]	22	22	22	22
K (year^{-1})[a]	0.4	0.18	0.13	1.5
A[b]	1.8	1.5	2.8	1.4
H	1[c]	0[d]	1[c]	1[d]
d	0	0	0	0

[a] the present study; [b] Fetahi and Mengistou (2007); [c] Worie (2009); [d] Alemayehu (2009).

The model comprises a set of simultaneous linear equations, one for each group under consideration, and assumes a mass balance where the production of the group is equal to the sum of all predation, non-predatory losses and export integrated in the master equation of Ecopath: $B_i*P/B_i*EE_i= Y_i + \sum B_j*Q/B_j*DC_{ij}$ (1), where B_i = the biomass of prey group i; P/B_i = production/biomass ratio of group i; EE_i = ecotrophic efficiency, i.e. the fraction of production consumed within the system by predation or fishing exploitation; Y_i = its yield (= fishery catch); B_j = the biomass of predator group j, the consumer of i; Q/B_j = the food consumption per unit biomass of j; and DC_{ji} = the fraction of i in the diet of j. Each compartment requires estimates of B, P/B, Q/B, DC and EE. However, one out of the parameters B, P/B, Q/B, EE can remain unknown for each functional group as it can be estimated by the model. Input data were standardized, B as wet weight (t km^{-2}) and P/B and Q/B as annual rates. EE has no unit and is usually estimated by the model.

Gross primary production (mean = 162.42 mg O$_2$ m^{-3} h^{-1}) and biomass (as Chlorophyll a = Chl a, 13 mg m^{-3}) were measured from Oct. 2007 to Oct. 2008 on a monthly basis (Fetahi et al., submitted-a) and the values were converted into wet weight (Table 3). The biomass of detritus was calculated using the empirical formula given in Table 3, which is a function of primary production (PP, g C m^{-2} y^{-1}) and euphotic layer depth (E, in meter), obtained from Fetahi et al. (submitted-a). Five major functional zooplankton groups were considered in the model: *Mesocyclops, Thermocyclops*, Nauplii, cladocerans and rotifers. Zooplankton abundance and biomass was determined weekly to biweekly from Oct. 2007 to Jan. 2009 (Fetahi et al., submitted-b). Zooplankton biomass was measured on a dry weight basis for Lake Hayq and then converted into wet weight (Table 3). Zooplankton production to biomass ratio (P/B) was calculated after Kuns and Sprules (2000) (Table 3). Bacteria biomass was calculated assuming a cell volume of 0.04 μm^3 and a density of 1, and ciliate biomass with an average dry weight of 0.04 μg (Wetzel and Likens, 1991); conversion factors to wet weight are given in Table 3. The abundance value was obtained from Fetahi et al. (submitted) and Kebede et al. (1992), respectively. Production/consumption (P/Q) ratio of 0.3 was used to estimate food consumption per unit of biomass (Q/B). Zoobenthos biomass was calculated based on abundances values (Assefa, 2010) and their weight are adopted from Fetahi (2005) for Lake Awasa, Ethiopia. P/B and Q/B ratios of zoobenthos for Lake Hayq were computed using Ecoempire (which is an interactive routine included in EwE containing several empirical relationships to facilitate parameterization) for benthic invertebrate populations (Christensen et al., 2005). Each fish species that inhabit the lake was considered as a functional group: Tilapia, Catfish, Carp and *Garra*. Catch statistics collected at 4 landing sites 3 times per week for 7 months were used for the model (Tables 2, 3). Furthermore, catch data from Amhara Regional Agricultural Research Institute (ARARI) were also included. Length-frequency data were analyzed using the ELEFAN procedure available in FiSAT II to estimate asymptotic length (L$_{inf}$) and the von Bertalanffy growth function (K). Total mortality (Z), under the condition assumed for the construction of mass-balance models, equals to production over biomass ratio (P/B) (Allen, 1971; Christensen et al., 2005) and Z was estimated from length-converted catch curves using FiSAT II software (Gayanilo et al., 2002). Natural mortality (M) for unexploited fish species (catfish, Carp and *Garra*) were estimated using FiSAT II software and considered as P/B since they do not suffer from fishing mortality. Annual stock biomass (B) was estimated using length-structured virtual population analysis (VPA), and yield Y was estimated assuming equilibrium conditions: Y=B x F, where F is the fishing mortality coefficient. Food consumption per unit of biomass (Q/B) was calculated using the multiple regression formula of Palomares and Pauly (1998) (Table 3).

Diet composition was obtained from recent studies conducted for the lake (Alemayehu, 2009; Worie, 2009). Fish-eating birds in Lake Hayq include Great Cormorants, White Pelicans, Sacred Ibis and the scavenger Marabou Stork (Mengistu Wondafrash, personal communication). As no data regarding actual abundance, biomass, consumption and mortality are available; we adopted data of Moreau et al. (1993) for Lake George, Uganda since the birds are assumed to be similar to Lake Hayq.

Table 3 Conversion factors and formula used to derive input parameters.

Items	Conversion factor/formula	References
Phytoplankton	Carbon to chlorophyll a 40:1 ratio Wet weight (WW) = 10xcarbon	Jones, 1979
Zooplankton	WW= 5xdry weight	Hall et al., 1976; Burgis, 1974
Zooplankton	*Log (P/B)= -0.73 – 0.23*log (w)*; CF=1.12, where P/B is per day, w is body mass (mg dry weight), and CF is a correction factor for the back-transformation from logarithmic units.	Kuns and Sprules (2000)
Detritus (D, g C m^{-2})	Log D= 0.954*logPP + 0.863*logE-2.41	Christensen and Pauly, 1993
Ciliate	WW = dry weight/0.59	
Bacteria	Carbon weight = 0.5*dry weight WW = dry weight/0.4	Bratbak and Dundas, 1984
Consumption/ biomass ratio	Log (Q/B) = 7.964 − 0.204 logW$_{inf}$ − 1.965T + 0.083A + 0.532h + 0.398d; where W_{inf} is the asymptotic weight (g); *T* an expression for the mean annual temperature of the water body, expressed using $T = 1000/K$ (K = ∘C+ 273.15); *A* aspect ratio (Ar = $h2/s$—of the caudal fin of fish, given height (*h*) and surface area (*s*); *h* a dummy variable expressing food type (1 for herbivores, and 0 for detritivores and carnivores) and; *d* a dummy variable also expressing food type (1 for detritivores and 0 for herbivores and carnivores).	Palomares and Pauly (1998)

The model was balanced by checking the values of EE and gross efficiency of food conversion (GE), a fraction between 0 – 1 and 0.1 – 0.3, respectively and input data (B, P/B, and particularly DC since it is the most uncertain parameter), were modified until we obtained acceptable runs (Christensen et al., 2005). The pedigrees were coded to quantify the uncertainty associated with input data (Pauly et al., 2000). Trophic levels (TL) are outputs of Ecopath; TL = 1 (first TL) by definition is assigned to primary producers and detritus; for consumers TL are estimated as 1 + (the weighted average of the TLs of the preys in the stomach content of the predators). EwE provides a mixed trophic impact routine that quantifies all direct and indirect trophic effects by summing the negative and positive

impacts for each group (Christensen et al., 2005). A modified Lindeman Spine was also used to demonstrate the contribution of detritus-based and grazing food chains. In ecological succession, a system will have some indices of maturity such as total primary production to total respiration (P/R), total primary production to total biomass (P/B), total biomass/total throughput (B/T) and total biomass of the system (B) (Odum, 1969), some were considered in the present study. Ascendency, system overhead and cycling indices are also considered as maturity and stability indices (Christensen et al., 2005). The ratio of fishery catch to net primary production (catch/NPP) and the system omnivery index (SOI) were also calculated.

Results

The basic input values accompanied with computed parameters estimated by EwE (bold) for Lake Hayq is given in Table 4, and the diet matrix presented in Table 5. Flows and biomass for the balanced lake ecosystem along with fractionated trophic levels are shown in Fig. 2. Most functional groups were between TL2 and TL3 since they feed on first trophic levels. The highest TL (> 3) was estimated for fish-eating birds, catfish and *Mesocyclops*, which are carnivore (Table 5). The mean TL of catches is 2.46, which corresponds well to TL of Tilapia and also shows a strong trophic link of Tilapia with plankton. Biomass and flows were aggregated into integer trophic levels *sensu* Lindeman (Fig. 3) using the modified Lindeman Spine, which indicated the importance of both phytoplankton and detritus in the food web of the lake. Furthermore, the modified Lindeman spine highlighted that flows at lower TLs in the grazing food chain (from I to II = 8868 t km^{-2} y^{-1} and from II to III = 1765 t km^{-2} y^{-1})

Table 4 Input parameters and basic estimates (bold) for trophic modeling of Lake Hayq, Ethiopia.

Species/group	TL	Yield (t km^{-2}y^{-1})	Biomass (t km^{-2})	P/B (y^{-1})	Q/B (y^{-1})	Q(t km^{-2}y^{-1})	EE	GE
Water Birds[a]	3.43		0.089	0.25	58.00	5.16	0.000	0.04
Catfish	3.32		**0.624**	0.42	5.69	3.55	0.763	0.074
Tilapia	2.46	4.8	10.800	1.20	21.82	235.66	0.666	0.055
Common Carp	2.34		**3.940**	0.36	20.26	79.82	0.900	0.018
Garra	2.33		**0.280**	2.68[b]	41.19	11.53	0.856	0.065
Zoobenthos	2.17		16.425[d]	3.24	36.60	601.16	0.900	0.089
Mesocyclops	3.18		4.092	180.00	506.67	2073.29	0.027	0.355
Thermocyclops	2.00		12.761	200.00	506.67	6465.62	0.272	0.395
Cladocerans	2.00		10.520	76.00	253.33	2665.03	0.808	0.300
Nauplii	2.41		3.067	306.00	972.75	2983.42	0.900	0.315
Rotifers	2.66		0.278	155.00[c]	516.67	143.63	0.811	0.300
Ciliate	2.26		0.149	200.00	516.00	76.88	0.900	0.388
Bacteria	2.00		5.615	280.00	**933.33**	5240.65	0.819	0.300
Phytoplankton	1.00		31.46	353.40			0.798	
Detritus	1.00		104.7				0.854	

[a]Moreau et al. (1993); [b]Fetahi and Mengistou (2007); [c]Talling and Lemoalle (1998); [d]Assefa (2010);

Table 5 Prey-predator feeding matrix of Lake Hayq, Ethiopia

Preys		1	2	3	4	5	6	7	8	9	10	11	12	13
						Predators								
1	Fish-eating birds													
2	Catfish[a]													
3	Tilapia[b]	0.73												
4	Carp[c]	0.21												
5	*Garra*[a]	0.06												
6	Zoobenthos		0.08		0.26	0.17	0.08							
7	*Mesocyclops*		0.26	0.09										
8	*Thermocyclops*		0.30	0.09		0.13		0.23						
9	Cladocerans		0.36	0.20	0.09		0.10	0.18						
10	Nauplii							0.29						
11	Rotifers							0.30					0.04	
12	Ciliates											0.36		
13	Bacteria										0.41	0.33	0.24	
14	Phytoplankton		0.50	0.36	0.60				0.49	0.8	0.59	0.31	0.11	0.3
15	Detritus		0.13	0.29	0.10		0.82		0.51	0.2			0.61	0.7

