KU LEUVEN

FACULTY OF SCIENCE

A comparison regarding the physico-chemical variables and zooplankton community characteristics of two Ethiopian Rift Valley Lakes: Lake Chamo and Lake Abaya

Arne DERIEMAECKER

Supervisor: Prof. L. De Meester

Co-supervisor: *P. Lemmens*

Mentor: *F. Eshetu Teferra*

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1 Introduction

1.1 The Geological history of the Ethiopian Rift Valley

1.1.1 The East African Rift System

The most extensive of all continental rift valleys are those of the East African Rift System, who started forming about 25 million years ago. This rift system takes place at an area where two events are happening at the same time: the African Plate is splitting up into two plates-to-be, and at the north of this diversion it is moving away from the Arabian plate. The two plates-to-be are being called the Nubian, which makes up the biggest part of Africa, and the Somalian plate. Their developing boundaries are extending from the Afar Depression up to Kenya, Tanzania and the Great Lakes region of Africa and have been raised more than 1000 m since the Miocene Era, and this gave the formation to two great rift valleys: The East African Rift Valley and the Ethiopian Rift Valley (Awulachew, 2006a; Wood and Guth, n.d.).

1.1.2 The Ethiopian Rift Valley

The Ethiopian Rift Valley is roughly northeast oriented. Most of the basin faults are oriented N-S and N40°E and at its margins the faults trend N30°E-N40°E (Boccaletti et al. 1998). This valley can be divided into three major rift zones with distinctive volcanic and tectonic features, from north to south: the Afar rift systems, the Main Ethiopian Rift and the broadly rifted zone of south western Ethiopia (WoldeGabriel, 2002). Our study domain lies in the second.

The seismically and volcanically active Main Ethiopian Rift runs northeast across the Ethiopian plateau, this Ethiopian plateau has less of the Proterozoic basement left because basalt eruptions covered most of it 31-29 Ma ago. The subsequent formed volcanic province was divided during the Miocene (23-5 Ma) by the Main Ethiopian Rift into the North Western and South Eastern Plateau. A slow-velocity mantle anomaly underlies the Main Ethiopian Rift at depths as shallow as 75 km or even less and the shallowest part of this anomaly is offset 25 km from the rift axis (Keranen & Klemperer, 2007; WoldeGabriel, 2002).

Based on geomorphology and geology the MER has been divided in three parts, namely the northern, central and southern sector. Lakes Abaya and Chamo are located in the last mentioned. This southern sector extends from Lake Awassa into the broadly rifted zone of Southern-Ethiopia. Faulting in this area was well-established around 18 Ma and volcanism began around 18-21 Ma. (Keranen & Klemperer, 2007) The sector is about 150-200km long and 30-65km wide. In this southern sector, unlike the other two sectors, pre- Tertiary crystalline basement rocks are exposed on the two rift-escarpments and the horsts. Red sandstone is overlaying these basement rocks in a packet from five up to ten meter. This red sandstone is of unknown deposition date and covers parts of the south sector and of the broadly rifted zone of south-western Ethiopia. The red sandstone is composed of well-sorted quartz arenite, mudstone and conglomerate layers. Also younger stratographic sections (early Eocene-Quaternairy) occur in the southern sector, and are formed by volcanic successions and eruptions, resulting into igneous rocks derived from basaltic flows (e.g. Amaro Basalt, Gamo Basalt, Nech Sar Basalt etc.), rocks composed of other volcanic products (vulcanoclastic deposits, Arba Minch Ignimbrite, Amaro tuff etc.) and stratographic sections due to erosional episodes, volcanic hiatus or both (WoldeGabriel, 2002).

All Ethiopian rift valley lakes (eight in total) were formed by water filling of the splits in the crust caused by the rifting, thus so did lakes Abaya and Chamo in the southern sector of the Main Ethiopian Rift (WoldeGabriel, 2002).

1.2 Hydrology and main characteristics of lakes Abaya and Chamo

The Abaya-Chamo drainage basin has a surface of 18599.8 km^2. It constitutes our two lakes, three medium rivers (Bilate, Gidabo and Gelana River) and a number of small and ephemeral rivers (Awulachew, 2007). Lakes Abaya and Chamo are separated by an approximately one km wide sill covered with swampy forests (Schütt, Thiemann, & Wenclawiack, 2005). The morphometric characteristics of Abaya and Chamo as they occur now are shown in Table 1.

Table 1: Morphometric characteristics of Lakes Abaya and Chamo (Awulachew, 2006), modified by Arne Deriemaecker

Parameter	Abaya	Chamo
Altitude (m)	1169	1110
Basin area, excluding lakes (km^2)	15219.62	1942.65
Lake area, including islands (km^2)	1108.9	328.63
maximum length (km) (L_{max})	79.2	33.5
Maximum width (km) perpendicular to L_{max}	27.1	15.5
Mean width (km)	14.13	10.1
Maximum depth (m)	24.5 (around the islands)	14.2 (near the middle)
Mean depth (m)	8.61	10.23
Shoreline (km)	268.78	108.1
Volume (m^3)	9.81×10^9	3.24×10^9

1.2.1 Hydrologic connectivity

Grove, Street and Goudie (1975) stated that 5000 years ago, or possibly earlier, Abaya, Chamo and Chewbahir were interconnected, and Chewbahir had an overflow into Lake Turkana. Lake Turkana and its basin lie in the zone between the Ethiopian Rift Valley to the north and the Kenyan Rift Valley to the south. In the early Holocene, coinciding with the African Humid Period (~12,000 and ~5000 BP), the lake-level of Turkana raised until it reached it highest point since the last glacial. This lake-level stabilized for a period from about 11,500 to about 8500 years BP, and during this period Lake Turkana exhibited a fluvial connectivity with the Nile basin (White Nile system) (Golubtsov & Habteselassie, 2010), which readily explains the similarities between the Abaya-Chamo Basin and the Nile (e.g. fish fauna).

At this moment lakes Abaya, Chamo and Chewbahir are connected via surface overflow (Awulachew, 2007). Water excess from Abaya enters Chamo through the Kulfo River (Awulachew, 2006). This Abaya water excess, entering the river, comes from a swampy depression at the south-western end of the lake (Golubtsov & Habteselassie, 2010). The swampy overflow is 300m wide and has a length of one km. The vertical extent of this barrier between the two lakes totals 65m (Schütt and Thieman, 2006**).** Last overflow of Abaya into Chamo dates from 1994 (eyewitnesses). Teklemariam (2005), however, states that overflow of Lake Abaya into Chamo stopped since December 1980. Before (1994), overflows regularly occurred during the rain seasons. The decrease in overflows is rather strange as Abaya's water levels are rising since 1987. And it can probably be explained by a higher deposition of sediments between both lakes. A large alluvial fan is deposited by the Kulfo River in the drainage zone between Lake Abaya and Lake Chamo. This alluvial fan exhibits a relict braided drainage pattern which indicates alternating drainage of the Kulfo River into both lakes. During flood events the river drains contemporary into both lakes. Runoff in all channels of the river show high concentration of suspended load, and high rates of soil erosion processes in the catchment are considered as the main cause. Deposition of sediment generally takes place in the floodplain between the Kulfo River and Lake Abaya, which is due to a low sediment carrying capacity of the river at this point. And this event eventually constructs a higher levee, making it harder for surface flow from Lake Abaya to reach Lake Chamo (Schütt & Thiemann, 2006).

When Chamo overflows, its water flows trough Metenafesha, joins the Sermale Stream and afterwards the Sagan River from where it finally ends up in Lake Chewbahir (Awulachew, 2006).

We conclude that the Lake Abaya - Lake Chamo system is endorheic, because in normal situation, without overflow that is, they lack an outflow to other water bodies (Blumberg and Schütt, 2004).

1.2.2 Lake Abaya

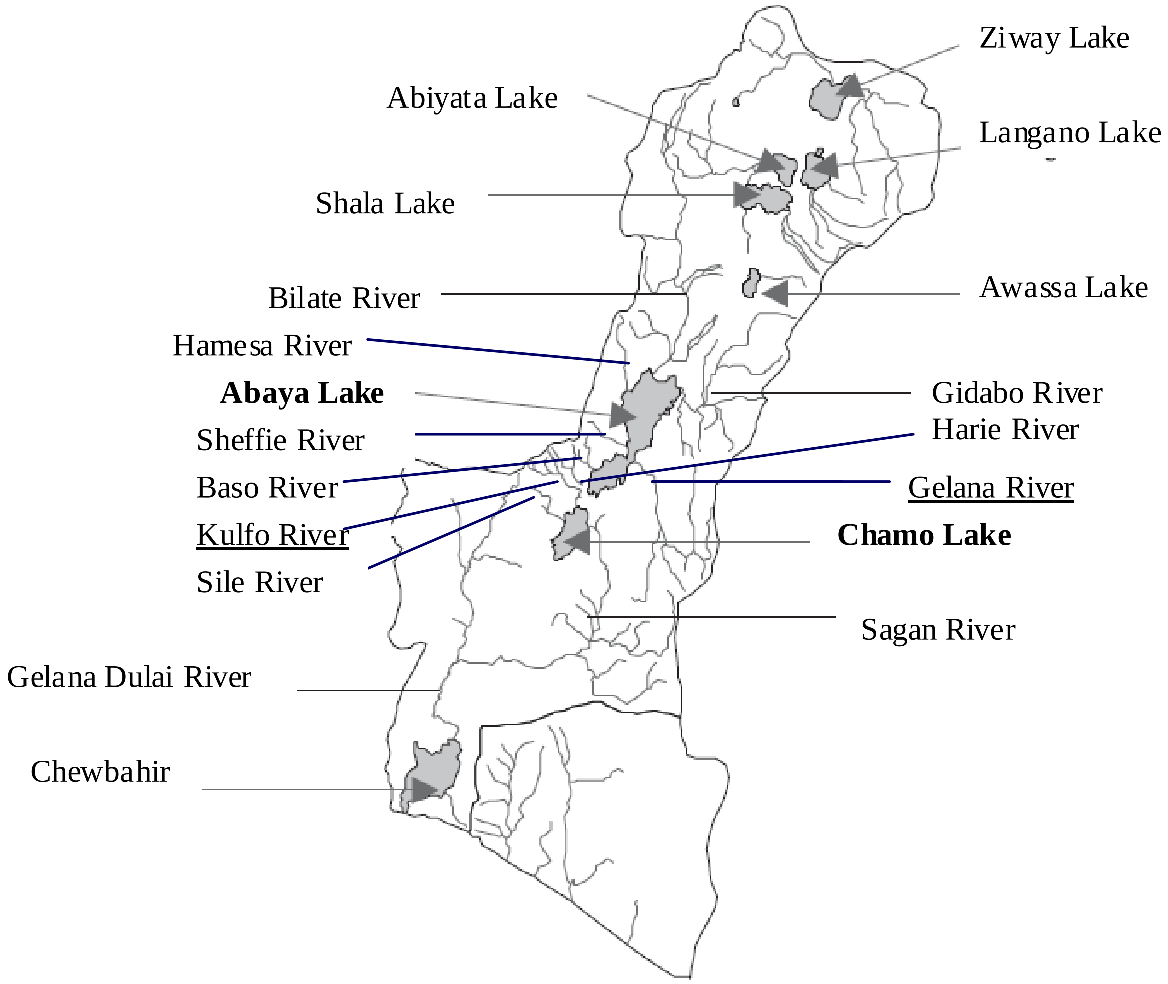
Lake Abaya (before: Lake Pagade or Margherita) is the largest lake in the ERV and can be included to the large lakes of the world (surface area > 500km^2). Lake Abaya's basin is composed out of a large northern sub-basin and a smaller southern sub-basin. The northern sub-basin has a maximum depth of 26m in comparison to the shallower southern sub-basin with a maximum depth of 14m. Both basins are connected with each other trough a bottle neck of about 8km wide, which possesses a maximum depth of 12m. Its water gains are dominated by surface water inflow, and water losses by surface water outflow and evaporation. (Abebe & Geheb, 2003; Awulachew 2007; Blumberg and Schütt, 2004; Golubtsov & Habteselassie, 2010; Grove, Street and Goudie, 1975; Kebede, Travi and Rozanski, 2009; Mackay, 2007; Shumbulo, 2005). This Lake is supplied by a major drainage system, the tributaries are the Bilate River from the north, the Gidabo and Gelana rivers from the east, and the Hare, Amessa and Basso rivers from the west (Fig. 1). The Bilate River its catchment area is the biggest of all Abaya's tributaries with 5224 km^2. The tributaries are the indirect cause of the reddish-brown colour of Abaya, they drain the volcanic slopes which are severely gullied and carry the silty to clayey soil sediments which give the lake its colour. (Ayenuw, 2004; Schütt, Thiemann & Wenclawiack, 2005; Grove, Street & Goudie, 1975). High sediment yields of the tributaries cause deposition of extended alluvial fans which evolve into deltas. These sediment yields are also the big contributors to the increasing water-levels of the lake since 1987, as discharge of the major tributaries decreased and the catchment annual precipitation did not vary significantly since 1987. The high yields are caused by soil erosion processes and this erosion's big contributors are changes in land-ownership, clearing of forest and bush-land as well as changes in cultivation (Schütt, Thiemann & Wenclawiack, 2005).

Seasonal stratification does not occur (Kebede, Travi and Rozanski, 2009; Blumberg and Schütt, 2004), as this is presumably caused by wind induced mixing, we can say this is most probably a shallow lake, so internal eutrophication might appear (De Meester, 2012).

1.2.3 Lake Chamo

Lake Chamo (before: Lake Ganjule or Ruspoli) is a clear blue lake receiving less sediment than Abaya (Golubtsov 2010; Grove, Street & Goudie, 1975). Water gains are dominated by surface water inflow, and water losses by evaporation (Kebede, Travi and Rozanski, 2009). As in Abaya, no seasonal stratifications occur (Kebede, Travi & Rozanski, 2009). All its tributaries drain the same mountains at the west, and the biggest one is the perennial Kulfo River, coming from the north (Fig. 1)**.** Lake Chamo is also fed by other, non perennial, rivers (e.g. Rivers Sile and Sego) (Golubtsov & Habteselassie, 2010; Shumbulo, ca 2005). The Kulfo River is a perennial river, but a lot of water is diverted for irrigation and mainly to the Arba Minch state farm, leaving the downstream without any water in dry season. Also the Sile River is used by a state-farm. (Teklemariam, 2005). Zinabu, Kebede and Desta, (2002) note, by personal observations and anecdotal information from the local people, that the Shoreline of Chamo receded by at least 1-2 km in the last 20 to 30 years.

Figure 1: Ethiopian Rift Valley Lakes including rivers surrounding Lake Abaya and Chamo (Awulachew, 2006; Teklemariam & Wenclawiac, 2004), modified by Arne Deriemaecker



1.3 Climate

The variation of rainfall regime, atmospheric temperature and evapotranspiration in Ethiopia shows a big coherence with the varying physiography and position of the Intertropical Convergence Zone (ITCZ)**.** This is a low pressure zone laying between the north-east Trade Winds bringing dry air from central Asia and the south-west Trade Winds bringing moist air from the Congo Basin. This zone might be the main contributor to the regional pattern of the seasonal rainfall distribution. The usually most cold and dry period in Ethiopia, November to February, coexists with the north-east Trade Winds. Other factors affecting the climate are topography, local convection currents, and air flow patterns over Africa (Tudorancea & Taylor 2002; Baxter, 2002**).**

The ERV climate exhibits a four month dry season from November until February and an eight month rainy season. However in the southern sector around Lakes Chamo and Abaya the rain follows another distribution, with two rainy seasons. The first rainy season occurs from April to May, with monthly rainfalls exceeding 140mm, and the second rainy season occurs from September until October with respectively total monthly rainfalls around 80mm and 110mm (Appendix 1A) (Abebe & Geheb, 2003; International Meteorological Station Region 63, 1974-2011). The rainfall pattern in 2012 was very similar (Appendix 1B). The annual rainfall in the drainage basin of lakes Abaya and Chamo is about 900mm, and the mean annual temperature at the two lakes is around 21.9°C (Tudorancea &Taylor 2002; Shumbulo & Assefa, ca. 2005).

Evapotranspiration is high in Ethiopia, in the southern sector of the ERV at lake Chewbahir (first lake to the south of our study site) extreme values exceeding 3000mm a year where obtained. This evapotranspiration in the ERV area exceeds the annual rainfall, which may cause water deficits in closed drainage basins (Tudorancea &Taylor 2002).

1.4 Water Quality Variables

1.4.1 Physical Variables

Temperature

Temperature gets influenced by latitude, altitude, season, time of the day, air circulation, cloud cover, flow, surface area, ground temperature, depth of the water body etc. It directly affects chemical, physical and biological processes. Chemical reactions increase with temperature and so does metabolic rate of organisms, it can even lie at the base of algal blooms. Increased temperature is also inversely correlated to the solubility of gases such as oxygen, carbon dioxide and nitrogen. (Deas & Orlob, 1999)

Light conditions

The intensity and spectral composition of light in aquatic systems changes greatly with depth. These changes arise from absorption and scattering of light by water and it's suspended and dissolved substances within. This underwater climate in lakes affects the temporal and spatial distributions of phytoplankton and submerged aquatic vegetation. (Zhang et al., 2012**)**

The measurement of Photosynthetically Active Radiation (PAR) is important as this is the range of the light spectrum used by plants (400-700 nm) (Alberta, 2006).

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Suspended solids and turbidity

"Suspended solids" refer to the mass or concentration of inorganic and organic (e.g. phytoplankton) matter which are held in the water column of a stream, river, lake or reservoir by turbulence. They are typically comprised of fine particulate matter with a diameter of less than 62 µm." However, transport of these solids frequently occurs in the form of larger aggregated flocks (Bilotta & Brazier, 2008).

Suspended solids occur in all natural waters but enhanced concentrations can lead to chemical, physical and biological alterations of the water body.

Physical changes include infilling of channels and reservoirs (if deposited), reduced penetration of light and induced temperature changes (e.g. reflection of the light). Associated with these alterations higher costs of water treatment, decreased longevity of the water body, deteriorated navigability and undesirable aesthetic effects occur.

Under chemical changes, we have alterations due to adsorption sites on the sediments. The sites can adsorb and release contaminants (e.g. heavy metals and pesticides) and nutrients (e.g. phosphorous). **S**ediments with high organic content may also deplete dissolved oxygen levels in the water. These sediments undergo anaerobic breakdown when they settle, and their breakdown products can react with dissolved oxygen. In low flow conditions this can produce critical oxygen shortage leading to fish kills.

Biological alterations include alterations in primary producers, aquatic invertebrates, and fish. And changes in these groups obviously influence each other (see further). Impacts on the primary producers are primarily caused by the reduction in light penetration, here it has to be considered that some primary producers prevailing at the surface (e.g. some cyanobacteria) are less affected. Effects on aquatic invertebrates include clogging of feeding structures, and abrasion, scouring and dislodgement in flows. Fish can be influenced directly by suspended sediments. Their delicate gill structures can get clogged or the fish can get stressed which suppresses their immunity system. Suspended solids deposition can also leads to smothering of fish eggs in gravel beds and even natural migration patterns of fish can be distorted.

It has to be noticed that not only concentration is the key factor affecting aquatic biota, also the duration of exposure, the chemical composition and the particle-distribution is. (Ryan, 1991; Bilotta & Brazier, 2008)

<u>Turbidity</u> is a measurement for the light scattering properties of water. It is often used as a surrogate for the Total Suspended Solids (TSS), but, turbidity measures not only concentration of suspended solids, it also gets influenced by size and structure of the matter, presence of phytoplankton and the presence of dissolved humic and mineral substances. That is why Bilotta and Brazier (2008) suggest turbidity records should always be checked and calibrated against TSS, building a rating relationship between the two variables. Lakes with a high input of nutrients often become turbid due to biogenic particles, including blooming phytoplankton, and this is most prominent in shallow lakes, in which a mechanism of internal eutrophication is operative by resuspension of their sediments (De Meester, 2012).

Turbidity fluctuation is high for Lake Chamo, and is related to rainfall. It quickly recedes during drier periods (Ugo, 2008; Teklemariam, 2005). Ugo (2008) also notices that turbidity in Chamo is more related to abiogenic factors then it is to algal biomass, however its biogenic turbidity is higher than Abaya’s. In the long term Lake Chamo is becoming more turbid as Secchi depth is declining since the 1980s (Ugo, 2008) In Lake Abaya, turbidity fluctuations are limited, staying above the levels of Lake Chamo for most of the dry season. Abaya has probably a very high ferric colloid suspension, as it has a Fe concentration of 5000 $\mu g.l^{-1}$, while the average of freshwater is around 50 $\mu g.l^{-1}$, and it is found that the turbidity in lake Langano is mainly caused by ferric colloid, while this lakes’ concentration ($550 \mu g.l^{-1}$) is much lower than Abaya’s (Taylor, Kebede & Zinabu, 2002). Turbidity peaks are different in both lakes and this could be due to the different periods of precipitation of Abaya’s different catchments (Teklemariam, 2005).

1.4.2 Non-nutrient chemical variables

Dissolved oxygen

Dissolved oxygen is oxygen gas (O_2) dissolved in water. It is one of the most important gases in water as sufficient concentrations are critical to the survival of most aquatic plants and animals. It is necessary for cell respiration and influences cycling of redox-sensitive elements as nitrogen. Oxygen is a key parameter when assessing the suitability of surface waters to support aquatic life. Oxygen solubility is a function of water-temperature, salinity and atmospheric pressure.

Dissolved oxygen levels should approach saturation for the maintenance of aquatic health. The freshwater saturation level at sea level is about 14.6 mg/l at 0°C and 8.2 mg/l at 25°C. But turbulence, photosynthetic activity, decaying of organic material and other oxygen demands also influence the concentration making the level generally below saturation. Function and survival of biological communities may already be adversely affected by concentrations below 5 mg/l and dead of most fish can occur at concentrations below 2mg/l. (Deas & Orlob, 1999; Helm, Jalukse & Leito, 2012)

Because of photosynthesis (e.g. phytoplankton) and respiration, precaution has to be taken while sampling, because O_2 and CO_2 make wide diurnal swings. This contributes to maximum pH and DO late in the afternoon and minimum values just before dawn (Deas & Orlob, 1999; Helm, Jalukse & Leito, 2012).