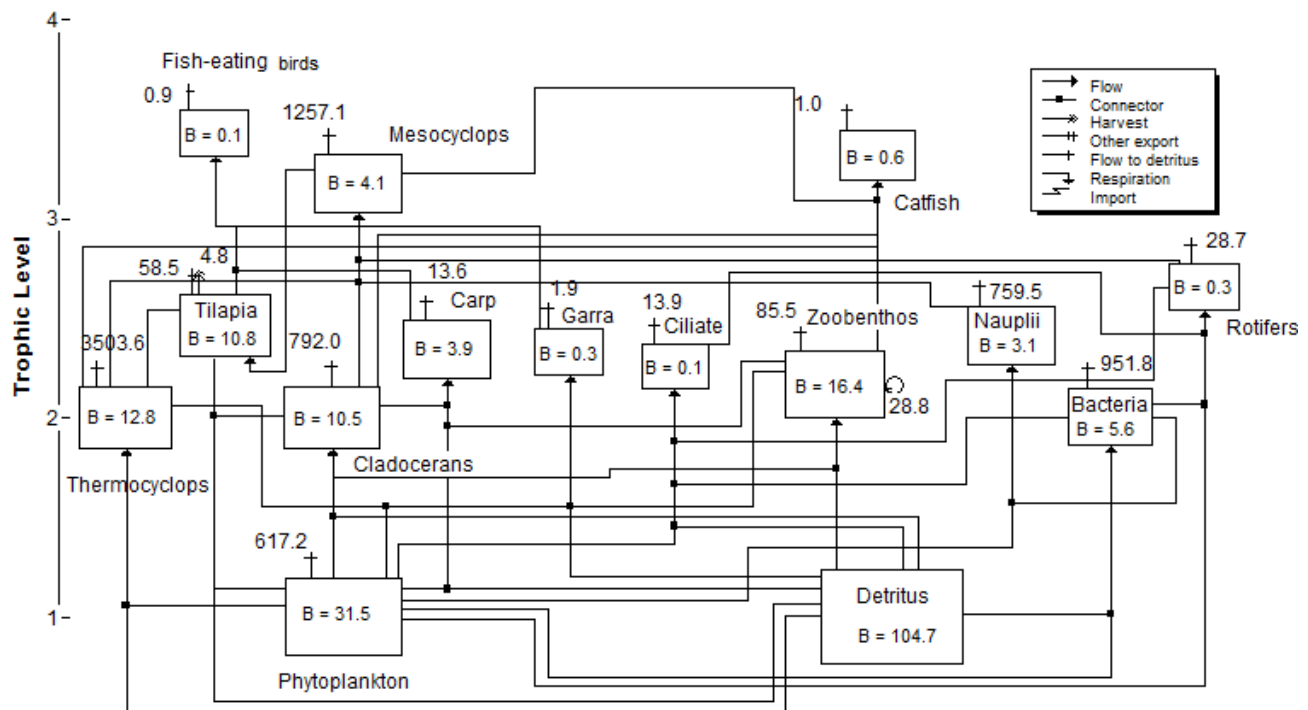[a]Alemayehu (2009); [b] Worie (2009); [c] Worie (personal communication).

Fig. 2. Flow diagram showing trophic flows in Lake Hayq, Ethiopia. Flows are expressed in t km^{-2}y^{-1}.

are larger than in the detritus food chain (8110 and 1419 t km^{-2} y^{-1}, respectively). Conversely, transfer flows for high TLs are smaller for grazing food chain (from III to IV = 124.4 t km^{-2} y^{-1} and from IV to V= 1.73 t km^{-2} y^{-1}) than detritus (264 and 3.64 t km^{-2} y^{-1}, respectively). These differences are reflected in the large difference in trophic efficiency (TE) for energy transfer between TL III and IV which is 7.1% for grazing food chain and 18.6% for detritus food chain. Total fish biomass of Lake Hayq is about 15.16 t km^{-2} and its yield was 4.8 t km^{-2} y^{-1}, basically caught from Tilapia.
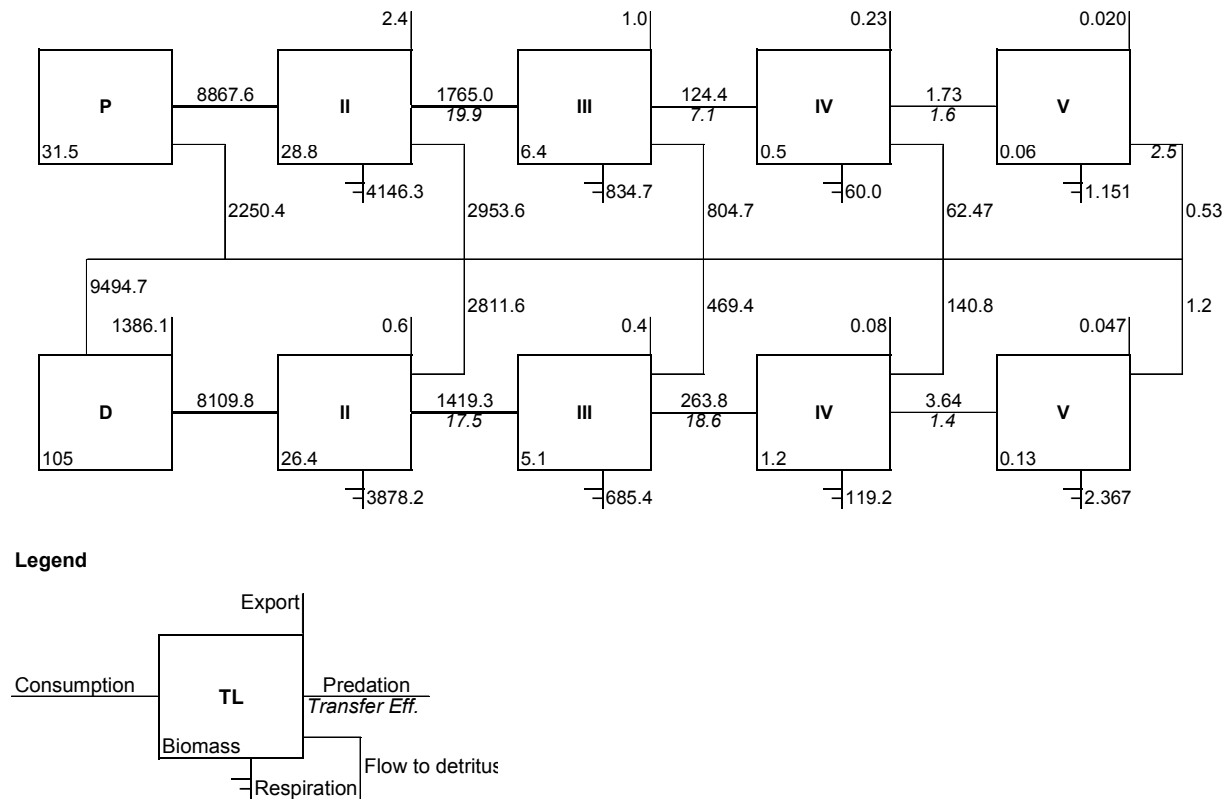

Fig. 3. Biomass, flows, transfer efficiencies are aggregated into integer trophic levels (TL) in the form of Lindeman spine. P stands for primary producers and D for detritus.

Ecotrophic efficiency (EE) is the fraction of production consumed within the system and ranges between 0 – 1, where 1 indicates total exploitation in a system. EE of both phytoplankton (0.8) and detritus (0.85) were high (Table 4). However, the EE values estimated for *Mesocyclops* (0.03) and *Thermocyclops* (0.30) were very low because these groups were mildly consumed by their predator, i.e. catfish. EE were high for catfish, *Garra* and common Carp even if they were not currently well-exploited in the commercial fishery, which could be related to the assumption of biomass accumulation of 0.3. However, EE for Tilapia fish was relatively low (~ 0.67), and it was calculated zero for fish-eating birds, because it is the top predator in the system.

The result of MTI exhibits both positive and negative effects among each other's (Figs. 4 and 5). Only phytoplankton and detritus have positive impact on most other functional groups, whereas other compartments show direct predator-prey interactions, cascading effects or competition. For instance,

Tilapia has a negative effect on Carp and *Garra* which can be seen as a result of competition since the larger portion (> 34%) of each of their diet comes from phytoplankton.
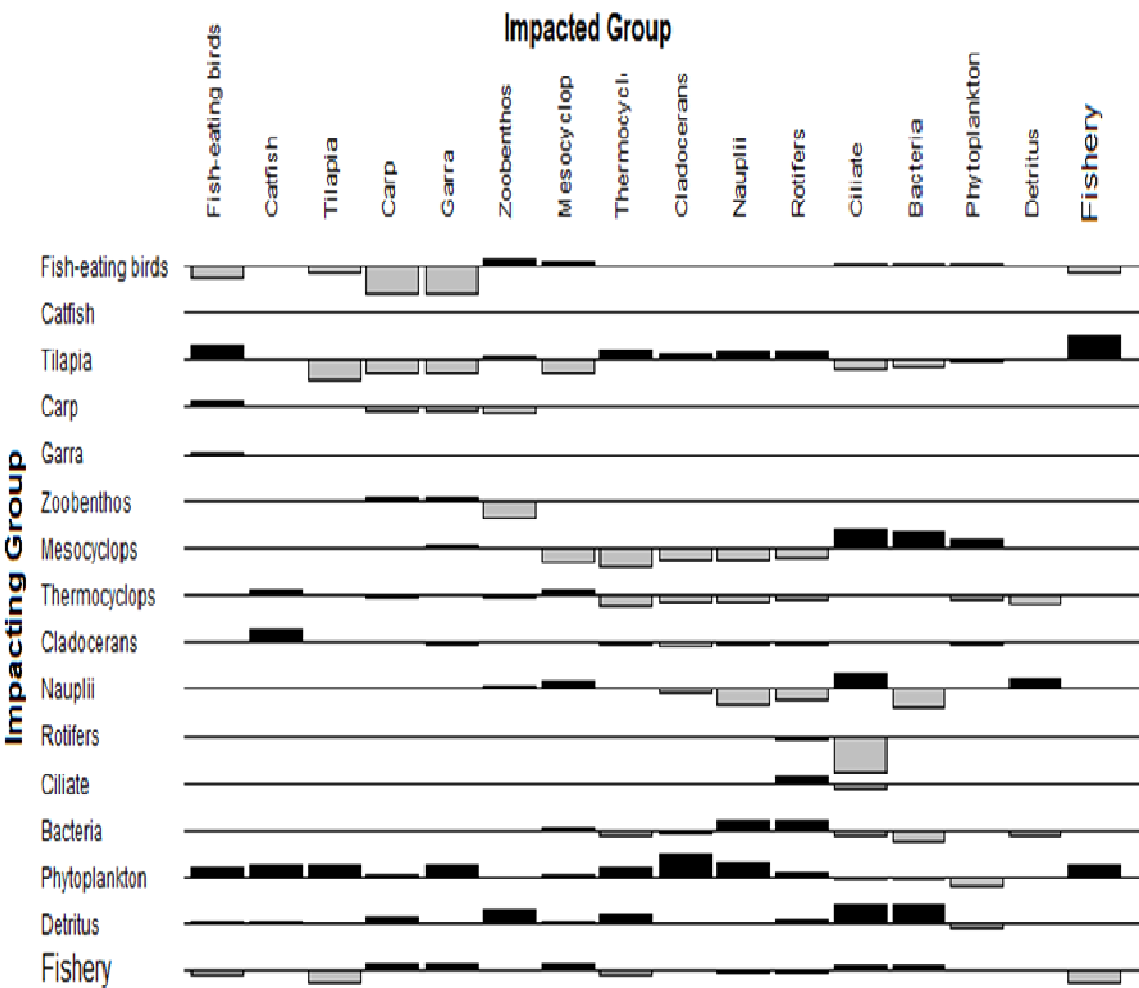
Fig. 4. Mixed trophic impacts (MTI) in Lake Hayq food web showing the combined direct and indirect trophic impacts. The black bars pointing upwards indicate positive impacts, while the grays pointing downwards show negative impacts. The impacts are relative and comparable between groups.

The positive impact of *Mesocyclops* on ciliate has a cascading nature, because *Mesocyclops* is consuming rotifers, which otherwise would feed on ciliates. The impact of catfish and ciliates on any other group is negligible, which could be due to their small biomasses – the former being estimated by EwE. Fishery has relatively strong negative impacts to fish-eating birds and Tilapia: the first indicates the result of competition for same resource and the latter indicates the direct impact of this important fishery in the region. Among the negative effects (top-down), fish-eating birds, *Thermocyclops* and rotifers have strong impact from an ecosystem perspective, whereas bottom-up effects are mainly exerted, as expected, by detritus and phytoplankton (Fig. 5).
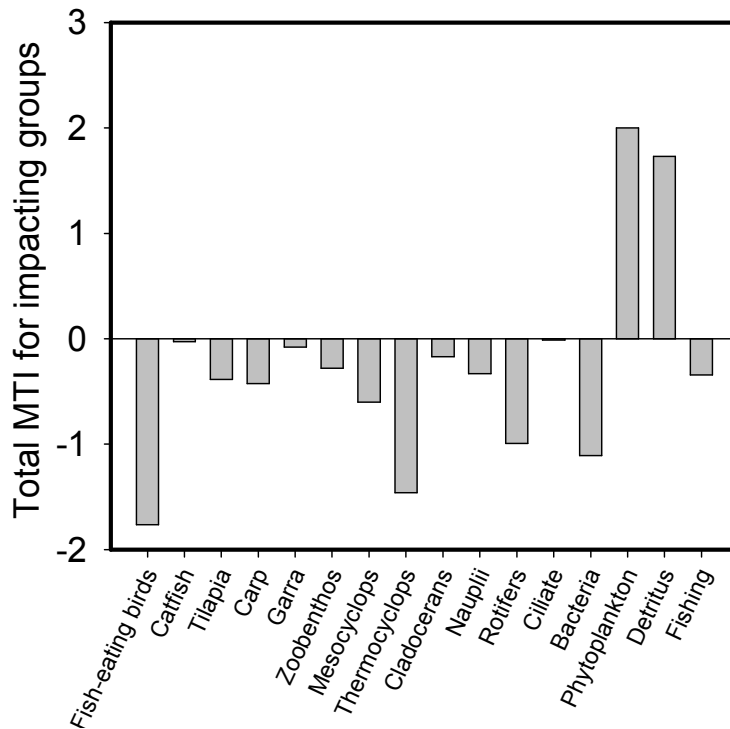
Fig. 5. Total MTI of each impacting groups on the ecosystem.

Table 6 presents the summary statistics and network flow indices. P/R approaches unity in matured ecosystem as energy fixed tends to be balanced by the energy cost of maintenance (Odum, 1969), and 1.05 was estimated for Lake Hayq. Finn's cycling index (FCI; Finn, 1976), 15% of total throughput obtained for Lake Hayq, expresses the percentage of the total throughput that is actually recycled and is a measure of maturity (Odum, 1969; Christensen and Pauly, 1993).

Figure 6 Summary of system statistics.

Parameters	Value
Sum of all consumption (t/km²/year)	21492.980
Sum of all exports (t/km²/year)	43.539
Sum of all respiratory flows (t/km²/year)	10062.830
Sum of all flows into detritus (t/km²/year)	8085.361
Total system throughput (t/km²/year)	39685.000
Sum of all production (t/km²/year)	17857.000
Mean trophic level of the catch	2.46
Gross efficiency (catch/net p.p.)	0.000475
Total primary production/total respiration	1.004
Total primary production/total biomass	100.974
Connectance Index	0.214
System Omnivory Index	0.220

Discussion

Lakes are often used as model ecosystems because they have clearly defined boundaries and identifiable connections with adjacent ecosystems (Forbes, 1887; Vadeboncoeur et al., 2002). With 0.64, the pedigree index of the present analysis falls within the range given for validating an Ecopath model (Christensen et al., 2005). In point of fact, several functional groups are represented at species level, and most of the input data were system-specific obtained from the present study. The food web of Lake Hayq is characterized by two important pathways: grazing and detritus-based food chains (Fig.2). Mass flows in the ecosystem based on the aggregated trophic level *sensu* Lindeman (1942) (Fig. 3) reveal the importance of both phytoplankton and detritus to the higher trophic levels. However, phytoplankton contributed higher to the primary consumers (57 %) than detritus (43%) indicating the preference of the consumer to living food, which is in agreement with the literature: Tilapia (Worie, 2009), *Garra* (Alemayehu, 2009) and cladocerans primarily feed on phytoplankton. Furthermore, copepods are also selective feeders even with the help of chemo-reception ('taste') (Lampert and Sommer, 1997), and we found the majority of copepods in Lake Hayq to be herbivore (Fetahi et al., submitted-b). MTI analysis also indicates the importance of phytoplankton for the fishery whereas detritus has only negligible influence (Fig. 4).

The main sources for biomass flow to detritus originate from TL1 and TL2 which altogether contribute about 80% of the total biomass flow (Fig. 3) which suggests the microbial loop to be an essential energy source for the planktonic food chain as pointed out already by Azam et al. (1983) and Suthers and Rissik (2009). Fetahi et al. (submitted-a) have reported high organic matter suggesting the presence of adequate substrate to microbes, which also indicates maturity of the ecosystem (Odum, 1969). In the grazer food chain, *Mesocyclops* consumes herbivorous zooplankton, and catfish exclusively feeds on both of them (i.e. catfish is a zooplanktivore). This link shows the transfer of energy from the primary producers to higher trophic levels. Usually, fish is an important component in the diet of catfish (Spataru et al., 1987; Dadebo, 2000), cichlids being the most preferred prey fish in most water bodies (Corbet, 1961; Dadebo, 2000). For instance in Lake Awasa, a freshwater lake in Ethiopian rift-valley, catfish feeds on Tilapia, *Garra* and *Barbus* fishes, the former being the larger (60%) contributor of its diet (Dadebo, 2000; Fetahi and Mengistou, 2007). Interestingly, the catfish of Lake Hayq is still zooplanktivore (Alemayehu, 2009), which can be explained by the feeding habit of long evolution that did not change to any fish diet in the last 30 years, even if the fish prey is available now.

Tilapia consumed about 24% of zooplankton and 68% of phytoplankton, and was assumed as a cause for the trophic status change of the lake (Kebede et al., 1992; Fetahi et al., submitted-a). The question arises how Tilapia could play the key role in changing the trophic status as its impact on zooplankton appears small in comparison to zooplanktivorous catfish. First, based on the summed-MTI analysis, Tilapia has a much stronger impact at the ecosystem level compared to catfish (Fig. 5). Second, the ecological niche of catfish and Tilapia are different; catfish is bottom dweller (Teugels, 1986) but Tilapia is pelagic. Phytoplankton (intuitively zooplankton) remains mostly in the euphotic depth of the upper water column, which is the fundamental niche of Tilapia. And hence, the positive effect of Tilapia by feeding on zooplankton cascade down to primary producers, which eventually resulted into eutrophication. Third, a large Tilapia biomass (10.8 tkm^{-2}) in comparison to catfish (0.624 tkm^{-2}) specifically feeds on cladocerans (Table 5), which are responsible for high filtering efficiency and clear-water phases (Lampert and Sommer, 1997). In Lake Hayq, there was massive Tilapia fish

kill that coincided with mixing, and consequently a large-size *Daphnia magna* appeared indicating the top-down control of Tilapia on large-sized cladocerans.

EE is high to several functional groups including phytoplankton (0.8) and detritus (0.85) which indicates the high utilization of the groups in the system. Contrarily, the EE of zooplankton in particular *Mesocyclops* (0.03) and *Thermocyclops* (0.30) was very low implying these huge resources were a 'sink' rather than a 'link' to higher trophic level. The low EE of *Thermocyclops* is reasonable as this taxon experienced high abundance and biomass in the lake (Kebede et al., 1992; Fetahi et al., submitted-b) but is only sparsely consumed by catfish due to its low biomass (Table 4). The abundance of cyclopoid copepods in Lake Hayq has reached a maximum of 577 Indl. L^{-1} (Kebede et al., 1992) and a mean of 92 Indl. L^{-1} for *Thermocyclops* alone, signifying the huge resource of this group. Though slightly, MTI indicated that fishery has negative effects on zooplankton, as fisheries can cause depletion of target and non-target species (Coll et al., 2008).

The gross efficiencies (GE), which correspond to the production/consumption (P/Q) ratio, are generally high for zooplankton (between 0.3 and 0.4), which is in agreement with literature (Christensen et al., 2005; Villanueva et al., 2006). However, GE is decreased for Tilapia which may be due to the inclusion of low food quality (detritus) in its diet. Catfish almost entirely consumes zooplankton and has somehow elevated GE in comparison to Tilapia, but GE still remains low. This can be explained by small–sized prey that requires longer time to satiate the energy demand of large-sized catfish. Generally, large-sized and long lived organisms have low GE as they respire most of the assimilated food stuff (Wolff et al., 2000).

Trophic transfer efficiencies of Lake Hayq (Fig. 3) show a similar trend compared to other lakes like Kinneret, Victoria and Malawi: higher efficiencies on lower trophic levels, and decreases in the upper trophic levels (Christensen and Pauly, 1993; Walline et al., 1993). This higher transfer efficiency on lower trophic levels could be related to the higher GE of zooplankton and/or fishery activity on the lower TL. Besides, the inclusion of high bacteria numbers could also result in such high efficiency (Walline et al., 1993). The computed average transfer efficiency of 11.5% for the first four trophic levels is within the range (10-15%) reported by Christensen and Pauly (1993) for highly efficient African lakes and also in the range (10-20%) reported in the other literature (Odum, 1971; Le Cren and Lowe-McConnell, 1980) but higher than some ecosystems (Table 7). This is consistent with the comparison of phytoplankton biomass, primary production and zooplankton biomass with other tropical lakes which places Lake Hayq at an intermediate position (Fetahi et al., submitted-a, b). Even though the transfer efficiency was good, this was not reflected in the overall ecological efficiency of the lake. The gross efficiency of the fishery (catch/NPP) of 0.05 % is lower than that for Lake Awasa, Ethiopia (0.144%) (Fetahi and Mengistou, 2007), which shows that the high amount of primary production in Lake Hayq (Fetahi et al., submitted-a) is not well-utilized for fishery. However, the efficiency of Lake Hayq is higher than the global average (0.02%) (Christensen et al., 2005).

At the ecosystem level, the top-down control seems weak as several consumers have a 'beneficial predation' on their prey (the direct negative impact on prey is out weighted by positive indirect impacts). The overall impact on the ecosystem (Fig. 5) reveals that only phytoplankton and detritus have positive and strong impacts suggesting the importance of bottom-up control on the lake ecosystem. The keystone species analysis also indicates the importance of phytoplankton in the lake ecosystem. The P/R ratio (1.05) of Lake Hayq falls within the acceptable range of Christensen and Pauly (1993) and Lewis (1981), and indicates the maturity of the ecosystem *sensu* Odum (1969). We calculated a high omnivery index (OI), which reflects a large feeding spectrum in the diet. An

increased OI also indicates the stability of the community (Pimm et al., 1991). Consequently, the SOI for Lake Hayq was relatively high (0.14, Table 7), indicating a high level of ecological maturity (Odum, 1969). Moreover, FCI also indicates the maturity of lake; the value obtained 15% of total throughput lies within the range reported by Christensen and Pauly (1993) for 41 lakes and it is higher than to several of them.

We also ran Ecopath by excluding Tilapia and with lower Chl-a concentration (2 mg m^{-3}) to reconstruct the food web of Lake Hayq before the introduction of Tilapia (Baxter and Golobtisch, 1970; Kebede et al., 1992). The analysis resulted in lower SOI (0.016) and P/R ratio (0.13), which describes the lake as immature ecosystem in former times. The introduction of Tilapia might have contributed to the maturity of the lake as a positive relationship between maturity and diversity in natural communities could be observed (Odum, 1969; Pe´rez-Espan and Arreguin-Sanchez, 2001). Indeed, Tilapia in Lake Hayq filled an ecological empty niche of pelagic planktivores and contributed for the higher transfer efficiency from primary production to fish yield. Additionally, Tilapia is a major success in the economy of the local people (Kebede et al., 1992). The diversity-stability hypothesis is often related to elasticity, the ability to return to the stationary condition particularly following a short disturbance (Lamper and Sommer, 1997). However long-lasting perturbations, such as addition of phosphorus through sewage or introduction of long-lived planktivorous fish species usually result into eutrophication. The latter was the case for Lake Hayq and in the meanwhile, the lake has changed into a new, stable, eutrophic status most probably as a result of food web interactions.