Oxygen may distribute a similar stratification as the horizontal temperature distribution in the lake. This temperature may have a superficial stratification in calm weather, which is probably diurnal, breaking down overnight and reforming in the course of the day. Longer lasting climatic cycle stratification has already been reported in Lake Turkana and Awassa, inflow of cold rainwater can be a cause in the latter lake (Baxter, 2002)

Ugo (2008) noted that dissolved oxygen in Lake Chamo is consistent over his study period from March to May, and that enough oxygen is available for biota. Teklemariam (2005), however, noticed a dissolved oxygen drop (in summer) below $3mg.l^{-1}$ in Lake Chamo. This condition occurred contemporary with a loss of soluble reactive phosphorus and an increase in the ammonia concentration.

pH

pH measures the hydrogen ion content of a water body ($-\log [H^+]$), and determines weather it is acidic (pH<7) or basic (pH>7). It's controlled by dissolved chemical compounds and biochemical processes. In unpolluted natural waters pH is controlled by the carbonate system (carbon dioxide, carbonate and bicarbonate), but industrial effluents, atmospheric depositions, and respiration can effect it. Ammonia, nitrate and toxicity of metals can be strongly affected by changes in pH. pH ranges from 6 to 9 occur in typical surface waters. (Deas & Orlob, 1999)

Most fish exhibit an average blood pH of 7.4, and since this blood comes in close contact with water they may become stressed and die if pH drops below five or rises above ten (Wurts & Durborow, 1992).

Due to tertiary and quaternary basaltic formations and the subsequent dominance of the calcium-magnesium-bicarbonate contents of the rivers, the alkalinity and pH of these lakes are normally high, but well buffered. There is a gradual and slight increase of the pH towards the end of the dry season and a decrease as the rainy season progresses. Changes are minimal in both lakes, but slightly higher in lake Chamo (Teklemariam, 2005; Ugo, 2008).

Total dissolved solids, Salinity and Conductivity

Specific chemical composition of lakes' water depend on the geology, lake's existence time, the volume and composition of the inflow, the rate of evaporation and the retention time of the water within. In general highest concentrations are found in closed basin lakes **(**Baxter, 2002).

Total Dissolved Solids (TDS) is the measurement of dissolved inorganic salts, organic matter and other dissolved materials in water.

Salinity refers to the amount of dissolved salts present in water. Changes in salinity can affect microbes, plants, invertebrates and vertebrates. The whole community structure can change through loss of sensitive species, and this lowers biodiversity or replaces freshwater species by salt tolerant ones. In plants it can inhibit germination, and diminish seedling survival and growth. Salinity can disturb the internal ionic balance of macro invertebrates and fish, causing most damage to their eggs and larval stages (Muschal, 2006).

Conductivity is the measure of water being able to conduct electric current. It is related to dissolved solids. It is affected by the degree in which dissolved solids dissociate into ions, the amount of electrical charge on each ion, ion mobility and the water temperature. Most waters range from 10 to 1000 $\mu S.cm^{-1}$. In polluted waters or waters receiving large quantities of land runoff the maximum value may be exceeded (Deas & Orlob, 1999).

Toxicity can be caused by an increase in salinity, changes in ionic composition and toxicity of individual ions. Composition change can cause shift in biotic communities, excluding some species wile promoting population growth of others. The order of toxicity from individual regularly occurring ions on biota is found to be $K^+ > HCO3^- = Mg^{2+} > Cl^- > SO4^{2-}$, while Ca^{2+} and Na^+ did not seem to cause any significant forms of toxicity (Weber-Scannell and Duffy, 2007).

Both Abaya and Chamo are alkaline, saline lakes with dominant ions of sodium, bicarbonate and chloride. Abaya has maintained it salinity levels over the last 40 years, but over recent years it has increased in a moderate rate. Due to drought, decrease in inflow, the rivers increasingly saline water quality, and increasing influence of evapotranspiration Lake Chamo possesses higher ion concentrations and increased its salinity levels 40% in the past 40 years (linear trend) (Teklemariam & Wenclawiak, 2004; Teklemariam, 2005; Zinabu, Kebede-Westhead and Desta, 2002). Ugo (2008) states that the TDS level is safe for it's freshwater organisms in Chamo, but that the lake's salinity showed concerns in terms of individual ion toxicity as there was found a general increase in major ion concentration.

1.4.3 Nutrient variables

Nutrients

Some elements are essential for life processes in aquatic organisms and are called nutrients. The nutrients phosphorus and nitrogen are usually critical for algal growth, and only their dissolved forms are directly available for this growth, and include ammonium, ammonia, nitrate, nitrite and orthophosphate (Deas & Orlob, 1999).

Nitrogen

Ammonium (NH_4^+) comes from the process called ammonification which transforms organic nitrogen to ammonium. This organic nitrogen comes from animal wastes and proteins remaining in bodies of dead animals and plants. The ammonification itself derives from processes as hydrolyses and biodegradation. Biodegradation is caused by bacteria under aerobic and anaerobic conditions. Ammonium is in equilibrium with the unionized ammonia (NH_3) and the relationship is pH dependent. At a pH above 9, elevated levels of ammonia can occur, which is the form toxic for fish. Levels of ammonium found in most natural waters are on the contrary innocuous. (Deas & Orlob, 1999).

Ammonium and ammonia released in excess of plant requirement will undergo nitrification which forms nitrite NO_2^- and nitrate NO_3^-, this by autotrophic bacteria called respectively the Nitrosomas and the Nitrobacter group. This process, nitrification, consumes oxygen and can significantly deplete DO in aquatic systems. Nitrification is a fast process, and high levels of ammonium and ammonia are normally indicative of a recent nearby source or high rates of decomposition in the absence of oxygen. Nitrates also serve as plant fertilizers and don not show high affinity with soils, which make them mobile in irrigation water for instance (Deas & Orlob, 1999).

Loss of nitrate and nitrite can occur through denitrification in anaerobic conditions (e.g. NO_3^- as electron acceptor). The nitrates can get reduced all the way to ammonium but most bacterially mediated reactions produces nitrogen gas, which can result in los of nitrogen to the atmosphere.

During photosynthetic growth of algae, algae assimilate and take up inorganic nitrogen, with a preference given to ammonium and ammonia over the oxidized forms.

Atmospheric nitrogen can be utilized through nitrogen fixation by certain nirtrogen-fixing algae and photosynthetic bacteria (e.g. blue-green algae), and this is, with some exceptions, a primarily light dependent process. This fixation is an important external nitrogen input and can affect nitrogen dynamics. In waters with high nitrogen content this fixation is suppressed, but this not always occur as N_2 diffuses more rapidly then the dissolved forms. In waters with high phosphorous loads, nitrogen levels can decline to the point where non-fixing algae will become nitrogen limited, giving nitrogen-fixing algae and bacteria a competitive advantage. This can lead to objectionable water quality characteristics as foam, toxicity and recreational hazard (Deas & Orlob, 1999).

Phosphorus

Phosphorus is important because it is usually in short supply relative to other macro-nutrients (e.g. carbon, oxygen, nitrogen). It has a low abundance in the earth's crust and a low solubility of its minerals. It also lacks atmospheric deposition, as it doesn't have a gaseous form. Furthermore, it sorbs strongly to fine-grained particles. The sedimentation of these particles together with organic particles containing phosphorus serve to remove phosphorus from the water body to its bottom's sediments, this way requiring anaerobic conditions and physical disturbance to bring the phosphorus back up again. Although this short supply, human activities can result in discharge of phosphorus to natural waters.

The only form of phosphorous that is readily available to most plants and microorganisms among inorganic phosphorus ($H_2PO_4^-$, HPO_4^{2-} and PO_4^{3-}) is orthophosphate (PO_4^{3-}). The percentage within the total phosphorus occurring as truly ionic orthophosphate is probably less than 5 percent in most natural waters while in nitrogen limited systems this may not even apply.

The phosphorus cycle starts with the organic phosphorus being available in animal waste and dead organic tissue. The organic phosphorus gets converted bacterially to orthophosphate without any oxygen demand of the system. The released PO_4^{3-} gets then incorporated into plant and animal tissue, where the cycle can start again

Generally a phosphate concentration of 0,01 mg/l will already support algal species. (Deas & Orlob, 1999).

Total P and total N

A good reason to use total nutrient concentrations is the fact that there are very short cycling times in aquatic systems, and also the nitrogen-phosphorus ratio can be measured with these total ratios. This ratio serves to know which one of the two nutrients is limiting to algal growth. Noting that algal cells contain 7-10 µg nitrogen and 0.5-2.0 µg phosphorus per µg chlorophyll-a, a rough N:P ratio can be formulated of 7:1, making nitrogen the limiting factor if the ratio is smaller than 7 en making P the limiting one if the ratio exceeds 7 (Deas & Orlob, 1999).

Nutrients in lakes Abaya and Chamo

Overall the inorganic nutrient concentration of lakes Abaya and Chamo is increasing, except for soluble reactive phosphorous in lake Chamo (Teklemariam & Wenclawiac, 2004). However, Ugo (2008) found a big increase of the latter nutrient in his recent study and proposes this could be attributed to intensification of fertilizer use and parallel clearance of vegetation infringing the lake's shore. Concentrations in Abaya and Chamo of Nitrite are always much lower than those of Nitrate and ammonium, as they usually are in African lakes (Shumbulo, ca. 2005).

According to seasonality, nitrate and nitrite levels in lake Chamo are higher in rainy periods than in dry. Overall seasonal changes were higher for Lake Chamo, this due to the flow reduction and decrease in water level, this seasonality may affect the lakes' ecology. In accordance with the nutrient and chlorophyll a data, both lakes can be classified under eutrophic lakes (Ugo, 2008; Teklemariam, 2005).

1.5 Trophic interactions in lakes

As all heterotrophs consume organic matter which directly or indirectly originates from autotrophs, one can construct a simple food-chain with the primary producers at the base followed by herbivores which, in turn, are preyed upon by predators. These trophic levels influence each others abundance and species composition. If a trophic level has a high production there will be more food for the higher trophic level which, if not negatively influenced by biota and the environment, will also get a higher productivity. This is called a bottom-up effect because the trophic level is influenced by its sources, these sources can also be abiotic (e.g. nutrients & light). A high predation or grazing pressure will contrariwise cause a lower abundance of prey/vegetation, and this higher up influence on a trophic level is called a top-down effect. A trophic level can also have an impact on more than one higher level, or in the opposite case, on more than one lower level, the latter is than called a trophic cascade.

Certain problems can be solved by investigating whether the trophic level is top-down or bottom-up controlled. If there are, for instance, problems with algal blooms, they can then be bottom-up controlled by lowering nutrient input or top-down by bringing in a predator that preys upon zooplanktivorous fish (De Meester, 2012). This top-down control works with a trophic cascade: as the predation towards zooplankton gets less, they increase in abundance, which subsequently increases zooplankton grazing pressure on phytoplankton. In turn, this phytoplankton will decline in abundance.

1.6 Phytoplankton

Algae are relatively simple photo-autotrophic organisms that do not belong to the Embryophyta. We will specifically focus on the planktonic intra-group called phytoplankton, which is the main primary producer of the pelagic water habitat of lakes (De Meester, 2012).

1.6.1 Community composition

Key factors

The community composition is structured by key factors that are important in regulating growth of phytoplankton species. A first key factor is 'light requirement'. Some species grade up their competitiveness by adjusting to light levels by changing the amount of pigments in their cells. Others prove to be better adapted by being able to use other wavelength arrays of the light spectrum (e.g. Cyanobateria cf. chlorophyta). As most light occurs at the surface (photic zone), buoyancy is also important to get enough light. This buoyancy can be achieved by the prevalence of flagella, a higher surface to volume ratio, mucilaginous sheaths (e.g. nearly all Cyanobactaria), accumulation of fats, or the presence of gas-vacuoles. The latter seems to be very efficient in Cyanobateria making some even flow on water, counteracting all shading-effects.

Another key-factor is 'temperature' as some species for instance have higher growth optima at higher temperatures (e.g. Cyanobateria).

A third key-factor is 'nutrient requirement' because the efficiency in which species can accumulate nutrients is very important in determining competitive outcome. Small spherical and motile cells are most efficient in capturing nutrients, but this morph has lower buoyancy and is highly susceptible for predation. This trade off between nutrient uptake and grazing resistance is a strong driver in shaping phytoplankton communities, for in oligotrophic lakes small motile spherical cells dominate whereas eutrophic lakes are often dominated by very large and often filamentous forms, because predation and not resources are the main problem in the latter. Although Cyanobateria have a mucilaginous sheath they exhibit a high competitive strength in highly eutrophic lakes. This is due to the ability of several species to fix nitrogen, which gives them an advantage in lakes where nitrogen instead of phosphorous tends to be the limiting factor. It should be noted that in the tropics N-limitation probably occurs more frequently than in the temperate zone.

A fourth key-factor is 'biotic interactions' as for instance competition for the same sources or grazing and predation. Some algal species even excrete inhibitory products that inhibit the growth of other species (i.e. allelopathy). This gives them more space and light, and can sometimes explain seasonal succession in natural phytoplankton communities. This phytoplankton allelopathy can also be targeted to macrophytes, bacteria and even zooplankton. Yet, allelopathy from other groups towards algae also occurs (e.g. macrophytes). Grazing by bacteria (e.g. amoeba), parasitism (e.g. chytrid fungi) and facilitation (e.g. excretions) are influential biotic interactions but lay outside the perspectives of this study (De Meester, 2012). Grazing by zooplankton, however, will be discussed.

Zooplankton grazing

Grazing of zooplankton is also an important biotic interaction, as it can shape communities and control seasonal patterns. Highly selective grazing zooplankton (cf. calanoid-copepodans) will promote algal species that are toxic or exhibit low nutritional quality. Largely unselective zooplankton (cf. cladocerans) will only tend to promote fast-growing algal species. Also body size distribution of the zooplankton (cf. cladocerans) community can have strong effects on the size distribution of phytoplankton. Presence of high densities of small or intermediate-sized cladocerans will often provoke a phytoplankton community dominated by relatively large algae (e.g. the colonial green algae *Pediastrum*). Change to larger cladocerans (e.g. D. magna) may consequently provoke the dominance of even larger species or the dominance of toxic species. In addition, the grazing pressure is very important, whereas a moderate grazing pressure of zooplankton promotes fast-growing species, high grazing pressure will eventually promote the development of inedible species. This inedibility is achieved by algal defence mechanisms as the production of thick cell walls (protection against digestion and biting forces (e.g. diatoms)), an increase in body-size, (counteracting size dependent grazing (e.g. colonial formation, increase in spine length)) and the production of toxins (depression of feeding activity and population growth in zooplankton). Another defence mechanism from phytoplankton towards zooplankton is the delay of their exystment when grazing pressure is high (De Meester, 2012).

Cyanobateria and flagellates

Cyanobacteria prevail in most ERV and tropic lakes. This may be ascribed to their resistance to grazing by zooplankton (cf. colonial or filamentous morphs, toxins), their capacity to fix nitrogen (heterocysts), relatively low light requirements (cf. additional pigments) and relatively high temperature optima. Most of the Ethiopian and tropic lakes lack an appreciable flagellate population which is contrary to temperate lakes. This may be attributed to the frequent mixing of their water columns, since flagellates are better adapted to stable water conditions (Taylor, Kebede & Zinabu, 2002; De Meester, 2012).

Community structure in Lakes Abaya and Chamo

In both Chamo and Abaya the highest species richness occurred in green algae, Cyanobacteria and diatoms (Taylor, Kebede & Zinabu, 2002 & Shumbulo, 2004**).** The biggest contributors to biomass in Lake Chamo are Cyanobacteria, whereas in Lake Abaya green algae and flagellates prevail. The Cyanobacterian *Microcystis aeruginosa* and the diatom *Melosira granulat* have been found dominant and persistent in Lake Chamo. The competitive advantage of *M. aeruginosa* is perhaps related to its buoyancy and colonial formation and to the high concentrations of Ammonium-nitrogen occurring during the study (non N-fixing Cyanobateria). *Melosira granulat* is rather fast sinking but its good adaptation to low light conditions is favourable in turbulent water conditions. Chamo Green algae populations were dominated by *Scenedesmus* and *Pediastrum* species. (Shumbulo, 2004)

1.6.2 Biomass and productivity

The classical seasonal algal succession of dimictic temperate lakes does not occur in tropic regions. On the one hand, total phytoplankton biomass and productivity are often both larger and more constant seasonally (cf. year-round high temperatures). On the other hand, numerous episodic changes in the annual phytoplankton succession and productivity may occur due to the abrupt changes in abiotic factors caused by wind-induced vertical mixing, and seasonality in rainfall with its associated nutrient loading and turbidity. In general, overall phytoplankton biomass in the tropics is often highest in the colder season. This contrasts with temperate lakes in which biomass is relatively low at winter. Changes in biomass during the year will normally not exceed a factor of five in the tropics while in temperate zones, it can be in the order of a thousand-fold.

The vertical distribution of phytoplankton productivity is often correlated with eutrophication, as in oligotrophic lakes the phytoplankton biomass is often in relative deep water in contrast with eutrophic lakes where the competition for light is higher because of the more particulate organic matter, biotic or abiotic. Also diurnal variations may occur as a reaction against predation and a search for nutrients. Zooplankton tends to hunt at the surface at night, and nutrients can be more abundant in the deeper parts (e.g. dimictic lakes) resulting in a migration to the surface at day and a migration to the bottom at night (e.g. flagellates). Horizontal distributions in big lakes are often associated with higher biomass and productivity closer to the littoral zone, mainly due to the near littoral higher nutrient load. In very large lakes the difference in productivity may vary several-fold. Other reasons for horizontal distribution include: basin morphometry, depth, extension of the littoral zone, variation in surface runoff, river inflow or wind induced aggregation of phytoplankton. (De Meester, 2012).

Biomass and productivity in Lakes Chamo and Abaya

Lake Abaya (except after bloom) is among the two lowest biomass containing lakes of the ERV fresh water lakes, while the eutrophic Lake Chamo is among the two highest**.** The high turbidity (e.g. high colloidal silt suspension) in Abaya may explain this low phytoplankton biomass (Taylor, Kebede & Zinabu, 2002).

According to Shumbulo (2004) chlorophyll-a concentrations in Lake Chamo have temporal changes over the year, only obviously correlated to total nitrogen, suggesting a N-limitation. The biomass of Chamo seems to be maintained to a larger extent by nutrient regeneration or turnover than by allochthonous nutrient input, which is facilitated by the high temperature and the wind-induced mixing (Tilahun & Ahlgren, 2010).

Spatial variation of phytoplankton biomass is absent (Shumbulo, 2004**)** in Lake Chamo,. this phenomenon appears to be related to the similar levels of nutrients and underwater light and temperature conditions throughout the lake. Presumably this results from the frequently horizontal mixing of the water body, and the macrophytes at the inflow of the river who may act as a nutrient filter moderating the seasonal input of nutrients in the lake.

Net photosynthetic activity in Lake Chamo is as biomass correlated with nitrogen containing nutrients but also with silicate. Minimum rates were associated with low levels of PAR. Highest photosynthetic capacity ($gC.m^{-2\cdot}d^{-1}$) was associated with low phytoplankton biomass, an inverse correlation often encountered worldwide (Shumbulo, 2004). Tilahun & Ahlgren (2010) note this could be explained by qualitative differences in algal populations. The eutrophic Lake Chamo has comparable production rates per day (annual average of 1–3$gCm^{-2}d^{-1}$) as other eutrophic temperate and tropical lakes (Tilahun & Ahlgren, 2010).

The high primary productivity of Lake Chamo is not or only to a small degree connected to the wet and dry season. Shumbulo (2004) again suggests this could be due to the buffering of nutrients by the extensive vegetation. Tilahnun & Ahlgren (2010) however, find a decline in primary productivity at optimum depth throughout the year (not seasonal), and address this phenomena to species composition, whereas in the beginning of the year diatoms are the dominant sp. and at the end Euglenoid *Lepocinclis sp.* prevail (Shumbulo, 2004; Tilahun & Ahlgren, 2010).

In the long-term, chlorophyll a values have shown an increase for Lake Chamo, while Lake Abaya has a more or less similar measurement (Teklemariam, 2004).

1.6.3 Algal blooms

Some phytoplankton species can form dense planktonic populations or “blooms” when they reside in optimal conditions. These blooms can be very harmful as some produce their own toxins. Furthermore, they can also provoke extreme variations in O_2-levels between day and night causing dead of aerobic organisms. High amounts of dead algal material may sink to the bottom resulting in an extreme O_2 usage by nitrifying bacteria, depleting oxygen even more. The anaerobic conditions can give the opportunity for anaerobic pathogenic bacteria to thrive (e.g. *Clostridium botulium*).

Although Elizabeth and Willén (1988) report fish kill due to algal blooming is a common event on Lake Chamo (Agriculture Bureau and African Parks, Ethiopia, 2007), not much specific information can be found when or where this fish kills have taken place. Amha and wood (1982), however, report a bloom in 1978 with *M. aeruginos* as dominant contributor, causing the dead of 75 zebras and an unusually high fish kill. In Lake Chamo at least three species of *Microcystis* have genes for toxin production: *Microcystis aeruginosa, M. botrys* and *M. panniformes*. *Cylindrospermopsis raciborski* also occurs and is known to contain toxin producing strains. (Shumbulo, 2004; Willen et al., 2011).

1.7 Zooplankton

Zooplankton, or truly planktonic animals are dominated by four major groups: one unicellular group of protozoans, and three multicellular groups including the rotifers and two crustacean taxa (cladocerans and copepods). We will focus on the main contributors to the mesozooplankton group (200µm – 2mm), namely the copepodans and cladocerans as they are the main contributors to zooplankton productivity and the main grazers of phytoplankton in the pelagic (De Meester, 2012).

1.7.1 Cladocera

Cladocerans range from 0.2 – 11 mm and reproduce with a cyclical parthenogenesis. When environmental conditions become unfavourable they get in the sexual phase, producing males, and subsequently sexual eggs. These eggs are dormant and can withstand a wide range of disturbances, which is important for overlapping unfavourable conditions and colonization of new habitats. Juveniles look like small adults and go trough four to five molts before they become sexual mature. Adults keep growing, in laboratories more than 20 adult instars can occur, and they can live for 60 days at 20°C. In each adult instar, a number of eggs are deposited in the brood patch, the eggs develop into embryos in about 2-3 days, and the juveniles are released when the mother molts. The cladoceran *Daphnia magna* for example can release more than 1000 offspring per individual, which in favourable conditions all will be females. As a result *Daphnia* populations can grow very fast, and will very soon, in the absence of predators, reach carrying capacity of the environment. In eutrophic habitats without predation, densities of several hundreds of *Daphnia* per litre can be observed. This has a result that Daphnia populations can have a strong impact on phytoplankton populations and efficiently control phytoplankton blooms. In most natural habitats however cladoceran mortality due to predation is high and only juveniles and young adults (first few adult instars) are found. Most planktonic cladocerans are filter feeders which feed mainly on algae, protozoa, bacteria and detrital particles. Depending on species, pelagial cladocerans filter particles ranging in size from < 1 µm to 70 µm, whereas the lower limit is depending on their filter combs, and upper limit is largely dependent upon mouth-size. Many littoral species have modified filtering structures used to scrape of periphyton that are growing on substrates (e.g. Chydoridae), and some species are carnivores feeding on rotifers and small crustacean zooplankton (e.g. Leptodora) (De Meester, 2012).