Table 7 Comparison of some parameters among different ecosystems. Transfer efficiency data, except Lake Hayq, were obtained from Christensen and Pauly (1993).

Systems	Transfer efficiency (%)	SOI	Gross efficiency of the fishery (Catch/npp)	Total pp/tot biomass	Total pp/total R	Mean TL of the catch
L. Hayq	11.5	0.140	0.0004	106	1.05	2.46
L. Awasa			0.0014	28.67	5.83	2.57
L.Kinneret	10.6		0.0015			4.07
L. Chad	11					
L. Kariba	4.6					
L. Malawi	7					
L. Turkana	4.3					
Tanganyika	12.1					
Victoria[a]	11.8					
Victoria[b]	15					
Ubolratana		0.121	0.0012	10.28	4.83	2.6
Pasak Jolasid		0.089	0.0016	19.5	1.21	2.37
Parakrama Samudra		0.031	0.0023	35.58	1.34	2.1
Venice-1998		0.228	0.44483	9.87	2.33	2.31

In conclusion, in this analysis we have been able to describe the structure and trophic interactions of the communities from a holistic point of view for the first time. Even though several functional groups were well-utilized in the system, *Mesocyclops* and *Thermocyclops* were under-utilized. The introduction of Tilapia is probably the major cause of the trophic change, and it might also have played a key role for the current maturity and stability. The stocked planktivorous fish occupied an empty niche and is a major success in the economy of the local people (Kebede et al., 1992). In the present analysis, we lumped benthic organisms as a single functional group and future study should inverstigate them more in detail. Fish-eating birds, though included, are adopted values; we recommend on site estimation as this group may consume large amounts of fish. Cormorants, for example, are usually blamed by feeding high fish biomass greater than or equivalent to fishery catches (Winkler, 1983; Schiemer and Duncan, 1988; Mavuti et al., 1996). This study is an essential step in understanding the ecosystem of this tropical highland lake, and can be seen as a baseline to devise ecosystem-based management in the future.

Acknowledgements

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Decadal changes in phyto- and zooplankton communities of Lake Awasa, Ethiopia

Age is a mirror (Ethiopian saying)

Decadal changes in phyto- and zooplankton communities of Lake Awasa, Ethiopia

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Abstract

We studied phyto- and zooplankton communities of Lake Awasa between November 2003 and August 2004, and compared with historical data since the 1980-ies to assess potential inter-decadal changes. The lake is located in the Ethiopian rift-valley in the vicinity of the growing city Awasa receiving adverse effluents from textile and ceramics industry and municipal sewage apparently with little treatment. In 2003/04, phytoplankton abundance comprised 54% Chlorophyta, 26% cyanoprokaryotes, 18% diatoms and 2% others, a proportion similar to previous records. However, the mean phytoplankton biomass in terms of Chlorophyll *a* (19 µg L^{-1}) was lower than reported from previous studies (e.g. 43 µg L^{-1}, KEBEDE and BELAY, 1994). In contrary, areal rate of gross photosynthesis has increased in the last two decades with higher values recorded at present (0.35 to 2.21 g O_2 m^{-2} h^{-1}). In a similar way, even though zooplankton community composition remained the same, the abundance and dominance of taxa have been changed in the last decades. In 2003/04, the mean abundance of cyclopoid-copepods was 58 000 ± 9200 (SE) Indl m^{-3} whereas cladocerans abundance (2 600 ± 640 SE Indl m^{-3}) was very low in the system. Interestingly, rotifers outnumbered other components with a maximum value of 264 000 Indl m^{-3} , which is about five-times greater than the previous reports. The adult cyclopoid to nauplii ratio of 0.27 in the present study suggested that cannibalism has diminished at present probably due to high number of rotifers as prey, contradicting a previous hypothesis.

Keywords: long-term change, Lake Awasa, phytoplankton, interactions, zooplankton

Introduction

An 'ecosystem distress syndrome' is widely prevalent (RAPPORT et al., 1998), and both internal and external drivers can affect aquatic ecosystems. The external driver can be thought of as a signal and the lakes as responders (MAGNUSON *et al.,* 2004) reacting in several ways: absorbing the signals, temporarily altered or changed into an alternate stable domain (e.g. eutrophic), or for the worst case, the system may disappear (e.g. Lake Alemaya, a history lake in Ethiopia, LEMMA, 2003). Changes are not abrupt but the sum of slow processes. A long-term view reveals a rich array of slow changes, and interannual and interdecadal dynamics (MAGNUSON *et al.,* 2006). Long-term data also provide an important baseline against which future changes can be assessed (KUNZ and RICHARDSON, 2006). Such long-term studies are well documented for temperate lakes (MAGNUSON *et al.,* 2006), however in tropical lakes long-term variability has been documented only sporadically (TALLING and LEMOALLE, 1998), and this holds true for Ethiopian water bodies. One exception is the comparatively well studied Lake Awasa, which was investigated extensively during the 1980s and early 1990s with particular emphasis on its biology. Phytoplankton biomass and primary production in relation to nutrients and light were studied during this time (KIFLE and BELAY, 1990; KEBEDE and BELAY, 1994) and some dominant phytoplankton species were identified including *Lyngbya nyassae* Schmidle 1902*, Botryococcus braunii* Kützing 1849 and *Microcystis* sp.. Zooplankton production, biomass and species identification were comprehensively studied by MENGISTOU (1989) with dominant taxa represented by *Mesocyclops aequatorialis* Van de Velde 1984*, Thermocyclops consimilis* Kiefer 1934*, Diaphanosoma excisum* Sars*, Brachionus* and *Keratella* spp.. Since then, there have been few studies done for Lake Awasa concerning plankton dynamics and their interactions. However, some changes are anticipated to have taken place based on demographic pressure and industrial developments around the lake. Lake Awasa is located in the vicinity of the growing city Awasa, and some of the many potential adverse effects facing the lake include lack of proper sewage treatment system, poor land-use management and high levels of recreational activity. Moreover, the nearby Awasa Textile Factory drains its effluent into the lake, apparently with little treatment. An experiment made by GEBRE-MARIAM and DESTA (2002) on the effluent from this factory showed that phytoplankton growth was either boosted or inhibited and fish fry and adult fish almost instantly died when exposed to the undiluted effluent. On the other hand, water level fluctuations of Lake Awasa were reported (MENGISTOU and FERNANDO, 1991; ZINABU *et al.,* 2002) with lake level increases. These water level changes could disturb the breeding ground of Tilapia (a commercially important fish) and other physical, chemical and biological parameters of the lake (TUDORANCEA and TAYLOR, 2002). Over-fishing of Tilapia (*Oreochromis niloticus* Linnaeus 1758) was also documented (LFDP, 1998), suggesting its preys might have relieved from the grazing pressure. Lake Awasa is now naturally changing to its ecological maturity stage, as evidenced from the concept developed by ODUM (1969) (FETAHI and MENGISTOU, 2007) and its water quality can easily be affected through anthropogenic effects.

In order to manage aquatic ecosystems, we need a broad understanding about plankton and its interactions with the environment. Plankton communities integrate various human and environmental impacts, thereby providing a benchmark for monitoring the synergistic effects of urbanisation and climate change (KUNZ and RICHARDSON, 2006). Accordingly, it is now common practise to use plankton as water quality indicator (MONA *et al.,* 2005). We therefore aimed to analyze and document the decadal changes of plankton in a tropical rift-valley lake where anthropogenic and environmental effect could be manifested. Phytoplankton changes were assessed in terms of

community composition, primary production and Chlorophyll a (Chl *a*). The zooplankton community structure and abundance was also examined to understand its long-term change and to lay down a baseline data for future managment. For this, we compared avialable historical data of Lake Awasa since 1980-ies, and attempt to account for some of the possible reasons for the changes.

Study site

The endorheic Lake Awasa is located at an altitude of 1680 m in the central part of the Ethiopian Rift Valley (6° 33' – 7° 33' N and $38^O22'$ – $38^O29'$ E; Fig. 1), 275 km south of the capital city Addis Ababa. GAMACHU (1977) documented that the Awasa area has a dry, subhumid climate and receives a mean annual rainfall of 1154 mm (Fig. 2). The annual potential evapotranspiration for the area is between 1100 and 1250 mm (KEBEDE and BELAY, 1994), so evapotranspiration sometimes exceeds precipitation. The lake has a surface area of 90 km^2 and a maximum depth of 22 m (Table 1), although the latter value is subjected to seasonal variation.
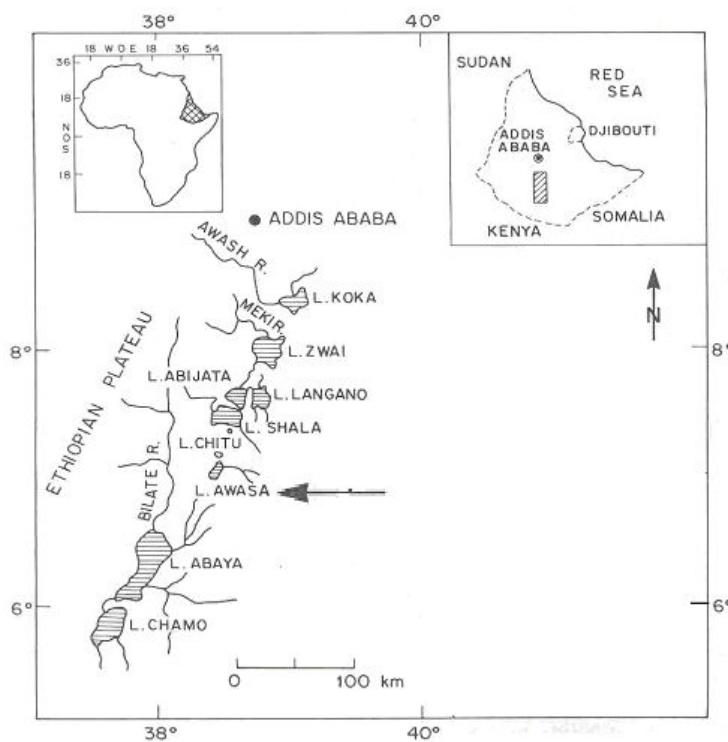

Figure 1. Map of Ethiopia (inset) and the Rift Valley Lakes with their drainage basin

pattern. The arrow indicates Lake Awasa (Modified after KEBEDE *et al,*. 1994).
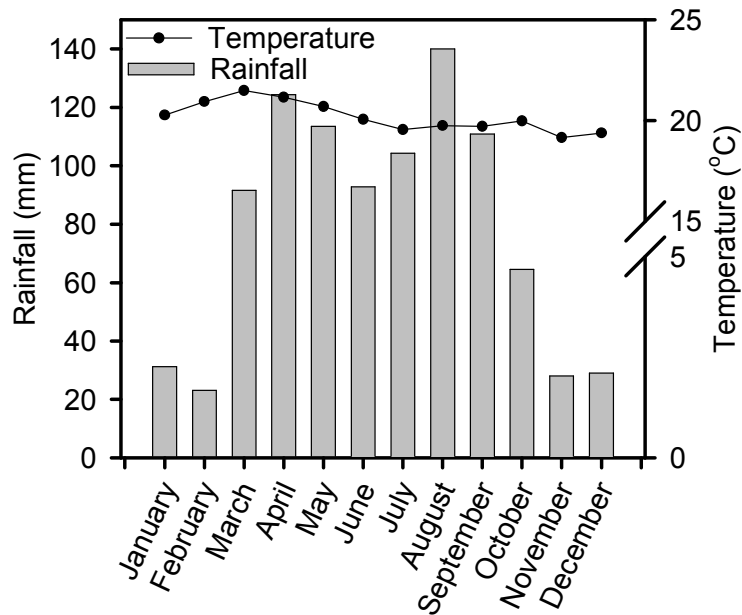
Figure 2. Air temperature and rainfall data near Lake Awasa during 1996 – 2006. Data from National Meteorological Services Agency.

Table 1. Morphometry of Lake Awasa (from Welcome 1972 and [a]Makin *et al.,* 1975)

Variables	Values
Catchment area	1250 km^2
Maximum Length	17 km
Maximum Width	11 km
Shoreline	52 km
Surface Area[a]	90 km^2
Maximum Depth	22 m
Mean Depth	11 m
Volume	$1.3*10^9$ m^3

A small river named Tikur Weha feeds the lake. The lake is classified as warm polymictic under the scheme proposed by Lewis (1983). A summary of the lake chemistry is presented in Table 2. The fish fauna of Lake Awasa consists of *Oreochromis niloticus, Clarias gariepinus* Burchell 1822*, Labeobarbus intermedius intermedius* Rüppell 1835, *Barbus paludinosus* Boulenger 1903, *Aplochelichthys* sp.*,* and *Garra* sp. (ADMASSU, 1996; Fishbase 2010). Juvenile and the last three fish species are regarded as planktivorous fish. The benthic fauna include Ostracods (dominant), Chironomids, Cyclopoids and Cladocerans. The macrophytes vegetation includes *Cyperus* sp.,

Nymphea caerulea, *Potamogeton* sp., *Typha angustifolia, T. latifolia*, and *Paspalidium geminatium* (KIBRET and HARRISON, 1989).

Table 2. The chemical characteristics of Lake Awasa, Ethiopia.

Characteristics	Values	Reference
Na^+	7.1 meq L^{-1}	Gebre-Mariam et al. (2002)
K^+	0.7 meq L^{-1}	»
Ca^{2+}	0.5 meq L^{-1}	»
Mg^{2+}	0.5 meq L^{-1}	»
Alkalinity	7.8 meq L^{-1}	»
Cl^{-1}	0.8 meq L^{-1}	»
$SO4^{2-}$	0.2 meq L^{-1}	»
SiO_2	42.6 mg L^{-1}	Kebede et al. (1994)
PO_4-P	12.4 µg L^{-1}	»
Total P	36.2 µg L^{-1}	»
NO_3/NO_2-N	34.9 µg L^{-1}	»
NH_4-N	5.7 µg L^{-1}	»
SiO_2	37.6 mg L^{-1}	Tilahun and Ahlgren (2009)
PO_4-P	15.4 µg L^{-1}	»
Total P	34.1 µg L^{-1}	»
NO_3/NO_2-N	2.5 µg L^{-1}	»
NH_4-N	118 µg L^{-1}	»
Conductivity	846 µS Cm^{-1}	Kifle and Belay (1990)

Material and Methods

Two sampling stations were selected: the shore station (SS, 200 m offshore) with a depth of 3 m and open station (OS, some 3 km offshore) with a depth of 18 m. The study was conducted from November 2003 – August 2004 at monthly intervals. Water transparency was measured with black and white painted disc of 0.20 meter diameter. Net phytoplankton (30 µm) samples were collected and immediately fixed with Lugol's iodine, and taxa identification was made using different guides including JOHN *et al.* (2002), ROTT and LENZENWEGER (1994), JEEJI- BAI *et al.* (1997), HINDAK (2000), and KOMAREK and CRENBERG (2001). Phytoplankton biomass was estimated from the Chl *a* concentration. Samples were collected with a 1 L container 10 cm below the lake surface and a defined volume was filtered through Whatman GF/C filters, ground and extracted with 90% acetone. After centrifuging, the supernatant absorbance was measured at 665 nm spectrophotometrically and corrected for turbidity by subtracting the corresponding reading at 750 nm (TALLING and DRIVER, 1963). Primary productivity was measured using light-dark bottles of Winkler titration method. Water samples were taken from the lake surface and were siphoned into 300 ml Pyrex light and dark glass bottles. Two light and dark bottles were attached at surface, 0.25 m, 0.50 m, 1 m and 2 m depth on a metal suspender, and incubated for about 2 hours.

Zooplankton samples were taken from the water column with 64 μm mesh townet having a mouth diameter of 0.3 meter. To determine abundance, the samples were hauled from 3 m depths for OS, and 0.5 m for SS. The concentrated samples were immediately preserved with formalin to yield the final concentration of approximately 5 %. Zooplankton taxa were identified using different guides including VOIGT and KOSTE (1978), DEFAYE (1988), and FERNANDO (2002). Numerical abundance was done using a Wild Microscope with 50 X magnification power. During counting, the developmental stages (nauplii and copepodites) were lumped together. Separate counts of nauplii and adults of cyclopoids was done in order to see the naupli-adult ratio. The trophic status of Lake Awasa was assessed using the trophic status index (TSI) of CARLSON (1977), which is calculated based on Secchi disk transparency (TSI (SDT) = 60 − 14.41 ln (SDT)) and Chl a concentration (TSI (Chl a) = 9.81 ln (Chl a) + 30.6). A TSI < 30 is commonly considered as indicative of oligotrophic conditions, between 50 and 70 the water body is eutrophic and values > 70 indicate hypereutrophic conditions (WETZEL, 2001).

Results

Water transparency readings ranged from 0.7 to 1.2 m and a mean of 0.9 m was recorded. We found an average Chl a concentration of 19 μg L^{-1} without significant differences between OS and SS (t-test, P = 0.635, DF = 14). The current phytoplankton biomass had one maximum in February and peaked again in August; lowest amounts were recorded in May 2004 (Fig. 3). A total of 39 phytoplankton taxa were identified, and their relative contribution to the total abundance comprised 54% Chlorophyta, 26% cyanoprokaryotes, 18% diatoms and 2% others (Fig. 4). Some taxa were new to the lake, e.g., *Pediastrum simplex* (two sub-species) and *Scenedesmus ecornis*. The depth profile of gross photosynthesis per unit volume (g O_2 m^{-3} h^{-1}; Fig. 5) of OS is a typical pattern for phytoplankton, displaying a single subsurface peak with maximum photosynthetic production occurring at a depth of around 0.5 m.
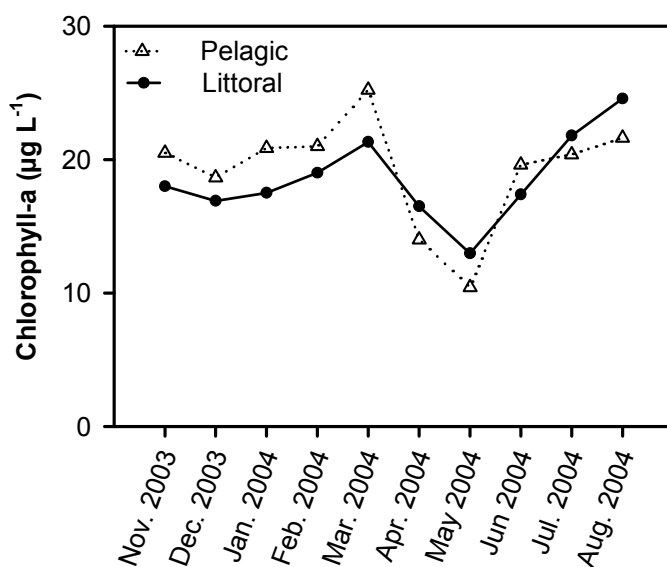

Figure 3. Temporal variation in phytoplankton biomass of Lake Awasa as indicated by Chl a at two locations in 2003/2004.
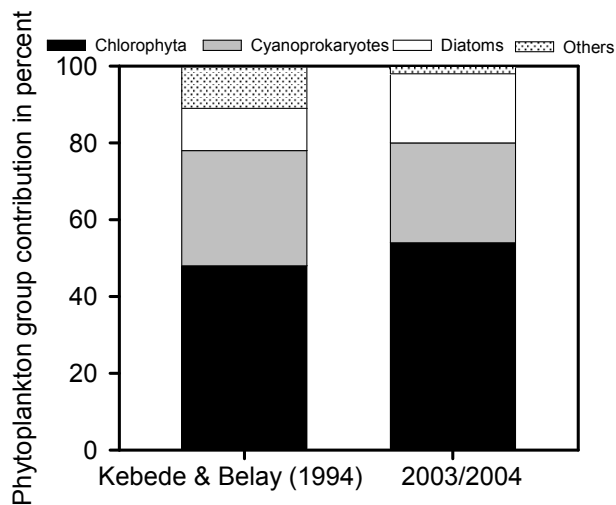
Figure 4. Relative algal proportion of major phytoplankton groups in Lake Awasa.

Large variations of the light-saturated photosynthetic rate (A_{max}) were recorded with values ranging from 0.4 – 3.4 g O_2 m^{-3} h^{-1}. Gross photosynthesis was also determined at SS for four months to compare it with the OS and no significant differences could be found. The daily areal photosynthesis ranged from 3.5 to 22.1 g O_2 m^{-2} d^{-1} exhibiting more than a six-fold variation.
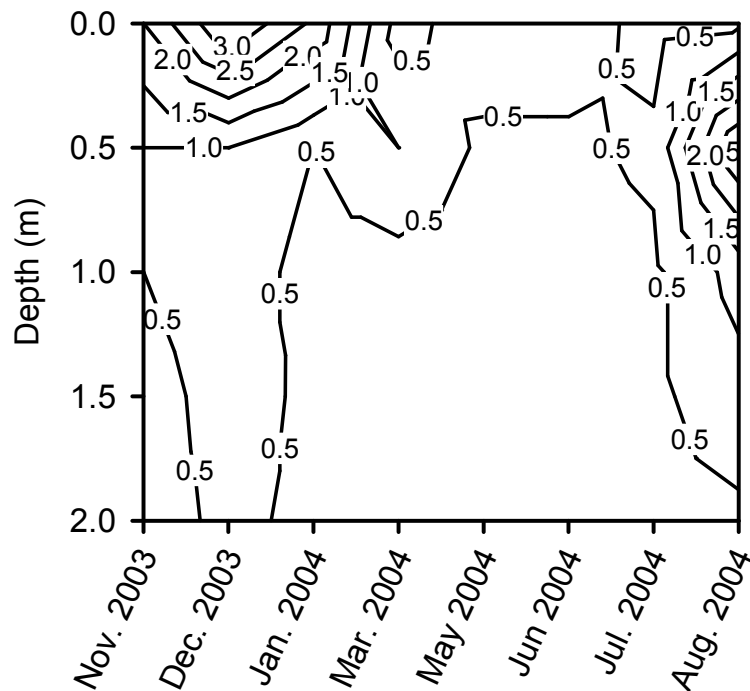

Figure 5. Gross primary productivity (g O_2 m^{-3} h^{-1}) of Lake Awasa, Open Zone, studied from November 2003 to August 2004.