1.7.2 Copepoda

Copepodans contain three Suborders of free-living animals. The first ones are the Harpacticoida which are almost exclusively littoral, scraping particles from sediments and vegetation. The second group consists of the Cyclopoida who are almost primarily littoral species, but they can be important in shallow lakes where they can dominate the zooplankton. Last group called ‘Calanoida’, are almost exclusively planktonic and are mainly specialized herbivores. Overall their importance declines with increasing eutrophication. All three former suborders are in comparison to cladocerans capable in picking out their food after judging its quality (Rieper, 1982, Rao & Kumar, 2001; De Meester, 2012). This is made possible by specialized appendages containing mechano-and chemoreceptors. Cladocerans in contrary, filter all particles of a given size range from the water and can only actively refuse a particle if it is too large or if a toxic substance is detected. If this happens all food that was collected will be removed at that specific moment by their post abdomen. Copepods first antennae are important organs, as they act as mechanoreceptors but are also used for jumping behavior (e.g. escape responses in the presence of predators). They can not, unlike cladocerans, form real images, but can differentiate between changes in light intensity by means of their ocellus. They are obligatory sexual, and some species can go in dormancy during a particular stage in their development (e.g. dormant egg or copepodid stage) to survive harsh conditions. In temperate zones cyclopoid copepods often go in diapause during winter months, probably to escape fish predation, and in many zooplankton communities of shallow lakes communities are dominated by copepods during winter months and by cladocerans during summer. Their life cycle involves six naulpiar stages and six copepodid stages, and maturity is only reached at the last stage. The time required to become adult is species specific and depends upon environmental conditions. Overall intrinsic rate of increase is lower than that of cladocerans, but since copepods are selective feeders, carrying capacities may under specific circumstances be higher, for example, when a large proportion of organic particles are not of sufficient quality as food (De Meester, 2012).

1.7.3 Predation on zooplankton

There are many predators feeding on zooplankton. They include vertebrates (e.g. fish, amphibian larvae and some bird species) as well as invertebrates. These invertebrates include omnivorous cyclopoid copepods, predatory calanoid copepods, aquatic insects and their larval stages, medusae, flatworms and water mites. The vertebrates and invertebrates both have their own size selectivity (De Meester, 2012). In temperate waters, both fish and invertebrates predators are important, but in permanent water bodies in the tropics, fishes are in general more important as predators (Sarma, Nandini & Gulati, 2005).

Negative size selectivity by invertebrates

Most invertebrates prefer to prey on small sized zooplankton, this because they are size limited themselves (more easy to handle small prey). Overall their mouth are too small (i.e. gape-limited) to consume the smaller zooplankton. Large-bodied zooplankton also suffers from invertebrates as they still lose considerable amounts of juveniles. However, this only occurs in a limited part of their life (one or two instars).

Against the negative size selectivity zooplankton can form swarms, or they have to become larger. This can be done by increasing their body-size or by the development of long thorns.

Seasonal changes in abundance are less easily predicted for invertebrate predators than for fish, and differ widely between taxa.

A number of invertebrate predators form an exception and prefer large bodied zooplankton (e.g. the backswimmer *Notonecta* and large beetles). *Notonecta* also rely on visual cues and exert similar selective forces on the zooplankton as predation by fish (De Meester, 2012).

Positive-size selectivity by vertebrates

Because most vertebrate predators hunt visually they look for conspicuous prey, and automatically select for large and/or pigmented prey. In this way they are considered *‘positive size-selective’* predators. Except those who are gape-limited, as is the case for fish- and amphibian-larvae younger than one or two months (most fish only a few weeks).

Planktivorous fish can be very numerous in freshwater ecosystems and can be highly selective. This may cause a big impact on zooplankton, affecting its density and community-structure. All planktivorous fish catch particles with their gill rakers. These have a mesh size as close as one mm, and all larger particles (e.g. zooplankton) are retained and eaten. Two different kinds of planktivorous fish exist, the particle-feeding and the filter-feeding fish. The first select particles by sight and swallow them while the latter are no visual hunters and filter everything by swimming around. Particle feeders will select the biggest prey while filter feeders eat all zooplankton above a certain mesh size. This makes particle feeders more efficient, but only when light intensities are high enough (visual hunters), high zooplankton densities also even out this advantage. There are a lot of fish with other feeding modes (e.g. pisci-, insecti- and benthivorous) but most young fish are particle feeders, even the juveniles of filter feeders. In addition most pisci- and benthivorous fish are planktivorous when young. Pelagic species are often dominated by planktivorous and piscivorous fish (De Meester, 2012).

Seasonality

In temperate lakes seasonality plays a strong role as fish are ectothermic animals, resulting in low activity if it’s cold (in winter they hardly eat at all). A second influencing factor is the large number of first year juveniles in summer, who are known to be veracious planktonic feeders as they are actively growing. As a result, in many lakes, young-of-the-year fish are more important predators on zooplankton than adult fish. This seasonality in the temperate zone often causes a zooplankton community shift to a smaller body size towards the summer.

In the tropics seasonality is less determined by temperature and overall fish predation-pressure is higher, because it occurs year-round. But changes in fish abundance occur and are often correlated with water levels or water quality (rainy season/dry season). In the high-water period water gets enriched as it flows over the floodplain area (rivers and lakes), with a resulting higher productivity of the system. Fish may produce their young as a consequence and expend rapidly, also building up fat-reserves for the subsequent dry period (De Meester, 2012).

Fish predation and zooplankton community structure

The impact of size-selective predation by fish on zooplankton community structure is proven by many studies. In most of these studies effects were observed on the size distribution within zooplankton species as well as on the relative abundance of large- and small bodied species. Within species, there was a reduction in the frequency of adults compared to juveniles, a reduction in the average adult size (e.g. less molts can occur), and a reduction in average size at maturity (i.e. smaller instar-body sizes), often accompanied by a reduction in average brood size. Among species there was a shift from large taxa (*Daphnia*, calanoids) to smaller taxa (e.g. *Ceriodaphnia* & cyclopoids). In case of strong fish predation pressure, the zooplankton community can be completely dominated by very small taxa as Bosmina and rotifers (De Meester, 2012).

Reduction of vulnerability to fish predation

Less vulnerability to visual predators (e.g. fish) can be obtained by becoming smaller (reduction in size), becoming more transparent (less pigments), engaging in diel vertical migrations (hiding in strata with low light intensity) and the formation of swarms. But these behavioral and morphological adaptations are often trade-offs. The reduction in body size makes them more susceptible for macro-invertebrates, and large bodied zooplankton are in general better competitors (see further). The major reason for zooplankton-pigmentation is protection to phototoxic effects from UVB and high light intensities (De Meester, 2012).

Outcomes of size-selectivity predation by invertebrates and fish

Three main situations occur on size-selectivity in lakes and ponds with different abundances of fish and invertebrates. The first takes place in fishless lakes where predation by invertebrates results in large-bodied herbivorous zooplankton. However, the superiority of large-bodied zooplankton over small-bodied may also be due to competitive superiority (see further). The second situation takes place in lakes with a moderate density of planktivorous fish, due to the presence of piscivorous fish, and a moderate density of invertebrate predators due to the predation of the planktivorous fish. Because of the density-reductions of both invertebrate predators and planktivorous fish, there is a moderate positive- and moderate negative-size selectivity on the zooplankton, which results in a zooplankton community dominated by medium-sized individuals. The third situation involves lakes with a high density of planktivorous fish, because piscivorous fish can not control their population. The high density of planktivorous fish completely eliminates invertebrate zooplankton predators, leaving only a positive size-selectivity of the fish. This lack of negative-size selectivity results in a high relative abundance of small zooplankton.

Another effect due to size selectivity of fish and macro-invertebrates is the evolution of zooplankton into small species (cf. large-body selectivity) that are artificially enlarged with transparent spines (cf. small-body selectivity). This makes them less edible for the small invertebrates while they are still less vulnerable to visual predation of the fish. In some cases the spines can make them also less edible for fish. This occurs in the tropical cladoceran *Daphnia lumholtzi* where its long tail and spiny helmet can hurt fish (De Meester, 2012).

1.7.4 Size-efficiency hypothesis

In fishless water-bodies, zooplankton tends to be dominated by large bodied species. Except for the presence of invertebrates and their negative-size selectivity, there is also a tendency of large-bodied zooplankton being a better competitor than small-bodied zooplankton. This has led to the size-efficiency hypothesis. The hypothesis is more pronounced in cladocerans than in copepods because copepods are selective in food collection which enables them to reduce the overlap in food resources with other species. This is not the case in non-selective filter-feeders. First reason for the better competition of large-bodied- over small-bodied zooplankton is the more efficient energy conversion of large-bodied species. They need less food (e.g. mg C/l) to contain their population size. Secondly, large zooplankton individuals have a higher starvation resistance. This makes them better adapted to food concentration fluctuations, for instance in environments with a high grazing pressure and a high competition between zooplankton species. Thirdly, large bodied species have a broader particle-range they can use as food (at least within the cladocerans). Finally, cladocerans seem to negatively affect small rotifer species by interference competition and even predation. The little rotifer species can be swept into the filtering chamber of the cladocerans, and may get damaged (interference competition) or even ingested. Although some caution has to be taken, as above mentioned generalizations do not hold between all species (De Meester, 2012).

1.7.5 Abundance of zooplankton in the ERVL

In general, zooplankton biomass in Ethiopian lakes is low compared to phytoplankton biomass, one might even expect much of the primary production to enter the decomposer pathway without passing through zooplankton. The most important food-fish in Ethiopia (i.e. Nile Tilapia) may contribute to this phenomenon. However Tilapia is herbivorous, they are known to exert higher clearance rates on zooplankton than on algae. When Nile tilapia was introduced to the Ethiopian highland Lake Hayq, larger zooplankton was eliminated and phytoplankton biomass increased (Taylor, 2002). Therefore it may be possible that abundant Nile Tilapia and the lack of effective predators contribute to the low biomass and small sized zooplankton. Low zooplankton- to phytoplankton biomass is also common in New Zealand lakes, and there it is ascribed to nitrogen limitation and the poly- or monomictic nature of these lakes resulting in persistent populations of grazing-resistant algae. This type of community, comparable to late summer communities in temperate lakes, may be a feature of the “endless summer” situation in African lakes (Taylor, 2002).

1.7.6 Spatial distribution of zooplankton

Vertical distribution

Some species have very specific vertical distributions in a lake and remain there all time (e.g. certain rotifer species). Others show vertical migration to reduce predation as the main reason. This is however a trade-off between predation on one side and food and temperature at the other, because the upper part of the lake often has a higher temperature (higher growth rates) and contains more food (phytoplankton in the photic zone) than the bottom part.

“Nocturnal migration” is the most abundant type of diel vertical migration. In this type the animals reside deeper in the water column during the day than during the night, doing so to prevent the visual hunters during daylight. Less common is the pattern of “reverse migration”, where animals reside deeper in the water column during night. This is to prevent zooplanktonic invertebrate predation who often express nocturnal migrations. Another reason is the avoidance of competition with the nocturnal migrators, that is why small-bodied zooplankton, who are less preyed upon by positive-size selective predators, often express reverse migration (e.g. rotifers). Nocturnal migration is often correlated with body-size, as zooplankton with a smaller body-size will suffer less from visual predation. This occurs between species (small species versus big), but also within. In copepods for instance, the nauplia often show no vertical migration while the copepodids do so.

These vertical migrations can except from being important to predator prey interactions also contribute to large scale consequences as primary and secondary productivity of lakes. Because of the absence of the zooplankton in the surface layers during the day, phytoplankton can grow to higher densities. Diel vertical migrations can therefore promote algal blooms (De Meester, 2012).

Horizontal distribution and migration

The horizontal distribution of zooplankton is often not homogenous. Heterogenity can be obtained trough a habitat preference of the animals (e.g. littoral or pelagic), the action of wind-induced currents, basin morphology of the lake and swarming. Diel horizontal migrations are also quite common, however they are less studied. Many zooplankton species form swarms during the day (often in the littoral) to reduce predation by fish, and they spread out to feed during the night.

Spreading out is a good defense mechanism (also in vertical migration) against all kinds of predators, it reduces the chance that a prey individual ‘bumps into’ a predator (De Meester, 2012).

1.7.7 Phytoplankton affecting zooplankton

Next to effects of zooplankton on phytoplankton (already mentioned), the opposite effects also exist. Increasing densities of phytoplankton (e.g. high-water period) will favour zooplankton species with highest intrinsic rate of increase. Another effect of phytoplankton is that large bodied-cladocerans are more vulnerable to the presence of cyanobacteria than small-bodied species. This is because they are capable of ingesting cyanobacterian filaments which may lead to intoxication. However, cyanobacteria mostly produce toxins only when they occur in high densities. As a result zooplankton populations often can not control blooms. (De Meester, 2012).

1.7.8 Diversity of zooplankton

Irrespective to latitude +50 species of cladocerans can be expected in an average lake, and this depends largely on the presence and the extent of a vegetated littoral zone. Because of the high fish predation (see further) *Daphnia sp.* are not common in the tropics and are largely replaced by the faster (cf. strong second antennae) and smaller *Diaphanosoma sp.* But when fish predation is not to high *Daphnia* will replace *Diapohanosoma* again, as they are better competitors in many circumstances.

Most plants and animals have a bigger diversity in the tropics but for zooplankton this gives mixed results.

Most zooplankton species are not cosmopolitan, contrasting to the statements of a lot of popular zooplankton guides, and as a result species identification in formerly less studied regions is far from easy (De Meester, 2012).

Dominance of small zooplankton in the tropics

In tropic lakes a dominance of small zooplankton occurs, and this could be due to the higher and more constant temperatures which cause fish to continuously recruit and forage. But also the community structure is different in the tropics (vs. temperate lakes), with more species and functional groups, and often a dominance of omnivores and detrivores. All this results in a more permanent and intensive predation by fish on primary consumers (e.g. zooplankton and algivorous macro-invertebrates), characterized by a large-bodied selectivity. (De Meester, 2012). Other reasons argued for the small body size, instead of higher predation, are direct temperature effects. The upper thermal tolerance of large, typically temperate, cladocerans (ca. 30° C) is often exceeded in (sub)tropical lakes (Iglesias et al. 2011)

Diversity of zooplankton in lakes Chamo and Abaya

Zooplankton fauna in Ethiopia is a mixture of species found throughout tropical Africa with a representation of Palaearctic species, this reflects the moderating effect of altitude on the tropic climate. The Ethiopian fresh water lakes are dominated by small forms although *Daphnia* are present in some lakes, and Calanoids are not abundant at all. Cyclopodids often dominate the crustacean zooplankton in terms of biomass, numbers and species. In Chamo zooplankton is mainly composed of copepods (*Mesocyclops sp., Thermocyclops sp., Eucyclops sp.*), rotifers (e.g. *Branchinous angularis*) and cladocerans (*Moina, Ceriodaphnia and Daphnia*). On species level (Lake Chamo) *Dapnnia magna* and *Moina micrura* were already determined (Shumbulo, 2004; Zone agriculture Bureau and African Parks, Ethiopia, 2007).

1.7.9 Influence of the fish community on zooplankton in lakes Chamo and Abaya

Because fish has a high impact on the zooplankton community we will take a closer look to the fish community structure in both lakes. Lakes Chamo and Abaya have respectively 18 and 20 species, together they hold a total of 21 species, and these are all native to the lakes. This Chamo-Abaya-basin is the most diverse of all basins in the Ethiopian Rift Valley and this is due to the former connection with the Omo-Turkana basin. The vast majority is from Nilo-Sudan origin and there are also some elements of the East-African ichthyofauna. During 1990-2010 intensive development of fisheries in Lakes Chamo and Abaya has driven local populations of commercial fishes (e.g. Mormyrus cashive, Labeo horie and Lates niloticus) to the verge of extinction (Golubtsov & Habteselassie, 2010).

The fish community in Lake Chamo is probably more balanced than in other ERV lakes, this caused by an occurrence of an appropriate mixture of fish species of different size classes. The occurrence of large piscivorous fish diminishes the population of smaller zooplanktivorous fish and allows great abundance of zooplankton.

The distribution patterns of zooplankton-consuming fish may limit diel zooplankton migration, as they occur all over the lake. For instance, zooplanktivorous Nile perch juveniles prefer shallow depths (littoral), *Hydrocynus forskahlii* juveniles (zooplanktivorous) are found in the pelagic of Abaya, and the omnivorous *Synodontis schall* is found in all parts of lake Abaya (but also in Chamo, (own findings)). Latter species also consumes zooplankton, there were copepods found in the stomach content in Lake Turkana and in Chamo, and it is a highly abundant species in both lakes. In experimental trawl catches (1984) on Lake Abaya, half of the total haul where *S. Schall*, in weight and in number, and in experimental and commercial gillnet catches in Lake Chamo they almost reach two thirds by number of individuals (Froese & Pauly, 2013; Golubtsov, Dgebuadze & Mina, 2002).

1.8 The clear-water and turbid-water equilibria of shallow lakes

Shallow lakes can over a broad range of nutrient concentrations occur in two alternative equilibrium conditions: a clear-water state and a turbid water state.

clear water state

This state is characterized by a low turbidity (biotic or abiotic), presence of macrophytes, a healthy piscivorous fish population, a relative (to the turbid state) low density of piscivorous fish, large-bodied and abundant zooplankton, and absence of phytoplankton blooms.

Feedback loops stabilize this system. Macrophytes play a major role here, as they provide a hunting-ground for a lot of piscivorous fish reducing omnivorous and planktivorous fish populations. Macrophytes also offer a shelter for large zooplankton (hiding for planktivorous fish) and compete with algae for light and nutrients (e.g. allelopathy). Finally macrophytes also stabilize the sediments so that wind action has less pronounced effects on nutrient recycling, which can be strong in shallow lakes (De Meester, 2012).

Turbid water state

This state is characterized by having the opposite characters mentioned for the clear water state, and it is also stabilized by various feed-back loops. The absence of macrophytes may decrease piscivorous fish species that rely on them for their hunting strategies. This results in an increase in plankti- and benthivorous fish. The planktivores contribute to higher zooplankton consumption and a shift to small-bodied zooplankton. The benthivorous fish stir up sediment which directly affects turbidity and nutrient load and may prevent germination of macrophytes. Small-sized zooplankton is a less efficient phytoplankton grazer than large-bodied zooplankton, the relatively low grazing and the high productivity of the system result in phytoplankton blooms. As blooming occurs light extinction is very strong, limiting successful germination of macrophytes (De Meester, 2012).

Nutrient range

At very low nutrient ranges only the clear-water state can occur, as nutrients are the limiting factor for phytoplankton blooms to occur. On the other side of the range, at very high nutrient concentration, only the turbid state will occur. This is due to the fact that phytoplankton outcompetes macrophytes in the struggle for light. Whereas algae can aggregate near the surface of the water to obtain light, macrophytes have to start growing from the bottom. Second, if there is to much light limitation, germinating macrophytes will soon die. And third, the macrophytes also suffer from dense periphyton (algae and bacteria) populations growing on their stems and leaves, which give them a reduction in photosynthetic efficiency.

The two alternative equilibria conditions can occur in lakes of intermediate nutrient level, and they are stabilized by the feed-back loops. External influences are necessary to change between states (De Meester, 2012).

Shifts towards the turbid state

Recent years, a lot of lakes have shifted to the turbid state which is the least preferable one. Cause in clear-water lakes with a rich aquatic vegetation and a healthy fish community, biodiversity is higher. Turbid lakes are also less economically profitable for many reasons. Phytoplankton blooms interfere with drinking water (bad taste and/or odour, toxicity) and its processing (e.g. clogging of sand-filters used to purify the water). Turbid waters are not preferred as swimming waters (recreation and tourism), and although the fish biomass is often higher, it is dominated by a few species that are often not appreciated by people as food, because they have a mud taste or are to small (De Meester, 2012).

1.9 Research question

This master thesis is part of a larger research project (PhD research of Fassil Teffera) that aims to fill the gaps in knowledge on the ecology of the major Ethiopian Rift Valley Lakes Abaya and Chamo. The overall aim of this research is to provide guidelines for sustainable management of these valuable ecosystems. This research aims to broaden the knowledge of the ecology, food web structure and water quality of these lakes. This master thesis essentially comprises a first explorative study on the ecology of both lakes and focuses in the first place on current differences in physicochemical variables and zooplankton community characteristics between lake Chamo and lake Abaya. Secondly, we investigate more in detail the spatial differences in physico-chemical variables and the spatial distribution of zooplankton communities within each lake. Finally, we aim to explore changes in major environmental variables of both lakes throughout recent decades by comparing our data with data from literature.

2 MATERIAL AND METHODS

2.1 Sample Collection

A transect line was drawn in both lakes between a major river inflow (Gelana and the Kulfo River) and the location where the lakes have their outflow at high water levels. Samples from each lake were collected at eight sampling stations (Fig. 2) and a distinction between "littoral", "pelagic" and "pelagic deep" locations were made. Two of the littoral stations were taken on the transect line at the inflow “Lake Littoral inflow one and two” (LLI1, LLI2) and the other two at the outflow (LLO1 and LLO2). From the four pelagic stations, three were taken on the transect line “Lake Pelagic one two and three” (LP1, LP2 and LP3), and one was taken (as close to the transect line as possible) at the deepest area of the lake “Lake Pelagic Deep” (LPD) (Fig. 2). Both lakes’ transects and exact locations are given in Appendix 2A and B.