Rotifers contributed 69% to the total zooplankton density, whereas cyclopoid copepods and cladocerans contributed 28% and 3%, respectively (Fig. 6). The mean abundance of cyclopoid copepods was about 58 000 ± 9200 (SE) Indl m^{-3} with a maximum of 134 420 Indl m^{-3} recorded in August 2004 and the minimum (31020 Indl m^{-3}) observed in May 2004. Cladoceran density was very low in the present study with an average of 2 616 ± 640 Indl m^{-3}. The number of rotifers in the present samples were high in comparison to the other two groups, with a mean value of 95 500 ± 25 600 Indl m^{-3} (maximum of 264 000 Indl m^{-3} in June 2004). A separate count of nauplii and adult cyclopoid was made in order to see the proportion of the adults to their juveniles. It was found that the open water of Lake Awasa had a mean of 22% and 78% of adult and nauplii, respectively, and the littoral had 14% and 86% of the same. In both sites in the present study, the major contributors to the total cyclopoid abundance were nauplii.
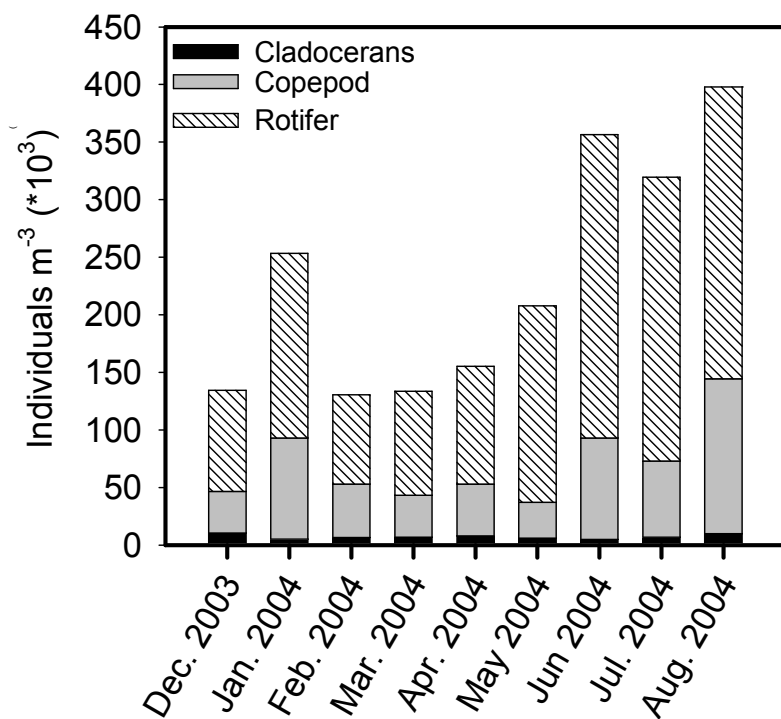

Figure 6. Mean monthly zooplankton abundance (individual m^{-3}) in Lake Awasa during 2003 to 2004.

Discussion

Based on TSI indices, Lake Awasa can be categorized as eutrophic water body (water transparency TSI = 62; Chl a TSI= 59.5). The chemistry of the lake was investigated by KEBEDE et al. (1994) and its long-term variations were discussed by ZINABU et al. (2002). Recently, TILAHUN and AHLGREN (2009) have also reported about the chemistry of the lake (Table 2). One obvious difference in the chemistry of the lake is that the primary form of nitrogen (NO_3-N) in KEBEDE et al. (1994) is replaced by NH_4-N in the recent investigation (TILAHUN and AHLGREN, 2009).

   The phytoplankton taxa were similar with KEBEDE and BELAY (1994), except some that are identified in 2003/04 (such as *Pediastrum simplex* (two subspecies) and *Scenedesmus ecornis*). The mean phytoplankton biomass of SS (19 µg L^{-1}) and OS (20 µg L^{-1}) were comparable. However, when taking a closer look at the temporal variations, OS experienced higher biomass than SS from November to June (except the depression point in May; Fig. 3), which was overcompensated later on. KEBEDE and BELAY (1994) observed a very similar seasonal variability of biomass in Lake Awasa. A first phytoplankton biomass peak (Fig. 3) could be associated with the effect of mixing. High biomass of phytoplankton was observed in February as there were enough sunshine and possibly high inorganic nutrients available. The second biomass rise in August 2004 coincided with the major rainy season (June to August) where nutrients are drained from the catchment; a complete mixing was observed as well. The biomass minimum at both stations occurred in May 2004 and could be related to stratification and nutrient depletion. Moreover, rotifers may have played a role in reducing phytoplankton biomass. Previously, TAYLOR and GEBRE-MARIAM (1989) suggested that rotifers and ciliates are important grazers of smaller phytoplankton forms in Lake Awasa. Additionally, a recent study showed that smaller-sized phytoplankton contributes much to the biomass of Lake Awasa (TILAHUN, 2007). However, high filtering efficiencey is ascribed to cladocerans particularly to large-sized ones (SCHEFFER, 1998; LAMPERT and SOMMER, 1997) and hence controlling of biomass by rotifer is unlikely.

   The relative contribution of the phytoplankton abundance is similar to the earlier report of KEBEDE and BELAY (1994) (Fig. 4), but when comparing the inter-annual variation of biomass between 1980-ies and the current values, a declining trend in the last 15 years is clearly visible (Fig. 7). This is probably associated with a decrease in nutrient availability, as ZINABU et al, (2002) showed that the concentration of Soluble Reactive Phosphorus (SRP) and Silicate decreased in the 1990-ies compared to previous data. These authors also demonstrated a significant decline of conductivity in the system.

   The daily integral gross primary productivity ranges from 3.5 to 22.1 g O_2 m^{-2} d^{-1} exhibiting more than six-fold variation between the minimum and maximum values. Compared to previous reports (3.0 - 7.3 g O_2 m^{-2} d^{-1} by KIFLE and BELAY, 1990; 9.9 g O_2 m^{-2} d^{-1} by GEBRE-MARIAM, 1988), it appears that the integral rate of gross photosynthesis of Lake Awasa has changed in the past two decades with some higher values in 2003/04 (Fig. 8). As the euphotic depth (derived from Secchi disc readings) remained more or less constant when the present study is compared with the previous works such as KIFLE and BELAY (1990), the present higher values were probably caused by the smaller-sized nanophytoplankton, which contributed >50% to the total biomass (TILAHUN, 2007), because small-sized organisms are more productive (WETZEL, 2001).
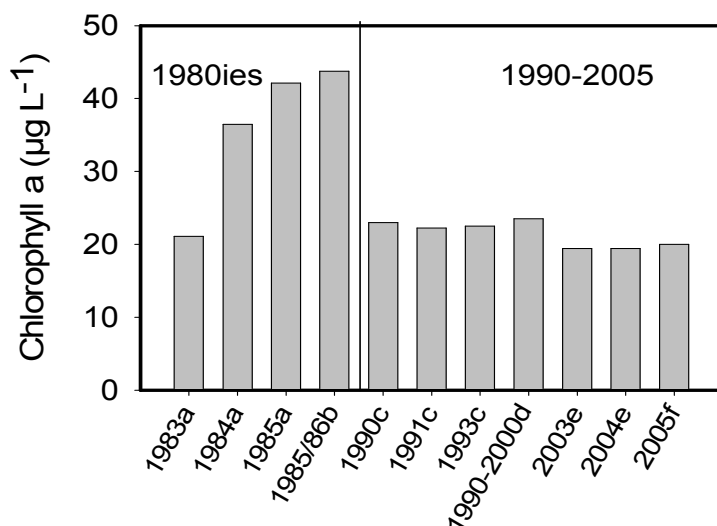
Figure 7. Inter-annual variation of phytoplankton biomass in Lake Awasa from 1980s to 2004. [a] KIFLE and BELAY (1990); [b]KEBEDE and BELAY (1994); [c]ZINABU and TAYLOR (1997); [d]GEBRE-MARIAM et al. (2002); [e]FETAHI (2005), [f]TILAHUN and AHLGREN (2009).
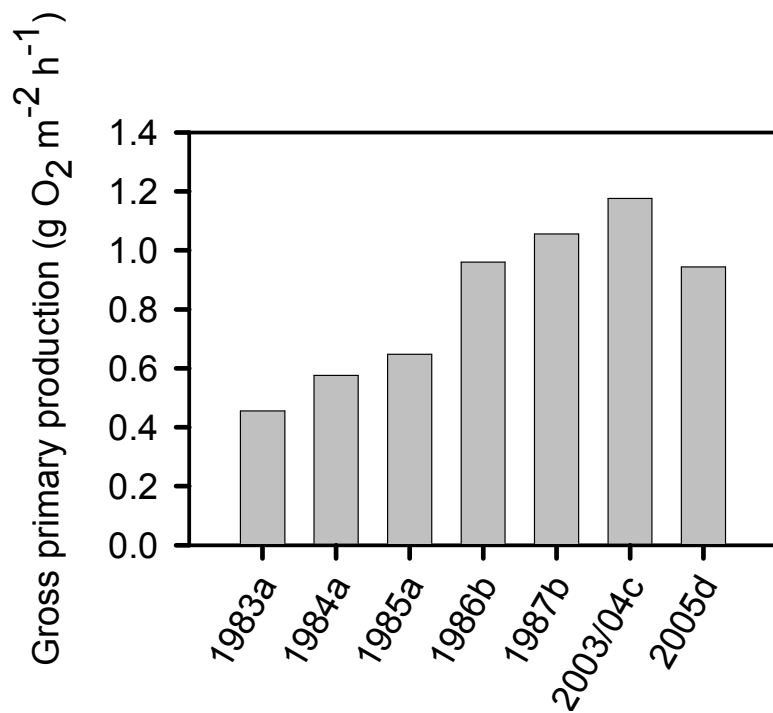

Figure 8. Inter-annual temporal variation of integral primary production of Lake Awasa from 1980-ies to 2005. [a] KIFLE and BELAY (1990); [b]KEBEDE and BELAY (1994); [c]FETAHI (2005), [d]TILAHUN and AHLGREN (2009).

Compared to previous studies, some differences of zooplankton numerical abundance are evident. We found a mean annual abundance of cyclopoid copepods of 58 000 ± 9200 (SE) Indl m^{-3}, whereas MENGISTOU (1989) reported 68 000 ± 4300 Indl m^{-3}. The average cladocerans density 2 600 ± 640 (SE) Indl m^{-3} was very low in the current study. In contrary, MENGISTOU (1989) reported a maximum of 18 000 Indl m^{-3}. The abundance of copepods and cladocerans in the present study is particularly low in the littoral zone, which is an area of nursery and feeding ground of juvenile and unexploited fishes that consume zooplankton at some stages of their developmental time (FERNANDO, 1994). A separate count of nauplii and adult cyclopoids showed that the major contributors for the total abundance of the taxa were nauplii. However, MENGISTOU (1989) reported that more than 90% of the total zooplankton was contributed by adult cyclopoids. It seems that the former larger contribution of adult cyclopoids is now replaced by nauplii indicating that cannibalism may be diminished at present conditions. The cannibalistic nature of cyclopoids may have been changed due to the presence of large number of rotifers in the current study, which is a potential prey in Lake Awasa (TAYLOR and GEBRE-MARIAM, 1989).

Large-bodied zooplankton affects rotifers in two ways: (i) it can compete with rotifers for available algal food through exploitative competition (NEILL and PEACOCK, 1980) and (ii) it can also feed on rotifers causing direct mortality in a form of interference competition (GILBERT and STEMBERGER, 1985), the latter interaction probably being more important (SCHNEIDER, 1990). TAYLOR and GEBRE-MARIAM (1989) suggested that rotifers are consumed by cyclopoid copepods in Lake Awasa, which might be an explanation for reduced rotifer abundances in former times. However, in the present study the small number of adult cyclopoids resulted only low grazing pressure on rotifers that may give a break time for rotifers to reproduce very well. As a result, we reported a maximum rotifer abundance of more than 263 600 Indl m^{-3} that is about five-times greater than that estimated by MENGISTOU (1989). A similar scenario was found by LEMMA (2003) for Lake Hora-Kilole where cladoceran populations were replaced by rotifers due to high predation pressure from the dominant juvenile *Barbus* species. The dominant rotifer taxa reported by MENGISTOU (1989) were *Brachionus* and *Keratella*, which however, were replaced by *Filinia* and *Trichocerca* in most months of the recent study. This species replacement may be due to predation pressure on *Keratella* and *Brachionus* by planktivorous fish and/or cyclopoids.