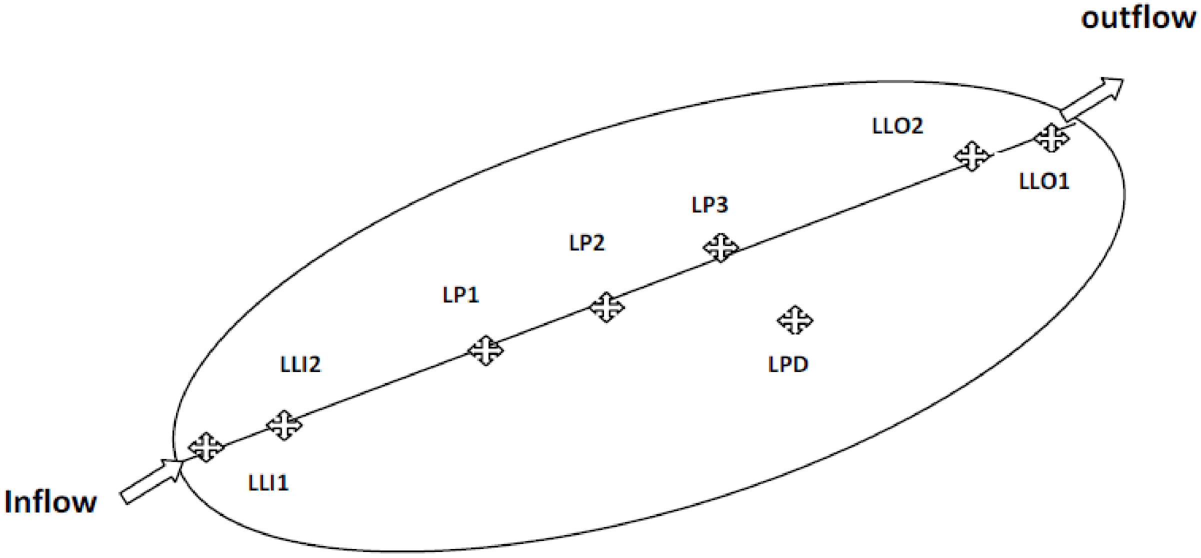


Figure 2: Sample station transect for both lakes, “L” = littoral, “P”= pelagic, “D” = deep “I”= inflow and “O” = outflow, different numbers denote different stations.

We sampled in both lakes at the end of the second dry season (second half of August - beginning of September). Temperature, turbidity, dissolved oxygen, pH, total dissolved solids (TDS), salinity, conductivity and chlorophyll-a concentrations were measured on the lake, at all sample stations at the surface (first 0.5m), the middle and the bottom of the water column, We also took depth integrated samples from these parameters, by mixing the water samples from different depth (Surface middle and bottom of the water column). Euphotic depth and Secchi depth were measured at all sample stations in both lakes, except for Secchi depth in Lake Abaya, were measurements were taken at the lake’s shore. Nutrient concentrations (available and total nitrogen and phosphorus) and total suspended solids were measured in the lab from depth integrated water samples within 24 hours after sampling.

Lake water was collected at specific depths by using a SEBA Van Dorn type water sampler. The depths were measured with a SEBA Hydrometrie (digital Multiparameterprobe MPS-D). Temperature, dissolved oxygen, pH, TDS, salinity, conductivity and turbidity, were measured with a HQ40D digital multi probes meter, Secchi depth, and euphotic depth respectively with a Secchi disc, and a LI-250A Light Meter. Chlorophyll-a concentrations and turbidity were measured in the field with a handheld fluorometer (AquaFluor™). The concentrations of total suspended solids in both lakes were determined gravimetrically by filtering a known volume of lake water on a GFF filter (Whatman). Nutrient concentrations (NO_3^-, NH_4^+ and PO_4^{3-}) were determined with a Portable Photometer 7100, and total nitrogen and phosphorous were measured with a Technicon Auto analyzer II (Technicon, Tarrytown, New York, USA) after alkaline persulphate digestion (Koroleff, 1970).

Five sediment samples per station were taken with a core sampler in both lakes at the upper 10 cm of the sediment. These 5 sediment samples were homogenized and analysed per station. Organic matter and carbonate content from the mixed sediments of each station were obtained by loss on ignition. This was performed by heating the samples in an oven at respectively 105°C (overnight), 550°C (four hours) and 950°C (two hours) and weighing them in between. The methods and calculations were obtained by the standard operating procedure of Rosenmeier and Abbott (2005).

Phytoplankton productivity was determined using in situ stable isotope ^{13}C addition experiments (Bouillon, Gillikin, & Connolly, 2012; Hama et al., 1983; Pimenov et al., 2008). The sample analysis were carried out using Stable Isotope Mass Spectrometry in K.U. Leuven, Faculty of Bioscience Engineering, Department of Earth & Environmental Sciences. Primary productivity was eventually calculated from obtained measurements via Dauchez, Legendre & Fortier (1995). Phytoplankton productivity measures in analyses are calculated per sample station, per µg Chl-a (µmol Carbon.h^{-1}.µg Chl-a^{-1}).

We sampled the zooplankton community from all sample stations in both lakes. Additionally, we took samples from the zooplankton community at three locations in the vegetation. The upper 2 meter of the water column was sampled by using a tube sampler and filtering 48 liter of lake water through a conical plankton net (mesh size 64 µm), while zooplankton at larger water depths was sampled by intervals of two meters up to the sediment of the lake by using a Schindler-Patalas sampler (64µm). Samples were preserved with formalin (4%)

Cladocerans were identified up to species level, copepods to suborder level and cyclopoids to genus level, using a microscope and zooplankton identification keys (Flössner, 2000; Korinek, 2000; Boxshall & Halsey, 2004) Zooplankton was counted and identified using a binocular (90x). At least 300 adult individual cladocerans and 300 individual copepods (copepod nauplii excluded) were counted from every sample to reduce the chance of missing any species, while counting these numbers also rotifers and copepod nauplii were counted. We measured minimum 10 randomly chosen individuals from each cladoceran species (out of the 300 individuals) and from every copepod suborder (out of 300 adult and copepodite copepodans) per sample. We note here that we not always found 10 individuals per sample per cladoceran species. Zooplankton body size was measured using calibrated binoculars. Data on zooplankton biomass were obtained by conversion from body size and abundance by using the equation $W = \alpha L^{\beta}$, (W = dry weight (µg), L= length (mm), α and β = conversion factors). Conversion factors were obtained from Azevedo and Dias (2012), McCaully (1971) and Watkins, Rudstam and Holeck (2001) (see table 2).

Table 2: Biomass conversion factors, the conversion factors of the taxa in the column under cf. were used to transform our taxa (left column).

Taxa	cf.	system	α	β
Ceriodaphnia cornuta	*Ceriodaphnia cornuta*	Azevedo and Dias (2012)	3.935	2.000
Daphnia barbata	*Daphnia sp.*	Watkins et al. (2001)	4.341	2.830
Moina mongolica	*Moina sp.*	Watkins et al. (2001)	12.962	3.340
Diaphanosoma australiensis	*Diaphanosoma sp.*	Watkins et al. (2001)	5.073	3.050
Daphnia magna	*D. magna*	McCaully (1971)	6.214	2.785
Macrothrix spinosa	*Macrothrix squamosa*	Azevedo and Dias (2012)	17.288	3.177
Ceriodaphnia laticaudata	*Ceriodaphnia sp.*	Watkins et al. (2001)	12.962	3.340
Cyclopoid copepodid	*Cyclopoid copepodid*	Watkins et al. (2001)	7.050	2.400
Calanoida	*Calanoida copepodid*	Azevedo and Dias (2012)	11.822	3.150
Leydigia	*Cladocera*	Azevedo and Dias (2012)	5.762	2.653

2.2 Long term data collection

We tried to find all long term data of all our sampled parameters, and these can be consulted in Appendix 4A, B and C. Only the average measurements, found in literature, were used, except for conductivity in Lake Abaya, here we also used a maximum range value of Lofredo & Malderra in 1938 (no average values given). From own data, only pelagic surface data are used (except for nutrient data (pelagic depth integrated) and Abaya Secchi depth (shore)), as most of the older measurements found in literature were taken at offshore stations at the top of the water column. The Conductivity data from all literature and our own values were corrected to conductivity at 25°C, this was done by using a temperature coefficient of 2.3% per °C (Tailing & Talling, 1965). Salinity data from old literature was measured as total major ion concentration (Na^+, K^+, Ca^{2+}, Mg^{2+},Cl^-,SO_4^{2-},HCO_3^- & CO_3^{2-}), since we did not do these kind of measurements, we had to convert our conductivity data to salinity data with a factor used for Ethiopian lakes made by Zinabu, Chapman & Chapman (2002). We highlight here that in further research conductivity data should always be multiplied with this factor, because widely used conversion factors are not high enough for Ethiopian lakes, as these lakes are bicarbonate/carbonate dominated.

2.3 Analyses

Environmental variables analyses

A Redundancy Analysis (RDA) was used to test for differences in major environmental variables between both lakes. The significance of this test was evaluated with Monte Carlo permutations (999 permutations under reduced model). We used Principal Component Analysis (PCA) to visualize patterns of environmental differentiation between both lakes, we applied logarithmic transformations on all variables, with the exception of pH, prior to these analyses

One-way ANOVA analyses were used to explore the differences in specific environmental variables between both lakes more in detail. For all analyses, surface samples were used, except for temperature and for total suspended solids and nutrients which only have depth integrated measurements. If assumptions for One-way ANOVA's were not fulfilled, we performed data transformations (i.e. log(x+1) and √(x)) and if assumptions could still not be met, we applied non parametric Kruskal-Wallis ANOVA analyses.

Univariate analyses (One-way or Kruskal-Wallis) were also used to analyse differences in important environmental variables between different sample locations along the horizontal transect within both lakes (from inflow to outflow). Analyses were only performed when at least three measurements within each zone were available.

Environmental characteristics were also analysed along the depth profile (surface, middle, and bottom) in pelagic sample plots using Repeated measurements ANOVA tests. If assumptions could not be met after transformation, Friedman ANOVA was used. We also analysed the depth profile of one pelagic station (CPD) of Lake Chamo, a linear regressions was taken of every meter until 10 meter deep. If assumptions for linear regression were not fulfilled a spearman correlation test was implemented.

Long term analyses

With long term data from literature, linear regressions were made to find changes in time. These analyses were only performed if at least three data points in time were available. If the assumptions of linear regression were not fulfilled, we performed logarithmic data transformations (log(variable+1), if assumptions could not be met after these transformations, we used a Spearman's rank correlation.

Zooplankton analyses

We investigated the distribution of zooplankton across the horizontal transect between and within both lakes. Within the lakes we looked for patterns in the horizontal transect, we did this by dividing the different sample stations into three major zones, namely the vegetated littoral (n=3), the littoral (n=4) and the pelagic zone (n=4). We used Redundancy analyses to test for differences in zooplankton abundance, relative abundance, biomass and relative biomass between both lakes and for zooplankton abundance and biomass differences between the three horizontal zones within each lake. As explanatory variables either lakes or the three subzones within each lake were used. The significance of this test was evaluated with Monte Carlo permutations (999 permutations under reduced model). PCA-plots were used to display the community differences between and within the Lakes. All data were logarithmic transformed prior to statistical analysis. We further used univariate analyses (One way ANOVA) to explore the found patterns (multivariate analyses) between and within the lakes more in detail. When the assumptions for these tests could not be met after data transformations (i.e. log(x+1) and $x^{0.5}$), Kruskal-Wallis ANOVA were used. These univariate analyses were also used to look for differences in cladoceran species richness and Shannon-Wiener diversity between and within both lakes.

The vertical zooplankton distribution within both lakes was investigated by using data from the pelagic sample stations (n = 4). We compared all depths (every two meter) with each other, only depths were used with data from minimum three different sample stations. RDA-analyses were used to test if there is a significant difference in zooplankton abundance or biomass over the pelagic water column, as explanatory variables we used the surface versus (0-2 meter) and the deep (2-10m). The RDA-test was analysed as above. PCA-plots were used to see community distributions in abundance or biomass over the pelagic depth profile.

Univariate analyses in depth were again used to explore the found patterns further in detail, but also to find patterns in zooplankton body-size, cladoceran richness and Shannon-Wiener diversity. For these analyses we used Repeated measures ANOVA. When the assumptions could not be met after data transformations (i.e. log(x+1) or $x^{0.5}$), Friedman ANOVA were implemented.

We further estimated the zooplankton grazing pressure on phytoplankton communities between both lakes (Kruskal-Wallis ANOVA), by taking the ratio zooplankton to phytoplankton biomass for every sample plot (Jeppesen, Jensen, and Søndergaard, 2002). For every sample plot, the depth integrated Chlorophyll-a data were taken and divided by the average zooplankton biomass of the total water-column.

3 RESULTS

3.1 Environmental characteristics of Lake Chamo and Abaya

3.1.1 Major environmental variable differences between both lakes

Redundance analyses (RDA) revealed a significant difference in major environmental variables between both lakes (Trace = 0.286, F-ratio = 5.602, P-value = 0.001). The first axis of the PCA-plot explains most of the variation (51.1%) in environmental variables and makes a clear distinction between Lake Chamo and Lake Abaya (Fig. 3). The sampling station CLI1 is an exception, as it is located closer to the cluster of Abaya stations. The second axis distinguishes the pelagic from the littoral sample stations. Lake Chamo is characterized by higher levels of salinity, conductivity, TDS, chlorophyll-a (Chl-a), phytoplankton productivity (PP), euphotic depth, pH, daytime oxygen concentrations ([O_2]day), and temperature, while Lake Abaya shows a positive association towards turbidity, total suspended solids (TSS), available nutrient concentrations (NH_4^+, NO_3^- and PO_4^{3-}), and organic matter content in the sediments. Total nutrient concentrations, (TN and TP) seem to be similar in both lakes, but available nutrient concentrations tend to be lower in Lake Chamo, especially for available nitrogen. It is remarkable that phytoplankton productivity is negatively associated with available nutrients, TSS, and turbidity, and positively associated with pH. The percentage of carbonates in the sediments is positively associated with depth, and subsequent with pelagic stations. Finally it is also remarkable that pelagic stations have lower concentrations of TN and TP compared to shallower sample locations nearby inflow and outflow of both lakes.

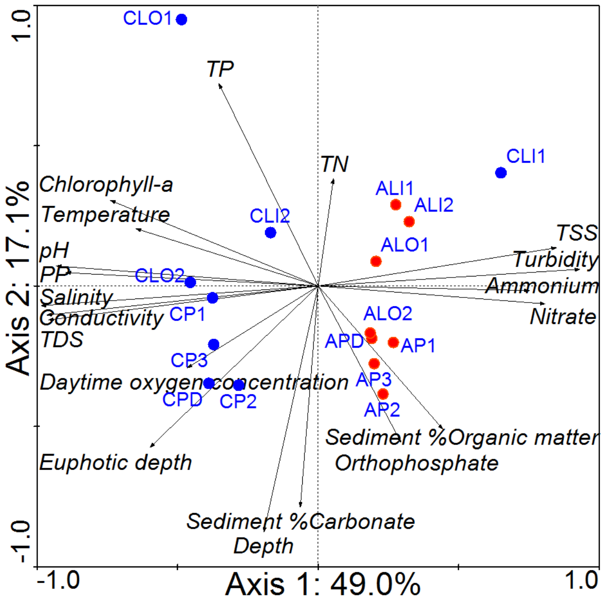


Figure 3: Biplot of a Principal Component Analysis (PCA) of the major environmental variables of lakes Chamo and Abaya (sample stations shown in blue and red respectively) are identified by a four-character code. “C”/ “A” = Chamo or Abaya, “L” = littoral, “P” = pelagic, “D” = deep “I” = inflow and “O” = outflow, different numbers denote different sampling stations. “PP” = Phytoplankton Productivity, “TDS”= Total Dissolved Solids.

Univariate analyses show that Chamo had a higher conductivity (Fig. 4G), higher TDS and a higher salinity compared to Lake Abaya. Chl-a, PP, pH, and [O_2]day were also higher in Lake Chamo (Fig. 4C, D, E, and F). Lake Abaya had a higher turbidity (Fig. 4A), and a higher suspension of solids (which is a lot higher when Chamo's inflow is excluded), however no significant difference was found for euphotic depth between the lakes. Total nutrients concentrations (TN and TP) do not differ between both lakes, although available nutrient concentrations are higher in Lake Abaya (i.e. NH_4^+, NO_3^- & PO_4^{3-}) (Fig. 4H & I). We found no difference in carbonate and organic matter concentrations in the sediments between both lakes (Appendix 3A). And finally we note that the total nitrogen: total phosphorous ratios are 1.21 and 1.31 for Chamo and Abaya respectively.

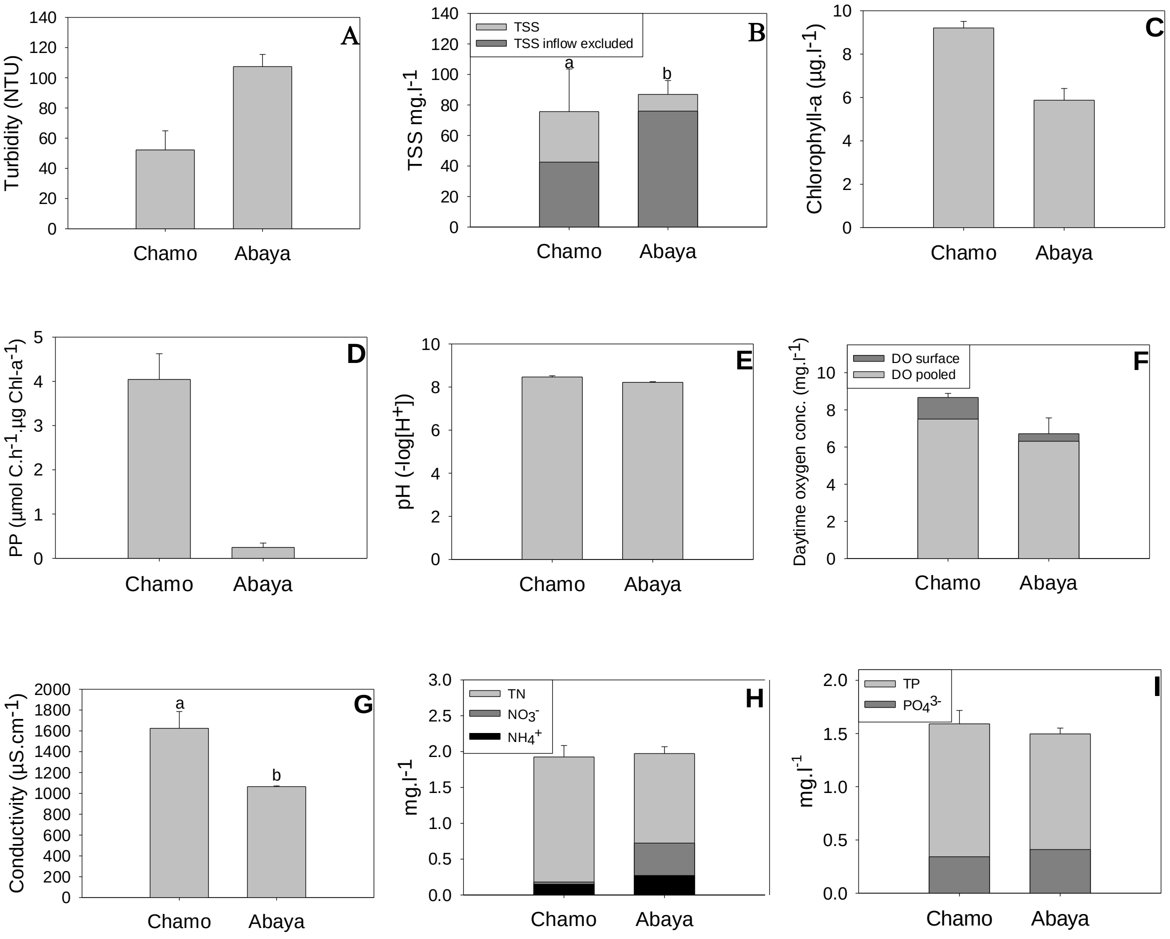


Figure 4 A-I: A. Turbidity, B. Total suspended solids, C. Chlorophyll-a, D. Phytoplankton productivity, E. pH, F. Daytime oxygen concentration, G. Conductivity, H. Total nitrogen, nitrate and ammonium, I. Orthophosphate and phosphorous. Each error bar denotes a standard error of the mean. With the exception of pooled daytime oxygen concentration, TP, and TN, all shown variables differ significantly between both lakes (p <0.05).

3.1.2 Major environmental variables in a horizontal transect

Conductivity, salinity and TDS levels in Lake Chamo were lower at the inflow compared to the pelagic and the outflow (Fig. 5A). In Lake Abaya, only TDS differed significantly, both the inflow and the pelagic were significant lower than the outflow (Fig. 5A) (Appendix 3B).

Turbidity in Lake Chamo was higher at the inflow compared to the pelagic and the outflow sample stations (Fig. 5B). TSS, seemed to have highest levels at the inflow and lowest at the outflow in accordance with the pattern of turbidity (Fig. 5C). In Lake Abaya, turbidity had the lowest mean at the outflow and this mean is only significant lower than the pelagic turbidity (Fig. 5B). TSS concentration in Lake Abaya described the same pattern as in Lake Chamo (highest at the inflow and lowest at the outflow (Fig. 5C) (Appendix 3B)

In Lake Chamo chlorophyll-a was significant lower at the inflow versus the outflow (Fig. 5D), and phytoplankton productivity seemed to follow the same pattern (no statistical analyses) (Fig. 5E). Conversely, we found no differences in chlorophyll-a concentration between inflow, pelagic and outflow in Lake Abaya (Fig. 5D), and Abaya PP seemed to be higher in the pelagic versus both the littoral zones, (Fig. 5E). A similar pattern for both lakes is found for daytime oxygen concentrations, levels are lower at the inflow versus both the pelagic and the outflow (Fig. 5F) (Appendix 3B).

Available nutrient concentrations (i.e. NO_3^-, NH_4^+ and PO_4^{3-}) in Lake Chamo did not differ significantly between the three zones, NO_3^- levels however, seemed to be higher at the inflow versus the pelagic and the outflow (Fig. 6A) (Appendix 3B). In Lake Abaya there was no visible trend from inflow to outflow, except that the NO_3^- level seemed to be lower at the inflow, while NH_4^+ seemed to be higher (Fig. 6B). For total nutrients in both lakes, we only notice a marked trend for TP in Chamo, the outflow seemed to have higher levels than both other zones, and this difference did not seem to be caused by high phosphate levels (Fig. 6C).

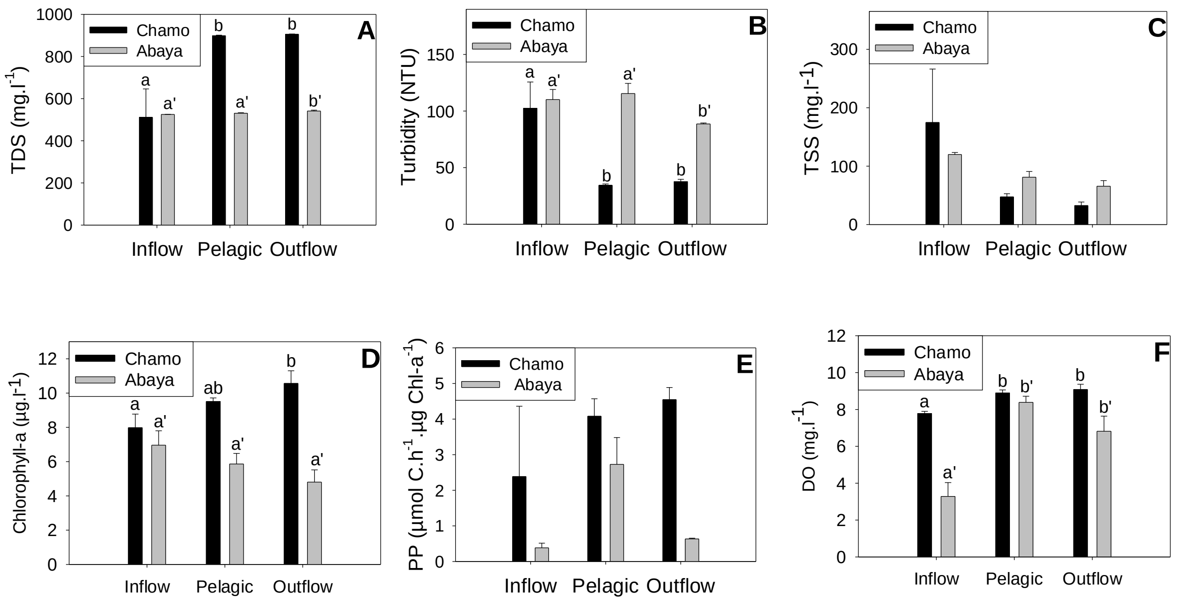


Figure 5 A-E: Environmental variables in a horizontal transect: A: TDS, B: Turbidity, C: Total suspended solids, D: Chlorophyll-a, E: primary productivity, F: Daytime oxygen concentrations. Each error bar denotes a standard error of the mean. Univariate analysed bars have a letter, bars with letters in common are not significant different from each other.

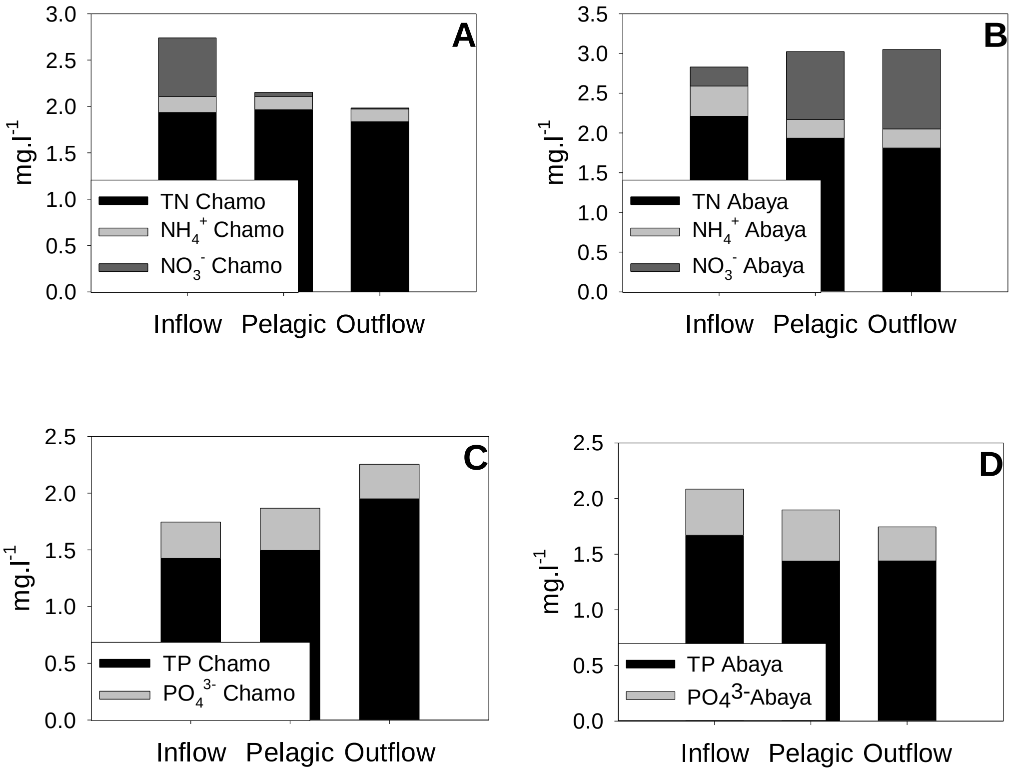


Figure 6 A-D: Stacked bar plots from the inflow to the outflow of A: total nitrogen, ammonium and nitrate in Chamo, B: total nitrogen, ammonium and nitrate in Abaya, C: total phosphorous and orthophosphate in Chamo, D: total phosphorous and orthophosphate in Abaya. Each error bar denotes a standard error of the mean. Only available nutrients of Lake Chamo were univariate analysed, no significant differences were found.

3.1.3 Major environmental variables in the pelagic water column

In Lake Chamo, conductivity was significantly higher in the surface versus both the middle and the bottom of the pelagic water column, (Fig 7A), and also had a negative association with depth in the deep pelagic station of Lake Chamo. At the depth profile of Chamo's pelagic deep station, we notice this significant difference in conductivity is due to a very superficial salinity stratification (Fig 8A). In Lake Abaya no conductivity differences were found between the three depths (Appendix 3C & D).

In Lake Chamo, turbidity was significantly lower at the surface compared to the middle and the bottom turbidity (Fig. 7B). However, in the depth profile of the pelagic deep station no significant regression was found. In Lake Abaya, turbidity did not differ at all. (Appendix 3C & D)

Chlorophyll-a concentrations differed significantly between the three depths in both lakes. The lower zone of the pelagic water column of Abaya had significant higher chlorophyll-a concentrations, compared to the surface and the middle (Fig 7C). In Lake Chamo, chlorophyll-a concentrations were significant higher in the surface versus the middle (Fig. 7C),

Daytime Oxygen concentrations did not differ in Lake Abaya, though in Lake Chamo the surface concentrations were significant higher versus the other two depths (Fig. 7D),

pH did not differ between the three depths in Abaya. and in Lake Chamo no correlation with depth was found in the pelagic deep station (Appendix 3C & D)

For the parameter temperature, all three depths in Chamo were significant different from each other, with the highest temperature at the surface and the lowest at the bottom. The pelagic deep station also gave a regression with depth (Fig 7E, 8B). If we look to Chamo's depth profile, we notice a superficial stratification. In Abaya only surface temperature was different, and higher, versus middle and bottom temperatures (Fig. 7E) (Appendix 3C, D).

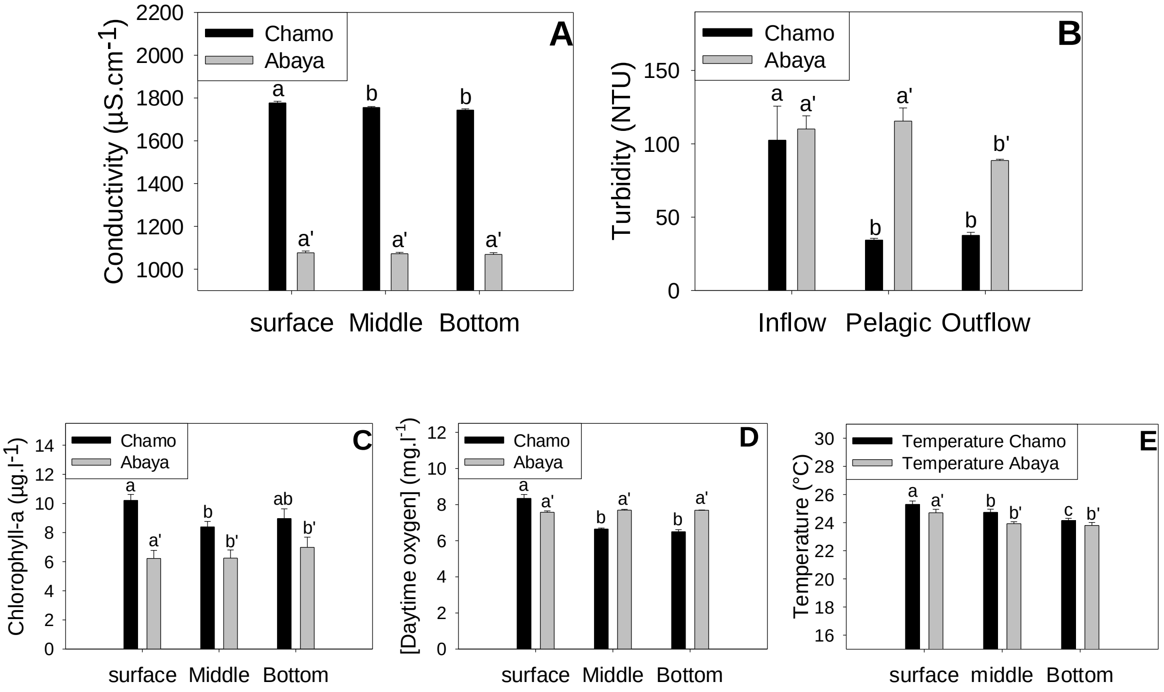


Figure 7 A-E: Environmental variables over the pelagic water-columns of both Lakes. A: conductivity, B: turbidity, C: chlorophyll-a, D: daytime oxygen concentration, E: temperature. Bars with letters in common are not significant different from each other, analyses were only performed within each lake. Each error bar denotes a standard error of the mean.

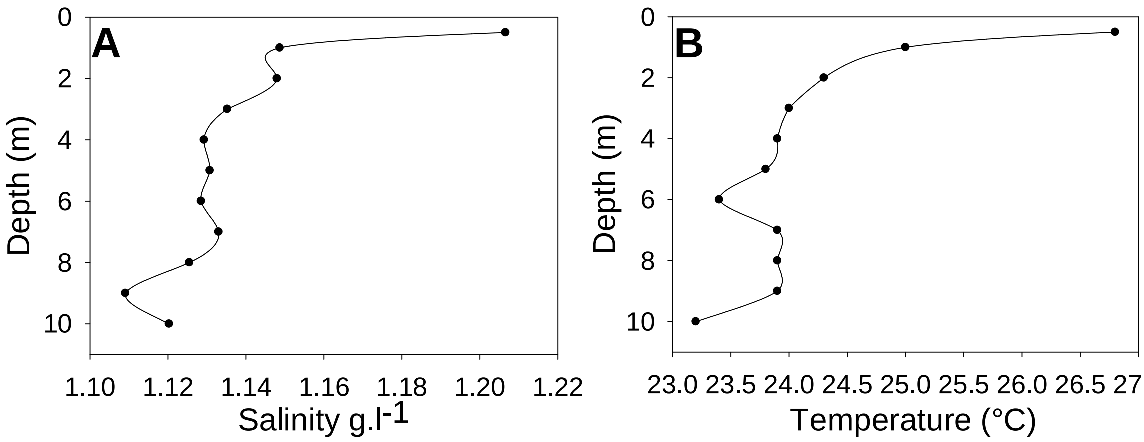


Figure 8 A & B: Two depth profiles at the pelagic deep station of Lake Chamo. A: Salinity ([major ions]), and B: temperature.

3.2 Long term variation in major environmental variables

Conductivity and salinity (as major ion concentration) are increasing significantly over time in Lake Chamo since the 1940s (conductivity: SS = 897212.3, MS = 897212.3, F = 23.447, $p < 0.001$, slope = 12.6; salinity: SS = 0.126, MS = 0.126, F = 10.135, $p = 0.015$). Lake Abaya does not seem to show any specific trend for these two variables, and our salinity value even seems to be lower than all measurements since 1961 (Fig. 9A & B).

For Secchi depth we found a negative change over time in Lake Chamo since 1984 (SS = 5841.722, MS = 5841.722, F = 37.911, $p < 0.001$), our values are less than one third of the first value, that still reached depths deeper than one meter. In Lake Abaya, there is no visible trend. We also notice that Chamo Secchi depth is evolving towards similar depths with Abaya (Fig. 9C). For turbidity we note that Chamo is trending downward, while turbidity tends to increase in Abaya (Fig 9D), but these changes are small, few data is available, and data only goes back to 2005. Secchi depth did not have marked changes nether from 2005 up till now. For TSS we have the lowest average data in Lake Chamo since 2002 (Appendix 4B). Chlorophyll-a levels show an insignificant but visible downward trend in both Lakes, this trend is a bit steeper in Lake Chamo than in Abaya (Fig. 9E). We also notice that we found the lowest average values in Lake Chamo since the first found measurements in 1966, and values in Chamo were extremely high from 1988 till 1990.

pH in Lake Chamo does not show a visible trend since 1966 up till now, Lake Abaya however, shows a negative trend since 1964 up till now (SS= 0.2766, MS = 0.277, F = 27.452, $p = 0.001$) (Fig. 9F), and in both Lakes our data are the lowest since first collected data.

We found no significant trends for available nitrogen containing nutrients: nitrite, nitrate and ammonium in Lake Chamo, total nitrogen on the other hand, seems to be 20 percent higher versus 2005 (Fig. 10A). For soluble reactive phosphorous and total Phosphorous all concentrations after 2005 were found to be higher than all values measured before (Fig. 10B)

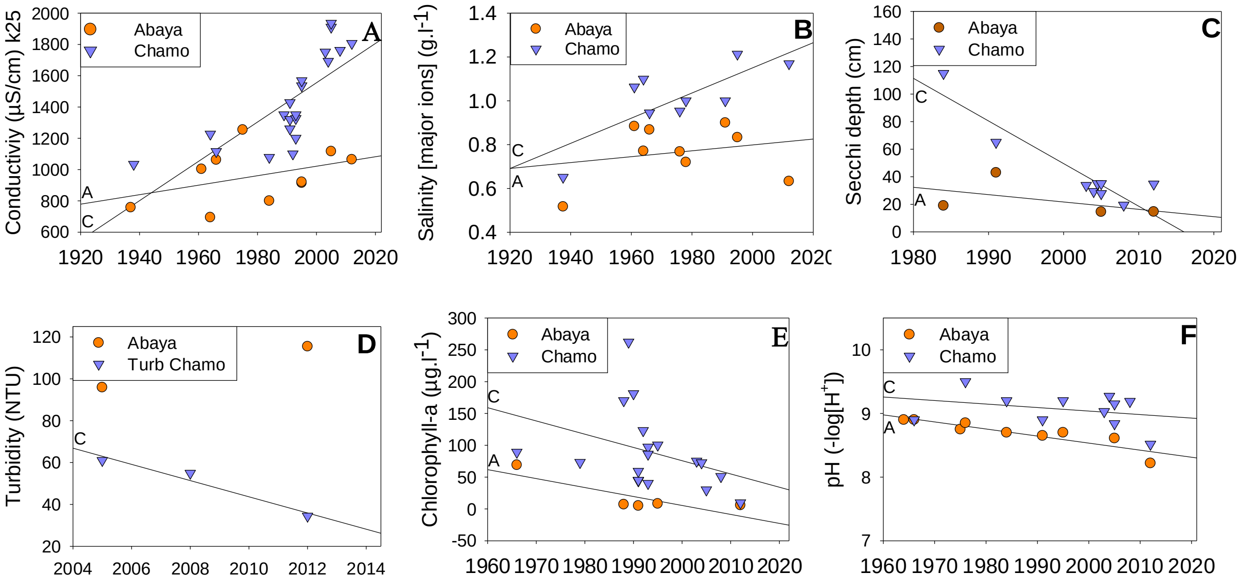


Figure 9 A - F: linear regressions of environmental characteristics, A: conductivity, B: total dissolved solids, C: Secchi depth, D: turbidity, E: chlorophyll-a, F: pH. X-axes denote time in years. Regression lines are characterised with letters A and C, which respectively denote Abaya and Chamo.

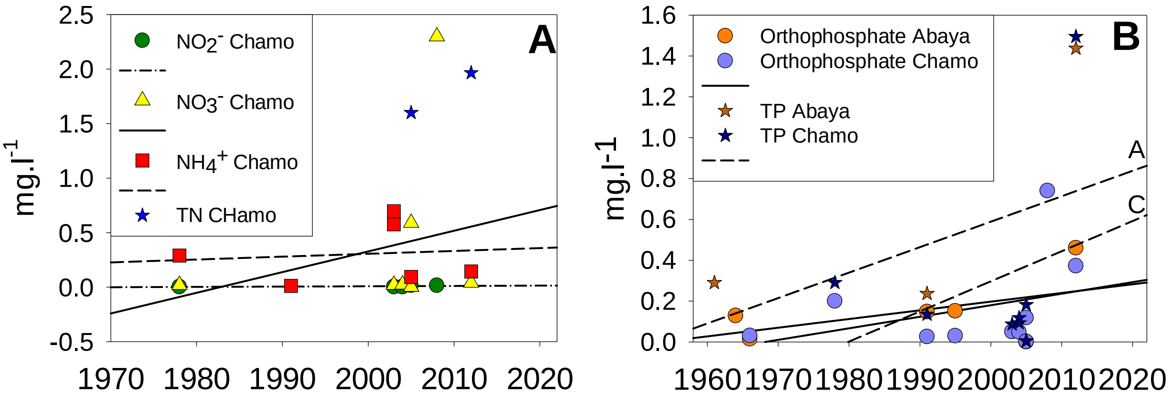


Figure 10 A & B: linear regressions of nutrients, X-axes denote time in years. In panel B regression lines are characterised with letters A and C, which respectively denote Abaya and Chamo.

3.3 Zooplankton Results

3.3.1 Zooplankton community characteristics between both lakes

We found ten zooplankton taxa over the entire set of samples (Table 3). Taxon richness in Lake Chamo and Abaya is the same (9 taxa), and cladoceran Shannon-Wiener diversity did not differ between the lakes. There are however important differences in zooplankton community composition, such as the absence of *Leydigia* sp. in Abaya and calanoid copepods in Chamo.

Table 3: The presence (+) and absence (-) of zooplankton taxa in Lake Chamo and Lake Abaya. (sp. = one species, spp. = species plural, "+" = presence of taxon, "-" = absence of taxon

Zooplankton taxa	Chamo	Abaya
Cladoceran species		
Ceriodaphnia cornuta	+	+
Ceriodaphnia laticaudata	+	+
Daphnia barbata	+	+
Daphnia magna	+	+
Diaphanosoma australiensis	+	+
Leydigia sp.	+	-
Macrothrix spinosa	+	+
Moina mongolica	+	+
Copepodan taxa		
Calanoida	-	+
Mesocyclops spp.	+	+

Redundancy analysis (RDA) revealed significant differences in zooplankton community abundances between both lakes (Trace = 0.631, F = 34.258, p = 0.001). Similar results were obtained for zooplankton community biomass (data not shown). The first axis of the PCA ordination plot explains 84% of the variation in zooplankton abundances and makes a clear distinction between both lakes (Fig. 11). The second axis explains 8.8% of the variation in zooplankton community abundance and differentiates Chamo's vegetated sample plots from its other plots. Most species were more abundant in Lake Chamo, while calanoid copepods and *Ceriodaphnia laticaudata* were more numerous in Lake Abaya. The strong positive association of CLI1 (Chamo littoral inflow station 1) with samples from Lake Abaya is surprising.

Univariate analyses revealed very similar results and indicate that total zooplankton abundance and the abundance of *Ceriodaphnia cornuta*, *Daphnia barbata*, *Moina mongolica*, *Diaphanosoma australiensis*, *Mesocyclops spp.*, copepod nauplii and Rotifera, were significantly higher in Lake Chamo compared to Lake Abaya. *Ceriodaphnia laticaudata* and calanoid copepods were more abundant in Lake Abaya (Appendix 5A). We found no significant differences in abundance between both lakes for other species.

Biomass univariate analyses gave the same outcome (Appendix 5B).

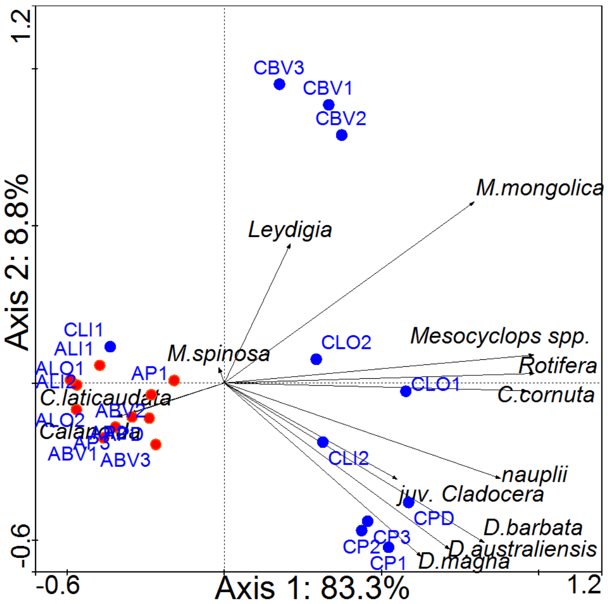


Figure 11: Ordination plot of a Principal Component Analysis (PCA) of the zooplankton abundance in Lake Chamo and Lake Abaya (samples shown in blue and red respectively)

The relative abundance of different zooplankton taxa differed significantly between both lakes (Trace = 0.208, F-ratio = 5.258, p = 0.005). Similar results were obtained for zooplankton relative biomass (data not shown). In the PCA-plot (Fig. 12) we can see that high relative abundances of *D. magna*, *D. australiensis*, *C. laticaudata*, Calanoida and copepod nauplii are positively associated with Lake Abaya, *M. spinosa* relative abundance is nearly the same in both lakes and higher abundance ratios for all other groups are positively associated with Lake Chamo.

Univariate analyses revealed that *C. laticaudata*, Calanoida and copepod nauplii were relative more abundant in Lake Abaya, *Mesocyclops spp.*, *C. cornuta* and *D. barbata* have higher relative abundances in Chamo, and the other taxa have similar relative abundances between both Lakes (Appendix 5A). The same patterns were found for relative biomass between both lakes, with the exception for *D. barbata*, wherefore no difference in relative biomass between both lakes was found, and we found a significant higher relative biomass for *D. magna* in the pelagic of Lake Abaya versus the pelagic of Lake Chamo (Appendix 5B).

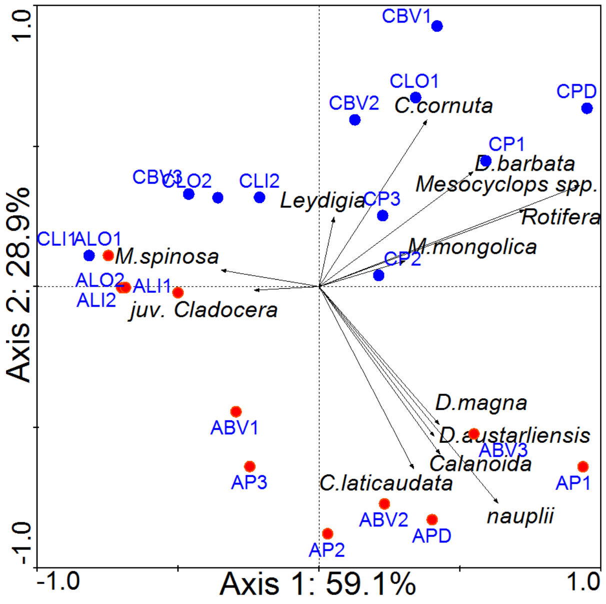


Figure 12: PCA-plot of relative abundance distribution between both lakes. Sample stations of Chamo and Abaya are shown in blue and red respectively

For body-size, we revealed that *D. australiensis* is larger in Lake Chamo compared to Lake Abaya, while *D. magna* was significantly larger in Lake Abaya compared to Lake Chamo. *Mesocyclops spp.*, *C. cornuta*, *M. mongolica*, *D. barbata*, and *M. spinosa* did not differ in size between both Lakes (Fig. 13).