In various lakes, strong top-down effects on phytoplankton biomass have been reported for cladoceran-dominated zooplankton (SOMMER, 1986; LAMPERT, 1988). Nevertheless, Lake Awasa did not follow similar trends, therefore large amounts of phytoplankton biomass were converted into detritus (FETAHI and MENGISTOU, 2007; MENGISTOU and FERNANDO, 1991). This can be explained, because the larger herbivorous *Daphnia* responsible for effective grazing is largely absent in Lake Awasa (MENGISTOU, 1989). Furthermore, the existing cladocerans (such as *Diaphanosoma*) are heavily consumed by the planktivorous fish species (FETAHI AND MENGISTOU, 2007), and thus very low in abundance (Fig. 6), which incapacitate their ability to utilize the available phytoplankton biomass. Additionally, large colonial and filamentous phytoplankton species may dominate sometime in the lake (KEBEDE and BELAY, 1994) and are more resistant against grazing than small r-strategists. The average phytoplankton biomass (34 t km^{-2}) is much greater than that of zooplankton (2.8 t km^{-2}) (FETAHI and SEYOUM, 2006) indicating that bottom-up (resource) control of phytoplankton is more significant than top-down effects. This supports the studies of TALLING and TALLING (1965), who have documented that bottom-up control is more important than top-down control in tropical systems.

In conclusion, the proportion of phytoplankton taxa and groups is quite similar to previous studies. Primary production has increased through time even though biomass has decreased in the system. The composition of zooplankton has remained the same but the abundance and the dominant taxa have changed in the long-term. The abundance of adult copepods and cladocerans is now very low but rotifers flourish in the system. Human impact is most likely as Lake Awasa is located nearby the fast growing town Awasa, where demographic pressure is high. The lake is used for fishing, and the commercially important *O. niloticus* is over-exploited (LFDP, 1998). The lake is also used for bathing and washing clothes, domestic use and recreational purpose. Moreover, the lake is surrounded by agricultural land, hence anthropogenic influences are inevitable. Besides, it receives affluent from industries. Once the concentration of pollutants passes the threshold limit, it will bring irreversible damage to the ecosystem. So care and appropriate management should be taken before such ecological damage happen, which would affect not only the biodiversity but the economy as well.

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Summary and Curriculum Vitae

Zusammenfassung von Plankton Gemeinden und Ökologie der tropischen Seen Hayq und Awasa, Äthiopien

Der im Hochland von Äthiopien gelegene Lake Hayq dient der ansässigen Bevölkerung als Trinkwasserreservoir, Nahrungsquelle sowie als touristisches Ziel. Der See wurde seit den 1930er Jahren sporadisch untersucht und als oligotrophes Gewässer eingestuft. Vor annähernd 20 Jahren änderte sich dieser Zustand und der See zeigte Eutrophierungserscheinungen. Für diese Verschiebung kamen zwei Hypothesen in Betracht: (i) ein erhöhtes Nährstoff-Volumen-Verhältnis und (ii) planktivore Tilapia Fische (*Oreochromis niloticus*), welche in den späten 1970er Jahren ausgesetzt wurden. Dies ist die erste Studie, die sich mit beiden Theorien auseinandersetzt, wobei historische Aufzeichnungen analysiert und mit neuesten Daten verglichen wurden. Primärproduktion und Biomasse, Zooplanktonabundanz, Nährstoffe sowie chemisch-physikalische Parameter wurden hierfür monatlich von Oktober 2007 bis Oktober 2008 an zwei Standorten gemessen. Die Ergebnisse zeigten, dass der pH-Wert sowie die Gesamtalkalinität während des letzten halben Jahrhunderts konstant blieben, die elektrische Leitfähigkeit jedoch sukzessiv zunahm. Die aktuelle mittlere Konzentration an gelösten, anorganischen Stickstoff betrug 305 µg L^{-1}, wobei Ammonium den Hauptvertreter stellte. Der löslich reaktive Phosphor betrug 22 µg L^{-1}, der Gesamtphosphor 58 µg L^{-1} und Si 3.7 mg L^{-1}, wobei letzteres eine höhere Konzentration als bei früheren Aufzeichnungen mit 2.4 mg L^{-1} zeigte. Die gegenwärtige Studie zeigte ein erhöhtes Aufkommen an Algengruppen und Taxa, während in den 1940er Jahren lediglich Diatomeen dokumentiert wurden. Von den 40 bestimmten Phytoplanktontaxa machten die Chlorophyten und Diatomeen 77% der Gesamtanzahl aus, wobei eine kanonische Korrespondenzanalyse (CCA) auf einen Zusammenhang ersterer mit Nährstoffen und Regen und letzterer mit Silikat und Zooplankton aufzeigte. Das Gesamtmittel der Phytoplanktonbiomasse von 1.10 mm³ L^{-1}, der mittlere Chlorophyll *a* (Chl *a*) Gehalt von 12.9 mg m $^{-3}$ und die Bruttoprimärproduktion von 7.12 g O_2 m^{-2} d^{-1} stellen den Lake Hayq - verglichen mit anderen tropischen Seen - in eine Übergangsposition zwischen meso- eutroph. Die Hauptkomponentenanalyse (PCA) gefolgt von einer Regressionsanalyse wiesen darauf hin, dass der Chl *a* Gehalt vor allem durch Regenfälle, Temperatur und Verfügbarkeit von Licht gesteuert wird. Lake Hayq kann aufgrund von verschiedenen limnologischen Produktivitätsindices als eutroph eingestuft werden. Als Ursache dürfte jedoch nicht das hohe Nährstoff-Volumen-Verhältnis in Frgae kommen, da bereits sehr hohe Nährstoffkonzentrationen (SRP 96 µg L^{-1} und NH_4-N 300 µg L^{-1}) vorlagen, als der See noch als als oligotroph eingestuft wurde. Vielmehr dürfte der Fischbesatz durch planktivore Tilapien die Hauptursache für die Veränderung des Trophiezustandes des Sees darstellen.

Die Veränderung der Zooplanktonzusammensetzung, z.B. das Verschwinden der Cladoceren ist laut verschiedenen Autoren ebenfalls auf Tilapia zurückzuführen. Um diese Hypothese zu bestätigen, bestimmten wir unter Berücksichtigung limnologischen Basisparametern die Zooplanktonzusammensetzung, die Abundanz und die Biomasse innerhalb Kurzzeitintervallen zwischen Oktober 2007 und Jänner 2009. Die dominanten Zooplanktonarten waren *Mesocyclops aequatorialis*, *Thermocyclops ethiopiensis*, *Ceriodaphnia reticulata*, *Daphnia magna*, *Diaphanosoma excisum* sowie die häufig auftretenden Rädertiere *Euchlanis parva*, *Keratella tropica* und *Polyarthra sp.*. Das Gesamtmittel der bestehenden Biomasse aus Crustaceen-Zooplankton mit 237 mg Trockengewicht m^{-3} ist durchaus mit anderen tropischen Seen vergleichbar. Unter den Copepoden war fast ausschließlich *Thermocyclops ethiopiensis* mit einem Maximalwert von 469 Indl L^{-1} und einem Mittelwert von 92 Indl L^{-1} zu finden. Diese Abundanzzahl stimmt mit anderen Autoren, die einen

Maximalwert von 577 Indl L-1 für cyclopoide Copepoden dokumentierten, überein. Die CCA deutete darauf hin, dass die zeitliche Variation von *Thermocyclops* durch die Verfügbarkeit von Nahrung und Wassertemperatur beeinflusst wurde. Die planktivoren Fische spielen eine Schlüsselrolle in der Strukturierung der Cladoceren, vor allem der großen *Daphnia magna*. Im Jänner 2008 beobachteten wir ein massives Fischsterben planktivorer Fische gefolgt von einer hohen Algenbiomasse, die von der großen *Daphnia magna* beweidet wurde. Dieser kaskadenartige Ablauf demonstriert die trophischen Interaktionen im natürlichen Ökosystem.

Wir entwickelten ein Massen-Gleichgewichts-Modell, um die pelagische Struktur des Nahrungsnetzes und die trophischen Interaktionen der funktionellen Hauptgruppen des Lake Hayq zu bestimmen. Die Studie bildet außerdem eine Datenbasis für zukünftige ökosystem-orientierte Untersuchungen und Managementpläne. Zwischen Oktober 2007 und Mai 2009 wurden ausführlich Daten gesammelt. Die ökotrophische Effizienz (EE) von verschiedenen funktionellen Gruppen inklusive Phytoplankton (0.8) und Detritus (0.85), war hoch, was auf eine Nutzung der Gruppen innerhalb des Systems schließen lässt. Der EE von *Mesocyclops* (0.03) und *Thermocyclops* (0.3) war jedoch sehr gering, was bedeutet, dass diese Ressourcen eher einen „Sink" in der trophischen Hierarchie darstellen. Stoffflüsse, die auf trophischen Niveaus sensu Lindeman basieren, lassen die Bedeutung von Phytoplankton und Detritus zu höheren Trophieniveaus erkennen. Die berechnete durchschnittliche Transfereffizienz von 11.5% für die ersten vier Trophieniveaus lag innerhalb des Bereichs für hocheffiziente afrikanische Seen. Die Primärproduktions-Respirations-Rate (P/R = 1.05) vom Lake Hayq spiegelt die das Klimaxstadium des Ökosystems wider. Wir modellierten unter Ausschluss von Tilapia ein Nahrungsnetz und reduzierten die Phytoplanktonbiomasse, um einen Einblick in das Massengleichgewicht zu bekommen, bevor Tilapia besetzt wurde. Die Analysen resultierten in einem geringeren System Omnivorie Index (SOI) (0.016) und einer niedrigeren P/R Rate (0.13), die den See als Ökosystem in Sukzession beschrieben und darauf hinweisen, dass Tilapia zur Weiterentwicklung des Sees beitrug. Tilapia füllte im Lake Hayq eine ökologisch leere Nische als pelagischer Planktivore und steuerte einen Beitrag zur besseren Transfereffizienz bei, die von der Primärproduktion bis zum Fischertrag beobachtet werden konnte.

Unter den Rift Valley Seen in Äthiopien wurde der verhältnismäßig gut untersuchte Lake Awasa herangezogen, um die Langzeiteffekte der anthropogenen und natürlichen Einflüsse auf Planktongemeinschaften zu untersuchen. Lake Awasa liegt in der Nähe einer wachsenden Stadt und erhält dadurch viele Industrieabflüsse und kommunale Abwässer. Rund um den See wird das Land wirtschaftlich genutzt, wobei ausreichende Managementpläne derzeit fehlen. Der See wird als Erholungsort mit vielen Freizeitaktivitäten genutzt. Wir untersuchten die Phyto- und Zooplanktongemeinschaft zwischen November 2003 bis August 2004 und verglichen unsere Daten mit den historischen Datensätzen seit den 1980er Jahren, um potentielle Veränderungen abschätzen zu können. Die Phytoplanktontaxa ähnelten sich mit den in früheren Studien, abgesehen von einigen Arten, die Neufunde in diesem System darstellen, wie z.B.: *Pediastrum simplex* mit zwei Unterarten und *Scenedesmus ecornis*. Die Phytoplanktonabundanz aus 2003/04 beinhaltete 54% Chlorophyta, 26% Cyanoprokaryota, 18% Diatomeen und 2% „sonstige Gruppen" und stellte eine proportionale Ähnlichkeit zu früheren Aufzeichnungen dar. Die mittlere Phytoplanktonbiomasse in Form von Chl *a* (19 µg L^{-1}) war jedoch geringer als in früheren Studien. Im Gegensatz dazu veränderte sich die flächenbezogene Rate der Bruttophotosynthese des Lake Awasa in den letzten zwei Dekaden nach oben (0.35 to 2.21 g O_2 m^{-2} h^{-1}). In ähnlicher Weise, trotz gleich bleibender Zooplanktongemeinschaft, unterschieden sich die Abundanz und die dominanten Taxa in den letzten Dekaden. Die mittlere

Abundanz der cyclopoiden Copepoden lag bei 58 000 ± 9200 (SE) Indl m^{-3} und die Cladocerenabundanz (2 600 ± 640 SE Indl m^{-3}) war 2003/04 im System gering. Die Rotifera übertrafen zahlenmäßig andere Komponenten mit einem Maximalwert von 263 670 Indl m^{-3}, der ca. das 5-fache von Werten von früheren Studien ausmacht. Die adult zu cyclopoid Nauplen Rate von 0.27 in dieser Studie deutet darauf hin, dass heutzutage der Kannibalismus möglicherweise durch die höhere Anzahl an Rotifera als Beutemöglichkeit abnimmt. Der menschliche Einfluss ist ahrscheinlich, da der Lake Awasa in der Nähe der schnell wachsenden Stadt Awasa liegt, in der der demographische Druck sehr hoch ist. Der See wird zu Fischereizwecken genutzt und der kommerziell wichtige *O. niloticus* ist stark überfischt (LFDP, 1998). Eine permanente Betreuung und ein angemessenes Management wären von großer Bedeutung, um ökologischen Schäden zu verhindern, die sich nicht nur auf die Biodiversität, sondern auf die gesamte Wirtschaft auswirken würden.