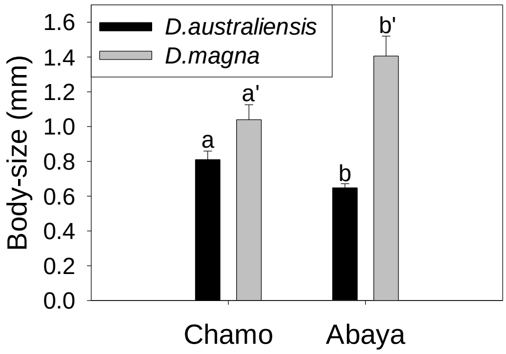


Figure 13: Differences in body-size between both lakes are shown for D. australiensis and D. magna. Bars with different characters are significant different from each other, analyses were only performed between the same species.

3.3.2 Zooplankton characteristics within each lake

Zooplankton abundance, biomass and body-size in Lake Chamo and Abaya

In both lakes we found a significant difference in zooplankton abundances between the three subhabitats (vegetated littoral, littoral and pelagic) (Trace = 0.472, F-ratio = 3.581, P-value = 0.011; Trace = 0.675 F-ratio = 8.304, P-value = 0.002, for Chamo and Abaya respectively). The similarities between both lakes (Fig. 14A & B) are: *M. spinosa* is associated towards vegetated littoral stations, *D. magna*, *D. barbata*, *D. australiensis* and *C. laticaudata* are highly associated towards the pelagic stations, and *C. cornuta*, *Mesocyclops spp.*, Rotifera and copepod nauplii have highest abundances within, and not different between, the pelagic and the littoral zone. The major differences between both lakes (Fig 14A & B) are: *M. mongolica* is highly positively associated towards the vegetated littoral station in Chamo while it is a pelagic species in Lake Abaya, juv. cladocerans are associated towards the pelagic in Lake Chamo, while they are highly negatively associated towards the pelagic sample stations of Abaya. Further we notice that, within lake Abaya, calanoid copepods are most abundant in the pelagic zone and within Lake Chamo, *Leydigia* sp. is positively associated with the between vegetation sample stations.

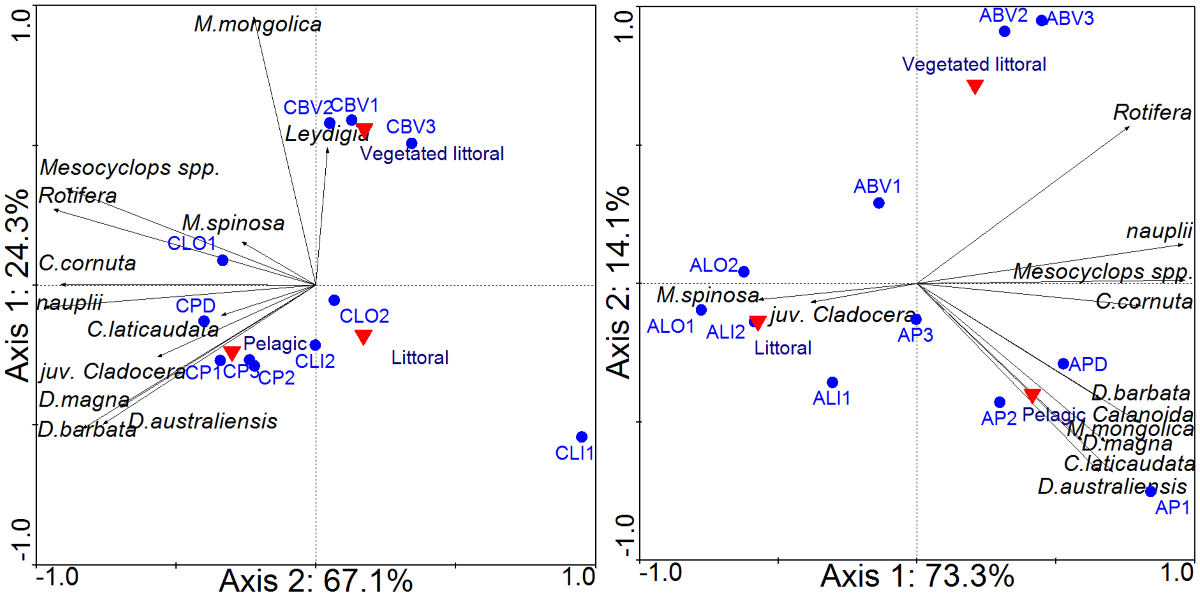


Figure 14 A & B: PCA-plots of zooplankton abundance distribution across different habitat types in respectively Lake Chamo and Abaya. The red triangles represent the centroids from the habitat types (pelagic, littoral, and vegetated littoral) and were plotted as supplementary variables to not influence analyses.

Lake Chamo

Univariate analyses (Appendix 6A) in Lake Chamo indicated that: *D. magna* and copepod nauplii were more abundant in the pelagic habitat compared to both littoral habitats, *D. barbata* had a higher abundance in the pelagic compared to the vegetated littoral, *M. mongolica* had a higher abundances in the vegetation compared to both other habitats (pelagic and littoral). The abundance of other species as well as the total zooplankton abundance in different habitats did not differ.

Biomass in Lake Chamo was only different for *D. magna* and *D. barbata* between the three habitats, and both *D. magna* and *D. barbata* are now significant higher in the pelagic compared to both littoral habitats (Appendix 6A).

We also found significant zooplankton body-size differences in Lake Chamo. Average cladoceran body-size was significant larger in the pelagic compared to the littoral habitats (open and vegetated), *Mesocyclops spp.* have a larger body-size between vegetation compared to open water habitats, and *C. cornuta* was on average larger in the pelagic compared to the littoral habitat with macrophytes. (Appendix 6A).

Lake Abaya

In Lake Abaya, total zooplankton abundances were lowest in the littoral zone compared to the pelagic and vegetated littoral, and only copepod nauplii, followed this same significant pattern, further we found a higher total cladoceran abundance in the pelagic versus the vegetated littoral habitat, a higher total copepod and calanoid copepod abundance in the pelagic versus the open littoral, a significant higher abundance for *D. barbata*, *D. australiensis* and *C. laticaudata* in the pelagic versus the two littorals separately, and a significant higher abundance in the vegetated littoral versus the open littoral for Rotifera. The other taxa do not differ in abundance across the three habitats (Appendix 6B). For biomass, we found some small differences in comparison to the former abundance results, as for total biomass (only significant higher in the pelagic versus the open littoral), *D. australiensis* biomass (only higher in the pelagic versus the vegetated littoral, and for *D. magna* and total cladoceran biomass (higher in the pelagic versus both littorals). All other results were similar, with the exception of calanoid copepods that did not differ between all three habitats (cf. calanoid copepod abundance) (Appendix 6B).

A Body-size difference was only found for *C. cornuta*, it had a higher body-size in the Pelagic versus the open littoral habitat. Body-sizes of *D. australiensis*, *Mesocyclops spp.*, *M. mongolica*, Calanoida, and average body-size of all zooplankton combined, all Cladodera combined, and all Copepoda combined did not differ between the three habitats (Appendix 6B).

Richness and Diversity within the lakes

We only found evidence for differences in cladoceran species richness between the three habitats in Lake Abaya (SS = 11.492, MS = 5.746, F = 13.455, p = 0.003), the difference is due to a higher pelagic richness compared to the vegetated littoral habitat (Fig 15A). The cladoceran Shannon-Wiener diversity in Lake Chamo, (SS = 0.432, MS = 0.216, F= 30.735 p < 0.001) was lower in the vegetated habitat compared to both open water habitats (Fig 15B), while we found no difference in diversity between the three habitats in Lake Abaya.

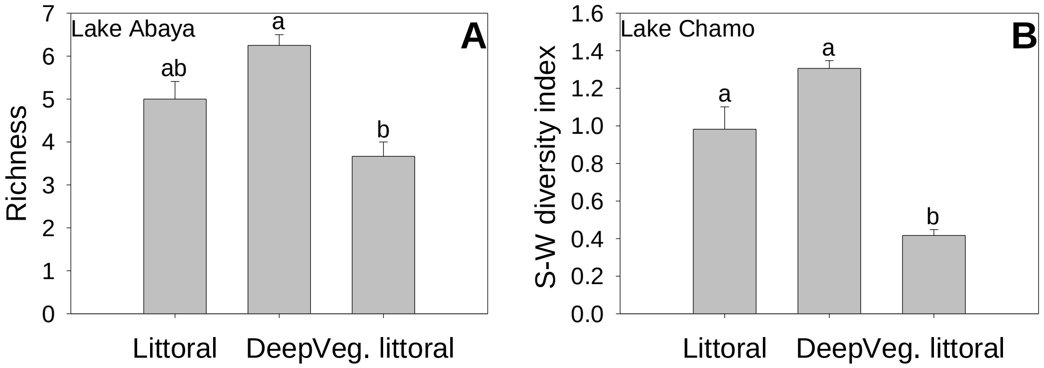


Figure 15 A & B: Vertical Bar Charts of the Cladoderan richness (A) and Shannon-Wiener (S-W) diversity index (B) between three different habitats (i.e. the littoral, the pelagic (deep), and the vegetated littoral. Error flags indicate standard errors of the means.

Dominant and largest sized species

Taxa with highest abundance, biomass and body-size are given in table 4 and 5 (Lake Chamo & Abaya respectively). Copepods seem to be the dominant group in both lakes, both in abundance and in biomass, and *D. magna* is the largest species in both lakes.

Table 4: Decreasing rank of abundance, biomass and body-size of al taxa in Lake Chamo, "# measured" = amount of individuals subject to body-size measurements

Rank	Abundance	#/l	Biomass	µg/l	Body-size	mm	# measured
1	*Mesocyclop spp.*	167.901	*Mesocyclop spp.*	442.930	*D. magna*	1.049	102
2	Copepod nauplii	59.470	*M. mongolica*	50.708	*D. barbata*	0.831	243
3	Rotifera	59.244	*D. barbata*	26.264	*D. australiensis*	0.792	181
4	*C. cornuta*	20.789	*D. magna*	15.524	*Leydigia sp.*	0.751	1
5	*M. mongolica*	12.960	*C. cornuta*	11.123	*M. mongolica*	0.704	259
6	*D. barbata*	9.016	*D. australiensis*	5.816	*C. laticaudata*	0.686	1
7	*D. australiensis*	2.436	*M. spinosa*	0.030	*Mesocyclop spp.*	0.603	296
8	*D. magna*	1.558	*Leydigia sp.*	0.003	*Ceriodaphnia cornuta*	0.367	300
9	Juv. cladocerans	0.590			*Macrothrix spinosa*	0.305	16
10	*M. spinosa*	0.088					
11	*Leydigia sp.*	0.007					
12	*C. laticaudata*	0.006					

Table 5: Decreasing rank of abundance, biomass and body-size of al taxa in Lake Abaya, "# measured" = amount of individuals subject to body-size measurements

Rank	Abundance	#/l	Biomass	µg/l	Body-size	mm	# measured
1	Copepod nauplii	8.549	*Mesocyclop spp.*	7.662	*D. magna*	1.425	210
2	*Mesocyclop spp.*	5.263	*D. magna*	5.307	*D. barbata*	0.912	110
3	Calanoida	1.621	Calanoida	4.541	Calanoida	0.907	276
4	*M. mongolica*	1.459	*M. mongolica*	4.275	*D. australiensis*	0.660	237
5	Rotifera	1.456	*D. australiensis*	0.930	*M. mongolica*	0.655	308
6	*D. australiensis*	0.601	*D. barbata*	0.332	*Mesocyclop spp.*	0.550	343
7	*D. magna*	0.314	*C. laticaudata*	0.308	*C. laticaudata*	0.526	150
8	*C. laticaudata*	0.192	*M. spinosa*	0.058	*C. cornuta*	0.367	96
9	*D. barbata*	0.088	*C. cornuta*	0.043	*M. spinosa*	0.352	22
10	Juv. cladocerans	0.086					
11	*M. spinosa*	0.079					
12	*C. cornuta*	0.072					

3.3.3 Zooplankton characteristics across the pelagic water column

Abundance, biomass and body-size distribution over the pelagic water column

RDA analyses for both lakes separately revealed a significant difference in zooplankton abundances between the surface layer and the deep layer of the water column (Trace = 0.379, F = 9.764, P = 0.002; Trace = 0.327, F-ratio = 10.198, P = 0.001, for Chamo and Abaya respectively) and overall patterns of differences were very similar for both lakes. In our PCA-plot (Fig. 16A and B) we see that all surface samples are clustered together, while the other depths are randomly positioned in clusters, and negatively associated towards the surface samples. We notice that all species are negatively associated towards the surface samples in both lakes. With univariate analyses (Appendix 7A & B), we found a lower total zooplankton abundance in the pelagic surface of Lake Abaya, versus all deeper depths until 10 meter. In Lake Chamo on the other hand, no differences were found between depths for total zooplankton abundance. For all taxa separately, no significant abundance differences were found between all depths in both lakes, except for copepod nauplii in Lake Abaya, here, all depths were only significant different with, and higher in abundance compared to the surface (Appendix 7B).

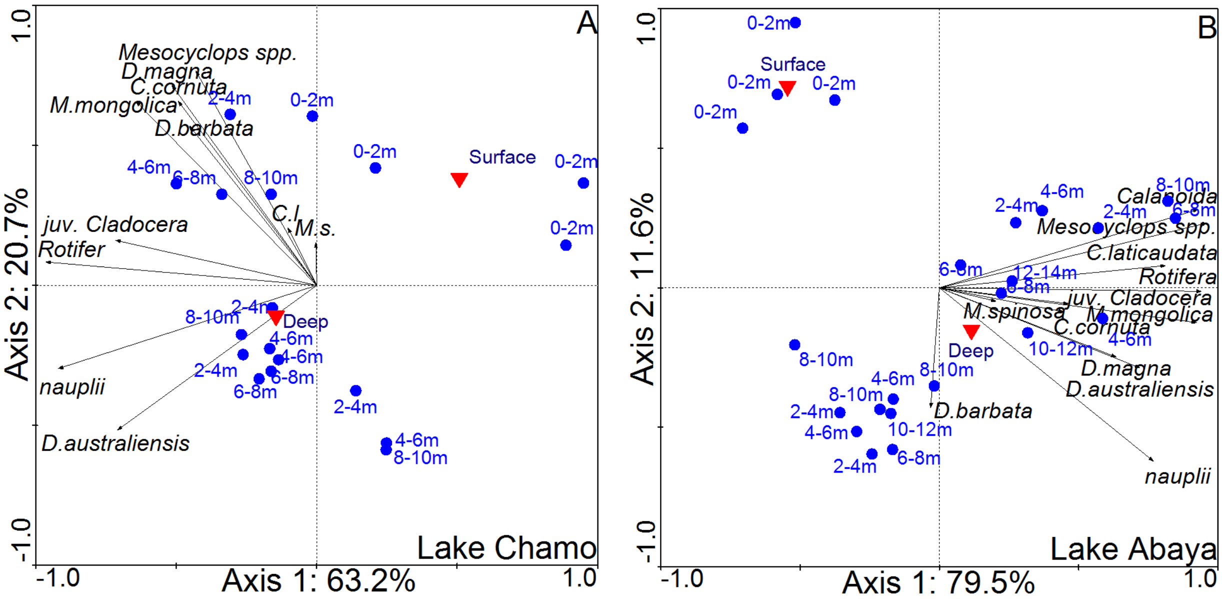


Figure 16 A & B: PCA-plots of zooplankton abundance over depth for Lake Chamo (A) and Lake Abaya (B). The red triangles represent the centroids from both depth types (surface and deep), and were plotted as supplementary variables to not influence the analyses.

Multivariate analysis of the biomass distribution along the vertical profile revealed very similar results for both lakes and the results of this analysis are therefore not shown. With univariate analyses we found, for Lake Chamo, that *D. australiensis* was significant lower in abundance at the surface versus depths 4-6 m and 6-8 m. In Lake Abaya total biomass did not differ between depths (cf. total abundance), but *D. magna* (Fig. 17), *D. australiensis* and *M. mongolica*, however, were all significant lower in biomass at the surface versus all depths separately.

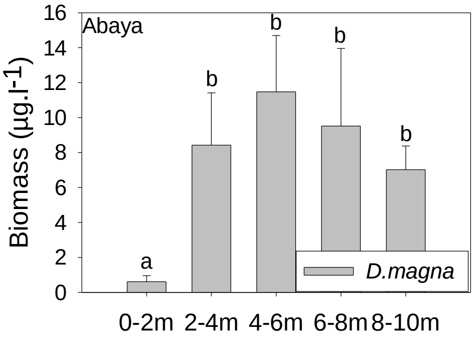


Figure 17: Biomass *D. magna* at different depths over the pelagic water column of Lake Abaya, Depths that do not have a letter in common differ significantly from each other

We found no effect of sampling depth on the average body size of the zooplankton community in both lakes, neither was there found a difference for any taxon separately (Appendix 7A & B).

Species richness and diversity index over the pelagic water column

Cladoceran species richness and Shannon-Wiener index were compared over all depths until 10 meter, no differences were found between depths

3.3.4 Visualisation of the zooplankton community in both lakes

Lake Chamo

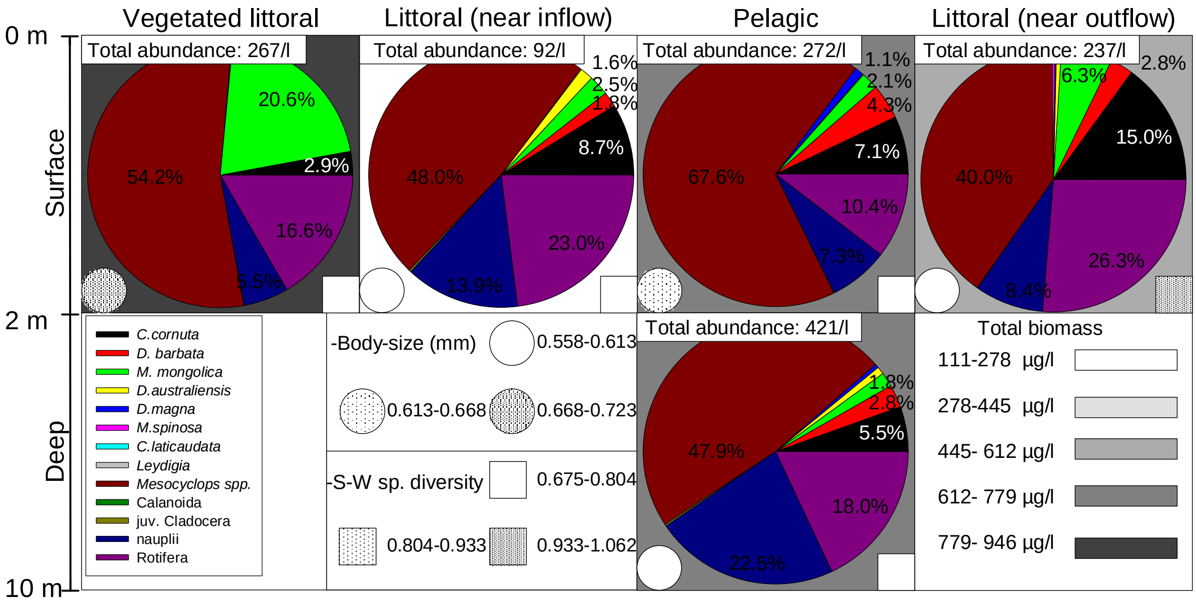


Figure 18: Abundance distribution of zooplankton in Lake Chamo (dry season, transect from inflow (Kulfo River) to outflow), the pie charts give the percentages of each taxon in a particular habitat (i.e. vegetated littoral, inflow, pelagic, outflow and pelagic deep (2-10m). Depths, beneath two meter, are taken together as no significant differences were found between them (RESULTS, section 3.3.3). Total zooplankton biomass, average zooplankton body-size and Shannon-Wiener diversity over all taxa are also included.

Lake Abaya

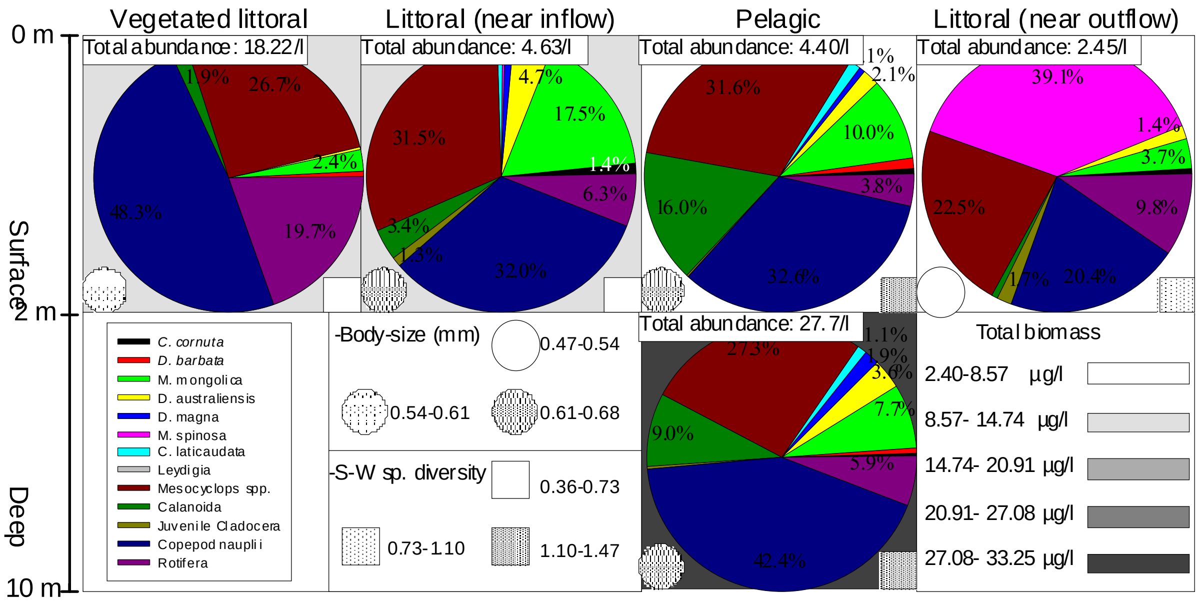


Figure 19: Abundance distribution of zooplankton in Lake Abaya (from inflow (Gelana River) to outflow), the pie charts give the percentages of each taxon in a particular habitat (i.e. vegetated littoral, inflow, pelagic, outflow and pelagic deep (2-10m). Depths, beneath two meter, are taken together as no significant differences were found between them (RESULTS, section 3.3.3). Total zooplankton biomass, average zooplankton body-size and Shannon-Wiener diversity over all taxa are also included.

For distribution patterns of cladocerans in particular see Appendix 8.

3.4 Biomass ratio of Zooplankton to phytoplankton

The zooplankton to phytoplankton biomass ratio is significantly higher in Lake Chamo versus Lake Abaya (p = 0.005) (Fig. 20).

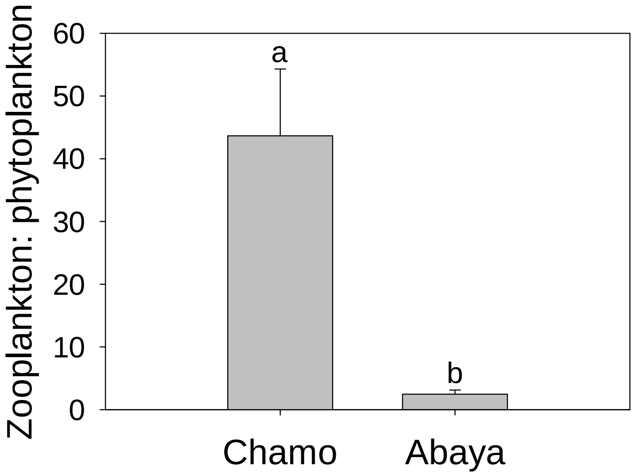


Figure 20: Zooplankton to phytoplankton biomass ratios between Lake Chamo and Abaya, error bars denote a standard error of the mean, significant different bars have no letters in common.

4 DISCUSSION

4.1 Environmental variables

Subsaline mixed lakes

Both lakes can be categorized as subsaline lakes (Hammer, 1986), with the most saline being Lake Chamo, and as expected its conductivity and total dissolved solids were also higher. Conductivity in both lakes exceeds 1000µS.cm^{-1}, which is a higher value compared to most water bodies, and may be addressed to a high input of land runoff (Deas & Orlob, 1999). This conductivity is not only higher in Lake Chamo, it is also increasing since the 1940s. Our values are 75% higher than the values from the 40s, and the trend of an average increase of 12.6 µS per year does not seem to stagnate. Salinity values in Chamo are also increasing significantly since the 1940s. This increasing trend may have major impact on Lake Chamo in the future, as salinity levels can change whole community structures (Muschal, 2006). Contrasting to Lake Chamo, no trends were found for salinity and conductivity in Lake Abaya. In the horizontal gradient we can see that water inflow from the Kulfo River seems to have a greater impact on lowering dissolved solids and ions in Lake Chamo compared to the impact of the Gelana River on Lake Abaya.

In the pelagic water column, conductivity differences between depths only occurred in Lake Chamo, and if we take a look to the depth profiles, we notice there is a very superficial saline stratification in this lake, which can probably be ascribed to evaporation at the surface of the water column, which leads to higher ionic concentrations. A similar superficial stratification was also visible for temperature in Lake Chamo, and we, as Baxter (2002), believe this stratification is diurnal and breaks of at night, as on average temperature drops more than 10 degrees at night in this area.

Turbidity

Lake Abaya is more turbid than Lake Chamo, and has more suspended solids, and if we exclude our samples taken close to the inflow, Abaya has approximately twice the amount of suspended solids compared to Lake Chamo. We can say the higher concentration of suspended solids in Chamo is not due to mesozooplankton and phytoplankton biomass ([Chl-a]) and is thus most probably higher because of abiogenic and dead biogenic matter. We can also conclude the higher turbidity in Abaya is not due to the former two biomasses and the dissolved solid concentration, as these are higher in Chamo. At the inflow stations of Lake Chamo we found a high turbidity most probably caused by the high concentration of suspended solids carried in the lake by the Kulfo River. In the long term we found that Lake Chamo is getting more turbid since 1984 as Secchi depth is decreasing since then, we hereby approve the findings of Ugo (2008). We also note that Secchi depth in Lake Chamo is evolving towards the same Secchi depth as Lake Abaya, which does not seem to differ in the parameter over time. This decrease in Secchi depth is not caused by higher levels of

Chlorophyll-a, as we rather see a downward trend in this parameter from the 1980's up to now, so the lower Secchi depth can be partly caused by the rising levels of dissolved solids but we strongly believe Lake Chamo's suspended solids levels are increasing with time.

Nutrients

Total nitrogen and phosphorous concentrations were relatively high in both lakes and did not differ between the lakes. However, we found significant higher concentrations of available nutrient concentration (N and P) in Lake Abaya compared to Lake Chamo. Because high phosphorous concentrations are already presumed around 0.2 $mg.l^{-1}$ and moderate nitrogen concentrations are presumed around 4 $mg.l^{-1}$ (Sagrario et al., 2005). We can conclude for both lake that phosphorous levels are high (around 1.50 $mg.l^{-1}$), and nitrogen levels are beneath moderate concentrations (around 1.90 $mg.l^{-1}$) in both lakes. The total nitrogen: total phosphorous ratios in both lakes suggest that both lakes are nitrogen limited, as the ratios are 1.21 and 1.31 for Chamo and Abaya respectively, which is far beneath the 7:1 ratio (Deas & Orlob, 1999). Available nutrients occurred less in Lake Chamo compared to Abaya, indicating that more N and P are accumulated in biota, and as expected, we indeed found higher Chlorophyll-a and zooplankton biomass in Lake Chamo. This also means that nitrogen, which is already limiting, is even less available in Chamo than in Abaya. Nitrogen limitation can give an advantage towards nitrogen fixing phytoplankton (i.e. Cyanobacteria) (De Meester, 2012), so this could be a major contributor towards the fact that Cyanobacteria prevail in phytoplankton biomass in Lake Chamo (Shumbulo, 2004).

Since the end of 1970s, available and total nitrogen nutrients do not have a significant trend in Lake Chamo, however the total nitrogen concentrations in Lake Chamo seem to be much higher than the measurement in 2005. We found no evidence for an increase in phosphate concentration over time in both lakes, but both total phosphorous and phosphate concentrations seem to get much higher after 2005 in both lakes. The increases in both lakes seem higher for the total nitrogen and phosphorous than for their available constituents, which could indicate that phytoplankton productivity got higher in both lakes from around 2005 until 2012, this is not reflected in chlorophyll-a increases over time since 2005, but productivity and biomass do not always go hand in hand (e.g. stronger grazing pressure by zooplankton).

In the horizontal transect of both lakes, NO_3^- and total phosphorous seem to be respectively negatively and positively associated towards chlorophyll-a biomass, NH_4^+, orthophosphate and TN do not seem to show any trend at al, except for a high NH_4^+ value at the inflow of the Gelana river, which could be caused by the inflow but can also be attributed to other sources (e.g. anaerobic decomposition as oxygen levels are found to be very low at the Gelana River inflow).

Phytoplankton

Both Phytoplankton productivity (16 times) and phytoplankton biomass (chlorophyll-a concentration) were higher in Lake Chamo compared to Abaya, and this higher phytoplankton productivity and biomass is most probably the reason why zooplankton biomass is much higher in Lake Chamo. In both lakes, phytoplankton biomass seems to decrease since the 1960s, and also very noticeable are the very high phytoplankton concentrations around 1990.

Spatial patterns were found for chlorophyll-a biomass in Chamo, in contrary to the findings of Shumbulo (2004), and in Lake Abaya. In Lake Chamo chlorophyll-a levels and primary productivity seemed to follow the total suspended solids pattern, and were lowest at the inflow and highest at the outflow, the high levels at the outflow could also be caused by the seemingly high TP values prevailing here. In Chamo's pelagic water column, significant higher phytoplankton biomass was found at the surface versus the bottom. In Abaya no significant phytoplankton biomass differences were found in the horizontal transect, phytoplankton productivity however, seemed to be much higher in the pelagic, this could be due to the seemingly lower suspended solid levels at the pelagic versus the inflow and the seemingly higher orthophosphate values compared to the outflow. In the pelagic water-column of Abaya, Chlorophyll-a levels were higher at the bottom versus the middle and the surface, which is rather surprising.

Influence of zooplankton on phytoplankton

We found a higher zooplankton to phytoplankton biomass ratio in Lake Chamo, indicating that there might be a higher zooplankton grazing rate in Lake Chamo compared to Abaya. This makes Lake Chamo more likely to have fast growing to inedible species than Lake Abaya. Further, the lakes did not differ in average zooplankton body-size, however the largest found copepod taxon (i.e. calanoid copepods) only occurred in Lake Abaya, and Abaya also had larger *D. magna* compared to Lake Chamo, which may promote larger and or toxic phytoplankton species in Lake Abaya (De Meester, 2012).

4.2 Zooplankton community characteristics

Different Taxa

Only 8 and 7 cladoceran species occurred in Chamo and Abaya respectively, and we seriously doubt if these lakes have more than 50 species of cladocerans in total, as average lakes normally do, irrespective to latitude (De Meester, 2012). This low species richness is in the agreement, that unlike terrestrial communities, phytoplankton and zooplankton communities do not show more complexity in low compared to high latitudes (Lewis, 1996). Tropical water bodies typically contain the predominantly herbivorous genera: *Moina*, *Ceriodaphnia*, *Macrothrix* and *Diaphanosoma*, and these were al found in our Lakes. The reasons why they are found in our lakes and reside better in tropical versus temperate lakes are generally thought to be: relatively higher rates of population increase (predominantly caused by their smaller body-sizes), higher threshold food levels (the food concentration at which animals can maintain a zero growth rate), higher filtering and ingestion rates, and greater tolerance to higher food levels and to temperature maxima. Their smaller body-size would also be an advantage towards predation, as macro-invertebrates are typically less abundant in tropical lakes compared to lakes in the temperate zone, and fish predation prevails (Sarma, Nandini & Gulati, 2005). *Diaphanosoma* would also have the advantage of being a fast species, which also gives an advantage against the high tropical fish predation (De Meester, 2012). We also found a singular, small sized species of the genus *Leydigia* with a very low abundance, which may be more abundant in another season, but it is also mentioned that they do worse in the tropics than the other small sized tropic species, as they need more time to reach maturity, which may be partly due to their thick carapace, which takes more time for formation compared with soft bodied taxa (e.g. *Moina*) (Sarma, Nandini & Gulati, 2005). At last we also found two *Daphnia* species (i.e. *D. barbata* & *D. magna*). We hereby approve findings of *D. magna* in Lake Chamo (Zone agriculture Bureau and African Parks, Ethiopia, 2007), and we believe we are the first who found them in Lake Abaya. We did not found any report of the occurrence of *D. barbata* in both lakes nether. The presence of *Daphnia* in both lakes (i.e. *D. magna* and *D. barbata*), is good news for further examinations of both lakes, as most life-history research of cladocerans was done on this genus (Sarma, Nandini & Gulati, 2005).

Two out of three free-living copepod suborders are represented in our lakes (e.g. Calanoida and Cyclopoida), but only cyclopoid copepods occurred in Lake Chamo. All found cyclopoid copepods in both lakes are from the genus *Mesocyclops*, and these are known to be biological controlling agents against mosquitoes, as this genus has been proven effective in controlling mosquito larvae at local levels in an introduction trial in Vietnam (Boxshall and Defaye, 2007). So this species may be of importance in controlling diseases, as malaria, in the area around the lakes. Calanoid copepod only occurred in Lake Abaya. We assume they reside better in Lake Abaya because of their high food-selectivity, which gives them an advantage towards cladocerans in this lake with a high abiotic turbidity (De Meester, 2012 & Kebede, 2002).

Dominant and largest sized species

Copepods dominated the zooplankton community in both lakes in terms of abundances and biomass, this might indicate that fish predation is high in both lakes, as copepods are known to be better in escaping fish predation than cladocerans (Drenner, Strickler, & O'Brien, 1978). The cyclopoid copepods (i.e. Mesocyclops spp.) were higher in abundance and biomass than the calanoid copepods. *Moina mongolica* was the most dominant cladoceran in abundance in both lakes, followed by *Ceriodaphnia cornuta* in Lake Chamo and *Diaphanosama australiensis* in Lake Abaya. *Moina* are often related to turbid water states, as their food intake decreases less with turbid water state in comparison to other cladoceran taxa (Hart, 2006) so this could already help explain the dominance in Lake Abaya.

In biomass *M. mongolica* was again the most dominant cladoceran species in Lake Chamo, followed by *Daphnia barbata*, however in Lake Abaya *D. magna* was the most dominant cladoceran in biomass, followed by *M. mongolica*, which shows *Daphnia* are residing well in both lakes. Because *D. magna* are filter-feeder their high biomass can not be explained by food selectivity (cf. Calanoida), and we rather think lower fish predation or the size-efficiency hypothesis are the most possible outcomes. As food is less abundant in Lake Abaya (less Chlorophyll-a biomass) it can be an advantage to be large, because large bodied zooplankton have a lower threshold food concentration and can also eat larger particles. The threshold food concentration decrease with size is only valid for individuals from about 1300 µm long and above (Sarma, Nandini & Gulati, 2005), and it seems *D. magna* is the only species in Abaya who meets this size on average (1.40 mm). *D. magna* was also the biggest species in both lakes followed by *D. australiensis* in Lake Chamo and *D. barbata* in Lake Abaya, and for copepods in Lake Abaya, calanoid copepods were larger than the cyclopoid copepods.

An Abundance, biomass and body-size comparison

Abundances and biomass of both cyclopoid copepods and cladocerans were high in Lake Chamo, compared to oligotrophic large and eutrophic small tropic water reservoirs, with the exception of cladoceran biomass who only reached a higher biomass compared with the large oligotrophic reservoirs. Lake Abaya’s cladoceran and cyclopoid abundances and biomass were rather low, as they did not reach the levels of both types of tropical reservoirs. Abaya’s calanoid-copepods biomass on the other hand, does not seem to be low for the tropics as it has a biomass in between the measures of tropical oligotrophic large reservoirs and tropical eutrophic small reservoirs (Pinto-Coelho et al., 2005). Cladoceran and copepod body-sizes in both lakes were rather small, all copepod and cladoceran taxa (accept *D. magna*) had an average body-size smaller than 1 mm, as is expected for tropical lakes (Lewis, 1996).

Zooplankton abundance and biomass is higher in Lake Chamo versus Lake Abaya, and this is most probably due to the higher phytoplankton biomass in Lake Chamo (chlorophyll-a biomass). Only Calanoida and *Ceriodaphnia laticaudata* were higher in abundance and biomass in Lake Abaya. The latter species seems to substitute the smaller *Ceriodaphnia cornuta* in Lake Abaya, as C. cornuta was the second most abundant species in Lake Chamo, and had a lower abundance than *C. laticaudata* in Lake Abaya.

Mesocyclops spp. have a higher relative abundance in Lake Chamo compared to Abaya and this may be due to calanoid copepods being their competitors for selective feeding on phytoplankton in Lake Abaya, and as *Mesocyclops spp.* eat small sized zooplankton, the higher relative abundance of small prey as C. cornuta and Rotifera (>64 µm) in Lake Chamo may also contribute to this pattern. Body-size differences between both lakes were found for *D. australiensis* (bigger in Chamo) and *D. magna* (bigger in Abaya). For *D. magna* we already mentioned the size-efficiency hypothesis as a possible explanation, *Diaphanosoma* on the other hand are known to be good adapted to living at high food concentrations (Sarma, Nandini & Gulati, 2005) which may give them an advantage in Lake Chamo, as phytoplankton productivity is much higher.

Horizontal distribution patterns

In the vertical transect of both lakes: *Daphnia*, *Diaphanosoma* and Calanoida were related to the pelagic zones**,** the chydorid- cladoceran *Leydigia* was found in the vegetated littoral zone and *Macrothrix* were associated towards the littoral zone, as was expected for these species (De Meester 2012; Declerck et al. 2007). *Ceriodaphnia* are normally littoral species, but C. cornuta did not seem to prefer any particular zone, and contradictory *C. laticaudata* was found to have a higher abundance in the pelagic of Lake Abaya. Cyclopoida are also known to be littoral species (De Meester 2012; Declerck et al. 2007) but our *Mesocyclops spp.* however did not seem to prefer any of the three different habitats**.** This pattern of littoral species not preferring this habitat is probably caused by these lakes being shallow, with the absence of a very deep pelagic zone. And at last *Moina* showed the most interesting pattern, as it was significantly higher in the littoral vegetated zone of Lake Chamo, while it showed a positive association towards the pelagic zone in Lake Abaya. Further we found for both lakes that C. cornuta differed across the horizontal transect in Body-size, and higher sizes versus other habitats were found in the pelagic.

Vertical distribution patterns

We believe it is the first time that both lake zooplankton communities were investigated over the water column in the pelagic zone, this to a depth of ten meters. Both lakes show a pattern of all species being less abundant in the first two meter versus the rest of the water column, and in Abaya it was significantly proven that the total zooplankton abundance was lower in the first two meter versus all deeper depth samples. The most probable explanation is an avoidance of visual predators at the surface of the water column**.** For all taxa, in both lakes, abundance and biomass differences were only found between the surface (first two meter) compared with the deeper samples, so no differences were found between depths deeper than 2 meter, which shows us that zooplankton is very homogeneous dispersed over the pelagic water column deeper than 2 meter. In Lake Chamo, *D. australiensis* had a lower biomass at the surface versus some deeper depths, further no differences were found in Lake Chamo, but in Lake Abaya however, *M. mongolica*, *D. magna* and *D. australiensis* were all significant lower in biomass at the surface versus all deeper depth (every 2 m). As *D. magna* has the largest average cladoceran body size in both lakes, it is highly susceptible to fish predation, which may cause a preference of *D. magna* towards deeper depths. Another explanation for *D. magna* being less abundant at the surface could also be the higher temperatures prevailing here during the day, because the upper thermal tolerance of large, typically temperate, cladocerans is around 30° C (Iglesias et al. 2011). In total, taxa in Abaya showed a higher tendency compared to Lake Chamo to stay out of the first two meters, which may be caused by a higher visual fish predation in Lake Abaya. We note here that in both lakes' water columns there would be no big trade off for vertical migration between predation on the one side and food and temperature on the other, as Chlorophyll-a levels and temperature do not differ a lot over depth.

Richness and diversity differences between lakes and subhabitats

No difference between both lakes occurs if it comes to cladoceran richness and Shannon-Wiener diversity. In the horizontal transect within the lakes we found a lower species richness in Abaya in the vegetated littoral versus the littoral and the pelagic zone. In Lake Chamo this was not true for richness, but here we found the same pattern for the Shannon-Wiener diversity (lower diversity in the vegetated littoral). We also did not find any different species in the vegetated littoral zone compared to the others, and this is rather strange as diversity in lakes normally to a large extent depends on the presence of a vegetated littoral zone. But this could be explained by the fact that in tropical areas, macrophytes seem to provide less refuge against fish predation, as small fish (both in species and abundance) seem to aggregate within the macrophytes in the tropics (De Meester, 2012; Teixeira, 2009).

4.3 Conclusion

In conclusion we found that both lakes in dry season were subsaline, had similar total nitrogen and phosphorous levels and are most probably nitrogen limited lakes. We also found that Lake Chamo is more saline, more limited in available nutrients (orthophosphate, nitrate, and ammonium) with an emphasis on available nitrogen, less turbid, has a higher phytoplankton biomass and productivity, a higher zooplankton biomass, a different distribution of its zooplankton species, and most probably has a higher zooplankton grazing pressure than Lake Abaya. We also found a superficial thermal and saline stratification in Lake Chamo which probable has a nocturnal breakdown. In the long term we found that Lake Chamo is increasing in conductivity and salinity ([major ions]), is becoming more turbid and, as Abaya, seems to be increasing in total nitrogen and phosphorous levels. Further, Abaya seems to decrease its pH levels, and both lakes seem to be decreasing in phytoplankton biomass. For the zooplankton community it seems that Lake Chamo has a high biomass and abundance of cladocerans and cyclopoid-copepods in comparison with the tropics, while these taxa are low in abundance and biomass in Lake Abaya, however biomass of its calanoid copepods seems to be averaged for the tropic zone. We further found that both lakes are dominated by copepod-zooplankton, and found that *Daphnia* species are well represented in biomass in both lakes, with the inclusion of a typical temperate species (i.e. *D. magna*). Both lakes had the same taxon richness and did not differ in cladoceran diversity, but we found important differences in zooplankton community composition (e.g. absence of calanoid copepods in Chamo) and distribution. In the pelagic water column we found (daytime) that species are homogeneous distributed beneath a depth of two meter (abundance and biomass), and seem to have a higher abundance and biomass within this depth. This pattern was strong for *D. australiensis* in both lakes, and further for *D. magna* and *M. mongolica* in Lake Abaya.

Overall we can conclude that both lakes have characteristics to promote toxic phytoplanktonic species, and show significant changes over time. That’s why we incest these lakes should be monitored, and measures should be taken concerning the inflow rivers and fisheries, for the well being of the area. For instance: Chamo’s high phytoplankton productivity and biomass is most probably higher than Abaya’s due to its less turbid state. And we found this lake is increasing its turbidity, and this, together with the fast salinity increase, could have a major impact on the lakes biotic community in the future, and so also on its highly valuable fish stock (i.e. yields and diversity) and water quality.

5 Summary

We compared the Ethiopian Rift Valley lakes Chamo and Abaya according to key environmental variables and mesozooplankton community characteristics in a horizontal (inflow to outflow) and vertical (pelagic water column) profile at the end of the second dry season. Additionally, we compared our data with older data from literature to investigate changes in lake characteristics through time. Our results allow us to draw some general conclusions:

1) Chamo has the highest salinity, and both lakes can be included in the range of subsaline lakes. Conductivity, and also salinity ([major ions]) are on an increase since the 1940's, with a strong trend in Chamo. Lake Chamo exhibits a superficial saline and thermal stratification, and we expect both stratifications have a nocturnal breakdown.

2) Abaya has a higher turbidity and suspension of solids than Chamo, the latter most probably caused by inorganic and dead organic suspended matter. The Kulfo River in Chamo carried much suspended solids with it. Turbidity in Chamo is on the increase since the 80's, and Secchi depth seems to evolve towards same levels as in Abaya.