Summary of Plankton communities and ecology of tropical lakes Hayq and Awasa, Ethiopia

Lake Hayq, located in the highlands of Ethiopia, offers its natural services to the local inhabitants including drinking water, fishes and tourism. Though sporadically, the lake has been visited since 1930-ies and used to be an oligotrophic water body. However, its trophic status changed some 20 years ago to an eutrophic level. For this shift, two hypotheses were proposed: (i) an increased nutrient to volume ratio and (ii) planktivorous Tilapia fish (*Oreochromis niloticus*), which were introduced in the late 1970-ies. This is the first study to disucss about these hypotheses and historical records were analyzed and compared with recent data. For this, primary production and biomass, zooplankton abundance, nutrients and physico-chemical variables were measured on a monthly basis from October 2007 to October 2008 at two stations. The results indicated that pH and total alkalinity have remained within the same range during the last half a century; however, electrical conductivity has shown a gradual increase over the last 5 decades. The overall mean actual concentration of dissolved inorganic nitrogen was 305 μg L^{-1}, with ammonium being the prominent species. Similarly, soluble reactive phosphorus was 22 μg L^{-1}, total phosphorus 58 μg L^{-1} and Si 3.7 mg L^{-1}, the latter shows higher concentrations than previous reports of 2.4 mg L^{-1}. In the 1940-ies only diatoms were reported; algal groups and taxa numbers in the present study have increased. Out of 40 phytoplankton taxa identified, chlorophytes and diatoms together contributed 77% to the overall taxa number, and Canonical Correspondence Analysis (CCA) indicated that the former were coincided with nutrients and rainfall, and the latter with silica and zooplankton. An overall mean phytoplankton biomass of 1.10 mm^3 L^{-1}, mean Chlorophyll *a* (Chl *a*) of 12.9 mg m^{-3} and gross primary production of 7.12 g O$_2$ m^{-2} d^{-1} gave Lake Hayq an intermediate position compared to other tropical lakes. Principal Component Analysis (PCA) followed by regression analysis indicated that Chl *a* was influenced by rainfall, temperature and light supply. Lake Hayq is categorized as eutrophic condition after employing various limnological productivity indices. However, the first hypothesis ascribed to eutrophication, high nutrient: volume ratio, is unlikely true since the nutrient concentrations (SRP 96 μg L^{-1} and NH$_4$-N 300 μg L^{-1}) were very high when the lake was reported as oligotrophic in the previous investigations. Hence, we support the second hypothesis that the stocked planktivorous fish was most probably the major cause for the trophic change of the lake. Hence, we support the second hypothesis that the stocked planktivorous fish was most probably the major cause for the trophic change of the lake.

Similarly, the change in zooplankton composition including the disappearance of cladocerans, were also related to the stocked Tilapia fish. To address this hypothesis, we determined zooplankton composition, abundance and biomass on short-time intervals, between October 2007 and January 2009, and the underlying limnological variables were also considered. The dominant zooplankton species were *Mesocyclops aequatorialis*, *Thermocyclops ethiopiensis*, *Ceriodaphnia reticulata*, *Daphnia magna*, *Diaphanosoma excisum* and the common rotifers *Euchlanis parva*, *Keratella tropica* and *Polyarthra sp.*. Total mean standing biomass of crustacean zooplankton was 237 mg dry mass m^{-3}, which gave Lake Hayq an intermediate position when compared with other tropical lakes. Of copepods, *Thermocyclops ethiopiensis* was almost an exclusive species, reaching a maximum value of 469 Indl L^{-1} and a mean of 92 Indl L^{-1}. This numerical abundance is somewhat in agreement with other authors who reported a maximum value of 577 Indl L^{-1} for cyclopoid copepod. CCA indicated that the temporal variation of *Thermocyclops* was influenced by food supply and water temperature. We refute the hypothesis that Tilapia was the cause for the seasonal disappearance of cladocerans, and attribute it to the adverse effect of episodic mixing. However, the planktivorous fish plays a key role in structuring

the cladocerans in particular the large-sized *Daphnia magna*. In January 2008, we observed a massive planktivorous fish mortality that triggered high algal biomass, which was later grazed by larger-sized *Daphnia magna* demonstrating the cascading trophic interactions hypothesis in a natural ecosystem.

We further generated a mass-balance model to figure out the pelagic food web structure and trophic interactions of the major functional groups of Lake Hayq. Moreover, the study lay down a baseline data for future ecosystem-based investigations and management activities. Extensive data collection have been taken place between Oct. 2007 and May 2009, and a number of parameters are system-specific. Ecotrophic efficiency (EE) of several functional groups including phytoplankton (0.8) and detritus (0.85) was high indicating the utilization of the groups within the system. However, the EE of *Mesocyclops* (0.03) and *Thermocyclops* (0.3) was very low implying these resources were rather a 'sink' in the trophic hierarchy. Flows based on aggregated trophic level *sensu* Lindeman revealed the importance of both phytoplankton and detritus to higher trophic levels. The computed average transfer efficiency of 11.5% for the first four trophic levels was within the range for highly efficient African lakes. The primary production to respiration (P/R) ratio (1.05) of Lake Hayq indicates the maturity of the ecosystem. We also modelled the food-web by excluding Tilapia and reduced phytoplankton biomass to get insight into the mass balance before Tilapia was introduced. The analysis resulted in a lower system omnivory index (SOI) (0.016) and P/R ratio (0.13) that described the lake as an immature ecosystem, suggesting the introduction of Tilapia might have contributed to the maturity of the lake. Tilapia in Lake Hayq filled an ecological empty niche of pelagic planktivore, and contributed for the better transfer efficiency observed from primary production to fish yield.

Of Ethiopian rift-valley lakes, the comparatively well-studied Lake Awasa was chosen to assess the long-term effect of antropogenic and natural impacts on plankton communities. Lake Awasa is located in the vicinity of the growing city receiving many potentially adverse effluents from factories and municipal sewage apparently with little treatment. Moreover, there are high levels of recreational activities and poor land-use management practices around the lake, and thus the lake system is exposed to intense human-induced pollution. Therefore, we studied phyto- and zooplankton communities between November 2003 to August 2004, and compared these data with historical data since the 1980-ies to assess potential inter-decadal changes. The phytoplankton taxa were similar with the previous study, except some species that are new findings to the system such as *Pediastrum simplex* with two subspecies and *Scenedesmus ecornis*. Phytoplankton abundance in 2003/04 comprised 54% Chlorophyta, 26% cyanoprokaryotes, 18% diatoms and 2% others, a proportion similar to previous records. However, the mean phytoplankton biomass in terms of Chlorophyll–*a* (19 μg L^{-1}) was lower than in previous studies. In contrast, the integral rate of gross photosynthesis of Lake Awasa has changed in the last two decades with higher values recorded at present (0.35 to 2.21 g O$_2$ m^{-2} h^{-1}). In a similar way, even though zooplankton community composition remained the same, the abundance and the dominant taxa differed in the last decades. The mean abundance of cyclopoid-copepods was 58 000 ± 9200 (SE) Indl m^{-3} and cladocerans abundance (2 600 ± 640 SE Indl m^{-3}) was low in the system in 2003/04. Interestingly, rotifers outnumbered other components with a maximum value of 263 670 Indl m^{-3}, which is about five-times greater than the previous reports.

The adult cyclopoid to nauplii ratio of 0.27 in the present study suggested that cannibalism has diminished at present probably due to high number of rotifers as prey, contradicting a previous hypothesis about high cannibalism in cyclopoids. Human impact is most likely as Lake Awasa is located nearby the fast growing town Awasa, where demographic pressure is high. The lake is used for fishing, and the commercially important *O. niloticus* is over-exploited (LFDP, 1998). The lake is also

used for bathing and washing clothes, domestic use and recreational purpose. Moreover, the lake is surrounded by agricultural land, hence anthropogenic influences are inevitable. Besides, it receives affluent from industries. Once the concentration of pollutants passes the threshold limit, it will bring irreversible damage to the ecosystem. So care and appropriate management should be taken before such ecological damage happen, which would affect not only the biodiversity but the economy as well.

Recommendations

The catchment land is cultivated intensively down to the lake shores with a variety of cereal crops including the indigenous cereal tef (*Eragrostis tef*), wheat, millet and maize, together with chickpeas, *Citrus* spp. and coffee (Darbyshire et al., 2003). The farmers use inorganic fertilizers (Urea and DAP) which ultimately reaches the lake. Furthermore, this lake is becoming one of the tourist destinations of the region and in a nutshell anthropogenic impact is intensified in the area. Hence:

- Appropriate sewerage system must be constructed.
- Catchment integrated research should be conducted in the future
- Afforestation on steep land of the catchment would be appropriate

Catch statistics data should be collected regularly in the future

Water birds, since they are one of the major functional groups of the lake, should be studied in detail including numerical abundance, biomass, mortality, feeding habit etc.

Benthic organisms (both animal and plant) should be studied in the future in detail to comprehend the contribution of these groups to the aquatic ecosystem and should be included in ecological model study.

The microbial loop needs further study in more detail, because it could be more important to the lake ecology in such deep and productive lake.

Ammonium is significantly higher than the other two forms of nitrogen (nitrate and nitrite), which demand further study to pin point the sources (internal or external) using stable isotope analysis, for instance.

The anthropogenic impact on Lake Awasa is very intense, and future intervention should include:
  ➢ Constructing sewerage system for the city.
  ➢ Appropriate treatment should be done before effluents are released from their respective factories.
  ➢ Awareness about the importance of the lake and the potential anthropogenic impact should be done urgently.

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Curriculum Vitae

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    Plankton communities and ecology of tropcial lakes Hayq and Awasa, Ethiopia
June 2005: MSc degree: Fisheries and Aquatic Sciences from Addis Ababa University
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    Trophic analysis of Lake Awassa using mass-balance Ecopath model
July 1999: I graduated with BSc degree from Awasa College of Agriculture, now Awasa
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Work Experience:
October 2005 – todate: Permanent staff of Addis Ababa University, Biology Department at lecturer
            position.

Duties and responsibilities
- Teaching and lab instructing for undergraduate classes
- Laboratory instructing and research follow-up of postgraduatestudents
- Prioritizing research problems and conducting research works

June 2000 - July 2005: Ethiopian Agricultural Research Organization (EARO) at Pawe Research
            Center as Researcher and Head of Animal Science Research Division.

Duties and responsibilities
- Identifying and analyzing research problems
- Prioritizing research problems based on National Strategy
- Preparing project document (s) according to the priority given
- Conducting research works considering the agro-ecology of mandate area
- Reporting and documenting research findings

Conferences and Training

- Aquatic ecosystem: processes and applications in IHE-UNISCO, the Netherlands
- Introduction to Geographical Information System (GIS) in Dar es Salaam, Tanzania
- The 6th European Conference on Ecological Modelling Trieste, Italy
- Training on Ecopath with Ecosim software model
- Diploma on Microsoft Application
- Certificate on Design and Analysis of experiments
- Certificate on biometrical methods and SPSS software package
- Certificate on Planning, Monitoring and Evaluation
- Scientific writing

Publications and unpublished documents

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Professional activities

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