3) Nitrogen is probably limiting in both lakes, and the most in Lake Chamo (available nitrogen levels). Furthermore, we see that available phosphorous and total phosphorous are getting higher since measurements after 2005 for both lakes, and total nitrogen shows the same rising trend in Lake Chamo.

4) Phytoplankton productivity and biomass are higher in Lake Chamo, probably due to its less turbid state. We also expect that the zooplankton grazing pressure on phytoplankton is much higher in Chamo, which can lead to faster growing and inedible phytoplankton (e.g. toxic). And since the 1960s, phytoplankton biomass seems to decline in both lakes.

5) Besides the typical tropical cladoceran genera we found two Daphnia species, including the typical temperate species *D. magna*. For copepods we only found cyclopoid copepods in Lake Chamo, while in Abaya, also calanoid copepods were found next to the former. Copepods (especially Mesocyclops spp.) dominated both lakes in abundance and biomass.

6) For the tropics, the overall cladoceran and cyclopoid density was high in Lake Chamo and low in Abaya. The average zooplankton body sizes for all taxa (*D. magna* excluded) were, as expected for tropical lakes, less than 1 mm.

7) Zooplankton taxa seem to be homogenised in distribution over the pelagic water column beneath two meter in both abundance and biomass. All taxa seem however to show a lower presence in the initial 2 meters from the pelagic water column, which is probably an avoidance towards visual predation. Strong patterns were found in Lake Abaya for *D. australiensis*, *D. magna* and *M. mongolica*, as they all had a significant lower biomass at the surface of the water column versus all deeper zones (every two meter).

Samenvatting

We vergeleken de Ethiopische Riftvallei meren Chamo en Abaya volgens belangrijke omgevingsvariabelen en mesozoöplankton gemeenschapskenmerken in een horizontaal (instroom tot uitstroom) en verticaal (pelagische waterkolom) profiel, op het einde van het tweede droogseizoen. Daarnaast vergeleken we onze gegevens met oudere gegevens uit de literatuur naar veranderingen doorheen de tijd. Uit onze resultaten kunnen we enkele algemene besluiten trekken:

1) Chamo heeft het hoogste zoutgehalte en beide meren zitten in het bereik van de subsaliene meren. Conductiviteit en saliniteit ([belangrijkste ionen]) zijn sinds de jaren 40 met een sterke trend aan het stijgen in Chamo. Chamo vertoont een zeer oppervlakkige saline en thermische stratificatie, en we verwachten dat beide straficaties ’s nachts worden doorbroken.

2) Abaya heeft een hogere troebelheid en suspensie van vaste stoffen dan Chamo, laatstgenoemde factor hoogstwaarschijnlijk veroorzaakt door anorganisch en dood organisch materiaal. De Kulfo rivier in Chamo droeg veel stoffen in suspensie met zich mee. Troebelheid in Chamo is aan het stijgen sinds de jaren 80, en Secchi diepte lijkt te evolueren naar hetzelfde niveau als in Abaya.

3) Beide meren zijn waarschijnlijk stikstof gelimiteerd, en deze limitatie lijkt het sterkst in Chamo. We zien ook dat beschikbaar en totaal fosfor in hogere concentraties aanwezig zijn na 2005, en dat de totale stikstof dezelfde stijgende trend vertoont in Chamo.

4) Fytoplankton productiviteit en biomassa zijn beiden hoger in Chamo, waarschijnlijk veroorzaakt door de lagere troebelheid in dit meer. We vermoeden ook dat de zoöplanktongraasdruk op fytoplankton veel hoger is in Chamo, wat kan leiden tot sneller groeiende en oneetbaar fytoplankton (e.g. toxisch).

5) Naast de typische tropische cladocere genera vonden we ook twee *Daphnia* soorten in beide meren, waaronder een typische soort uit gematigde regio’s (i.e. *D. magna*). Voor de copepoden vonden we enkel cyclopoide copepoden in Lake Chamo, terwijl we in Abaya, naast de cyclopoide copepoden ook calanoide copepoden aantroffen. Copepoden (vooral *Mesocyclops spp.*) domineerden beide meren zowel in abundantie als in biomassa.

6) Voor de tropische regio was de cladoceren en cyclopoide copepoden densiteit hoog in Chamo, en laag in Abaya. De gemiddelde lichaamsgrootten voor alle taxa (D. magna uitgesloten) lagen, zoals verwacht voor tropische meren, onder 1 mm.

7) Zoöplankton taxa lijken gehomogeniseerd verspreid te zijn over de pelagische waterkolom onder 2 meter (abundantie en biomassa). Alle taxa lijken echter lager aanwezig te zijn in de eerste 2 meter van de pelagische waterkolom, wat waarschijnlijk gelinkt kan worden aan een vermijden van visuele predatie. Sterke patronen werden gevonden in Lake Abaya voor *D. australiensis*, *D. magna* en *M. mongolica*, die allemaal een significant lagere biomassa aan het oppervlak van de waterkolom vertoonden versus alle diepere zones (om de 2 meter).

7 REFERENCES

Abebe, Y.D.; Geheb, K., ed., 2003. *Ethiopian Wetlands.* 1. Kenya: IUCN. Nairobi, Kenya

Alberta Environment, 2006 *Aquatic Ecosystems Field Sampling Protocols* [pdf]: Government of alberta. Available at: http://environment.gov.ab.ca/info/home.asp

Awulachew, S.B, 2006. *Investigation of physical and bathymetric characteristics of Lakes Abaya and Chamo, Ethiopia, and their management implication*s. Lakes & Reservoirs: Research and Management, 11, 73–82

Awulachew, S.B, 2007. *Abaya-Chamo Lakes Physical and Water Resources Characteristics, including Scenarios and Impacts.* Siegen: University of Siegen.

Ayenuw, T., 2004. *Environmental implications of changes in the levels of lakes in the Ethiopian Rift since 1970.* Reg. Environ Change, 4, 192–204

Azevedo. F.,D., Dias, J.D., 2012. *Length–weight regressions of the microcrustacean species from a tropical floodplain.* Acta Limnologica Brasiliensia, 24 (1), 1-11

Baxter, R.M., 2002. Lake morphology and chemistry. ln: C. Tudorancea, W.D. Taylor, eds. 2002. *Ethiopian rift valley lakes.* Leiden: Backhuys Publishers. Ch.3

Bilotta, G.S., Brazier, R.E., 2008. *Understanding the influence of suspended solids on water quality and aquatic biota.* Water research, 42, 2849 – 2861

Blumberg, S., Schütt, B., 2004. *Character of lake floor sediments from central Lake Abaya, South Ethiopia.* Lake Abaya Research Symposium, 4,.

Boccaletti, M., Bonini, M., Mazzuoli, R., Abebe, B., Piccardi, L., Tortorici, L., 1998, *Quatanary oblique extensional tectonics in the Ethiopian Rift (Horn of Africa).* Tectonophysics, 287, 97-116

Bouillon, S., Gillikin, D., & Connolly, R. I. W. E., McLusky D. (Eds.), Treatise on Estuarine and Coastal Science Volume 7: Functioning of Ecosystems at the Land–Ocean Interface (pp. 143-173). Elsevier. (Eds.). (2012). *Use of stable isotopes to understand food webs and ecosystem functioning in estuaries.*

Boxshall, G.A., Halsey, S.H., 2004, *An Introduction to Copepod Diversity (2 Vol. Set),* Ray Society

Boxshall, G.A., Defaye, D., 2008. *Global diversity of copepods (Crustacea: Copepoda) in freshwater.* Hydrobiologia, 595,195–207

Dauchez, S., Legendre, L., Fortier, L., 1995, *Assessment of simultaneous uptake of nitrogenous nutrients (15N) and inorganic carbon (13C) by natural phytoplankton populations.* Marine Biology, 123, 651-666

Deas, M.L., Orlob, G.T., 1999. *KLAMATH RIVER MODELING PROJECT,* Center for Environmental and Water Resources Engineering, Report No. 99-04

Declerck, S., Vanderstukken, M., Pals, A., Muylaert, K., De Meester, L., 2007. *Plankton biodiversity along a gradient of productivity and its mediation by macrophytes.* Ecology, 88, 2199-2210

De Meester, L., 2012. Advanced Aquatic Ecology, *B-KUL-I0D28A.* KU Leuven, unpublished

Drenner, R.W., Strickler J.R., O'Brien W.J., 1978. *Capture Probability: The Role of Zooplankter Escape in the Selective Feeding of Planktivorous Fish.* Journal of the Fisheries Research Board of Canada, 35(10): 1370-1373

Flössner, D., 2000. Die Haplopoda und Cladocera Mitteleuropas Leiden: Backhuys Publishers.

Froese, R., Pauly, D., Editors. 2013. FishBase. World Wide Web electronic publication. www.fishbase.org, version (02/2013).

Golubtsov, A.S., Habteselassie, R., 2010. *Fish faunas of the Chamo-Abaya and Chewbahir basins in southern portion of the Ethiopian Rift Valley: origin and prospects for survival,* Aquatic Ecosystem Health & Management, 13(1), 47–55.

Golubtsov, A.S., Dgebuadze, Y.Y., Mina, M.V., 2002. Fishes of the Ethiopian Rift Valley. ln: C. Tudorancea, W.D. Taylor, eds. 2002. *Ethiopian rift valley lakes.* Leiden: Backhuys Publishers. Ch.10

Grove, A. T., Street, F. A., Goudie, A. S., 1975. *Former lake levels and climatic change in the rift valley of southern Ethiopia*, The Geographical Journal, 141 (2), 177-194.

Hama, T., Miyazaki, T., Ogawa, Y., Iwakuma, T., Takahashi, M., Otsuki, A., & Ichimura, S., 1983. *Measurement of Photosynthetic Production of a Marine-Phytoplankton Population using a Stable C-13 Isotope*. Marine Biology, 73(1), 31-36.

Hammer, U.T., 1986. Saline Lake Ecosystems of the World: Springer

Hart, R.C., 1988, *zooplankton feeding rates in relation to suspended sediment content: potential influences on community structure in a turbid reservoir*. Freshwater Biology, 19(1), 123–139

Helm, I., Jalukse, L., Leito, I., 2012. *A highly accurate method for determination of dissolved oxygen: Gravimetric Winkler method.* Analytica Chimica Acta, 741, 21– 31

Iglesias, C., Mazzeo, N., Meerhoff, M., Lacerot, G., Clemente, J.M., Scasso, F., Kruk, Car., Goyenola, G., 2011. *High predation is of key importance for dominance of smallbodied zooplankton in warm shallow lakes: evidence from lakes, fish exclosures and surface sediments.* Hydrobiologia 667: 133–147

Jeppesen, E., Jensen. J.P., Søndergaard, M., 2002, *Response of phytoplankton, zooplankton, and fish to re-oligotrophication*: *An 11 year study of 23 Danish lakes.* Aquatic Ecosystem Health & Management, 5:1, 31-43

Kebede, E., Zinabu G.M., Ahlgren, I., 1994, *The Ethiopian Rift Valley lakes: chemical characteristics of a salinity-alkalinity series*. Hydrobiologia 288, 1-12

Kebede, S., Travi Y., Rozanski K., 2009. *The* $d^{18}O$ *and* $d^{2}H$ *enrichment of Ethiopian lakes*. Journal of Hydrology, 365, 173–182.

Keranen, K., Klemperer, S.L., 2007. *Discontinuous and diachronous evolution of the Main Ethiopian Rift: Implications for development of continental rifts.* Earth and Planetary Science Letters, 265, 96–111

Klein, A.E., 1977, A study of heavy *metals in lake Abbaya, Ethiopia, and the incidence of non-parasitic elephantiasis*, water research. 11: 323-325.

Korinek, V., 2000. *A guide to the limnetic Cladocera in African inland lakes (Crustacea, Branchiopoda)*. Prague: Charles University

Koroleff, F., 1970, *Determination of total phosphorus in natural waters by means of persulfate oxidation*. International Council for the Exploration of the Sea (ICES*)*, Report No. 3

Lewis, W.M., 1996. *Tropical lakes, how latitude makes a difference*. Perspectives in Tropical Limnology, 43-63

Mackay, A.W., 2007. Large Lakes, *Encyclopedia of Quaternary Science*, 548–557

McCauly, E., 1971. The Estimation of the Abundance and Biomass of Zooplankton in Samples. ln: J.A., Downing, F.H., Rigler, eds. 1984. *A manual on methods for the Assessment of Secondary Productivity in Fresh Waters*, Oxford, London, Edinburgh,
Boston, Melbourne: Blackwell Scientific Publications, Ch. 7.

Muschal, M., 2006. *Assessment of risk to aquatic biota from elevated salinity—A case study from the Hunter River, Australia*. Journal of Environmental Management 79, 266–278.

Pimenov, N., Zyakun, A., Prusakova, T., Lunina, O., Ivanov, M., 2008, *Application of 13C mineral carbon for assessment of the primary production of organic matter in aquatic environments*. Microbiology, 77(2), 224-227

Ryan, P.A., 1991, *Environmental effects of sediment on New Zealand streams: a review.* New Zealand Journal of Marine and Freshwater Research, 25, 207-221

Pinto-Coelho, R., Pinel-Alloul, B., Méthot, G., Havens, K.E., 2005. *Crustacean zooplankton in lakes and reservoirs of temperate and tropical regions: variation with trophic status*. Fish. Aquat. Sci. 62: 348–361

Sagraria, M.G., Jeppesen, E., Sondergaard, M., Jensen. J.P., Lauridsen, T.L., Landkildehuis., F., 2005. *Does high nitrogen loading prevent clear-water conditions in shallow lakes at moderately high phosphorus concentrations?*. Freshwater Biology, 50, 27–41

Sarma, S.S.S., Nandini, S., Gulati R.D., 2005, *Life history strategies of cladocerans: comparisons of tropical and temperate taxa*. Hydrobiologia, 542, 315–333

Wood, J., Guth, A., nd. *East Africa's Great Rift Valley: A Complex Rift System.* [online] Geology.com, Available at: < http://geology.com/articles/east-africa-rift.shtml >

WoldeGabriel, G., 2002. An overview on volcanic, tectonic, rifting, and sedimentation processes. ln: C. Tudorancea, W.D. Taylor, eds. 2002. *Ethiopian rift valley lakes.* Leiden: Backhuys Publishers. Ch.2.

Rao, T.R., Kumar R., 2002. Patterns *of prey selectivity in the cyclopoid copepod Mesocyclops thermocyclopoides*, Aquatic Ecology 36: 411–424.

Rieper, M., 1982. *Feeding Preferences of Marine Harpacticoid*, Marine ecology - progress series, 7: 303-307

Rosenmeier, Abbott, 2005, *S.O.P. – Loss On Ignition*, University of Pittsburgh, Loss_On_Ignition_Protocol.doc

Shumbulo, E., 2004. *Temporal and spatial variations in biomass and photosynthetic production of phytoplankton in Lake Chamo, Ethiopia*. Master of Science in Biology, Addis Ababa University.

Shumbulo, E., Assefa, F., ca. 2005. Phytoplankton Biomass in Relation to Water Quality in the Lakes Abaya and Chamo, Ethiopia ln: G. Förch, ed. 2009. *Summary of Master Theses from Arba Minch University, Ethiopia.* Universität Siegen: Centre for international capacity development. Ch.7

Schütt, B., Thiemann, S., Wenclawiack, B., 2005. *Depostion of modern fluvio-lacustrine sediments in Lake Abaya, South Ethiopia – A case study from the delta areas of Bilate River and Gidabo River, northern basin.* Zeitschrift fuer Geomorphologie, 138, 131-151

Schütt, B., Thiemann, S., 2006 Kulfo River, *South-Ethiopia as the regulator of lake level changes in the Lake Abaya – Lake Chamo system.* Zeitblad Geologie Paläontologie, Heft ½, 129-143

Study team from Arba Minch University, Gamo Gofa zone agriculture Bureau and African Parks, Ethiopia, 2007, *A Report on the Investigation of the Cause of the Immense Fish Kill Occurred between April 30 Night and May 01, 2007 Dawn in Lake Chamo, Arba Minch,* Arba Minch: unpublished

Talling, J.F., Talling, I.B., 1965, I.B., *The Chemical Composition of African Lake Waters.* Int. Revue ges. Hydrobiol. 50, 221-463

Taylor, W.D., Kebede, E., Zinabu, G.M., 2002. Primary and Secondary Production in the Pelagic Zone. ln: C. Tudorancea, W.D. Taylor, eds. 2002. *Ethiopian rift valley lakes.* Leiden: Backhuys Publishers. Ch.5

Teklemariam, A., Wenclawiak, B., 2004. *Water quality monitoring within the Abaya – Chamo drainage basin.* Lake Abaya research symposium - proceedings

Teklemariam, A., 2005. *Water Quality Monitoring in Lake Abaya and Lake Chamo Region.* Ph.D. University of Siegen

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

Tudorancea C., Zullini, A., 1989, *Associations and distribution of benthic nematodes in the Ethiopian Rift Valley lakes.* Hydrobiobgia 179: 81-96

Ugo, Y., 2008. *Evaluation of water quality parameters and their implications to fishes and fisheries in lake Chamo, Southern Ethiopia,* master in environmental science. Addis Ababa University.

Watkins, J., Rudstam, L., Holeck, K., 2001, *Length-weight regressions for zooplankton biomass calculations – A review and a suggestion for standard equations.* Cornel Univeristy: http://hdl.handle.net/1813/24566

Weber-Scannell, P. K., Duffy, L. K., 2007. *Effects of Total Dissolved Solids on Aquatic Organisms: A Review of Literature and Recommendation for Salmonid Species.* American Journal of Environmental Sciences, 3 (1), 1-6.

Willén, E., Ahlgren, G., Tilahun, G., Spoof, L., Neffling, M., Meriluoto, J., 2011. *Cyanotoxin production in seven Ethiopian Rift Valley lakes.* Inland Waters, 1, 81-91

Wurts, W.A., Durborow R.M., 1992. *Interactions of pH, Carbon Dioxide, Alkalinity and Hardness in Fish Ponds.* SRAC Publication, No. 464

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

Zhang, Y., Liu, X., Yin, Y.,Wang, M., Qin, B., 2012 *Predicting the light attenuation coefficient through Secchi disk depth and beam attenuation coefficient in a large, shallow, freshwater lake.* Hydrobiologia, 693, 29–37

Zinabu, G.M., Taylor, W.D., 1997. *Bacteria-chlorophyll relationships in Ethiopian lakes of varying salinity: are soda lakes different?*. Journal of Plankton Research, 19(5), 647-654,

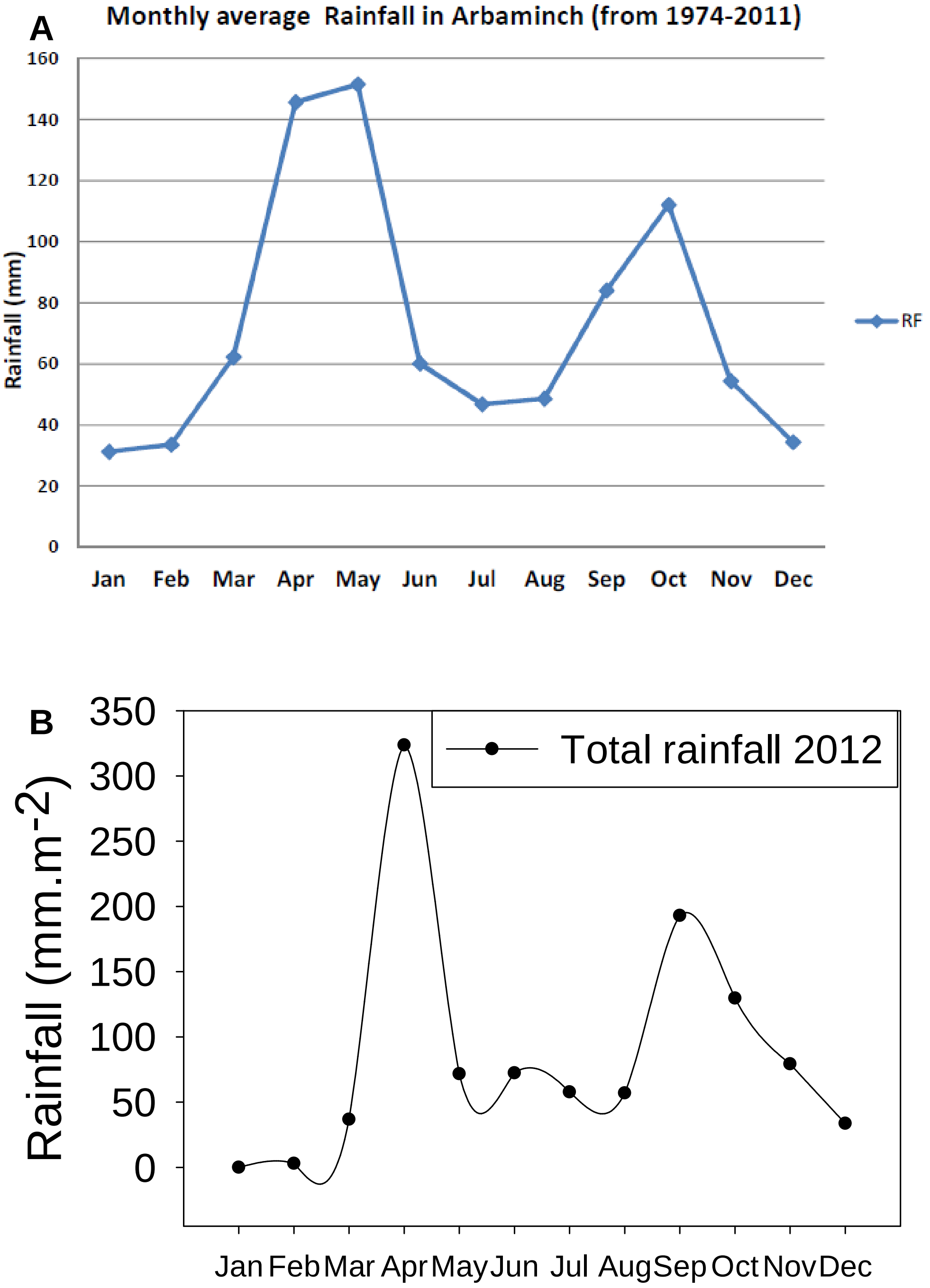
Zinabu**,** G.M., Chapman, L.J., Chapman, A.C., 2002, *Conductivity as a predictor of a total cations and salinity in Ethiopian lakes and rivers*: *revisiting earlier models.* Limnologica 32, 21-26

Zinabu, G.M., Kebede-Westhead, E., Desta, Z., 2002. *Long-term changes in chemical features of waters of seven Ethiopian rift-valley lakes.* Hydrobiologia, 477, 81–91.

8 ADDENDUM

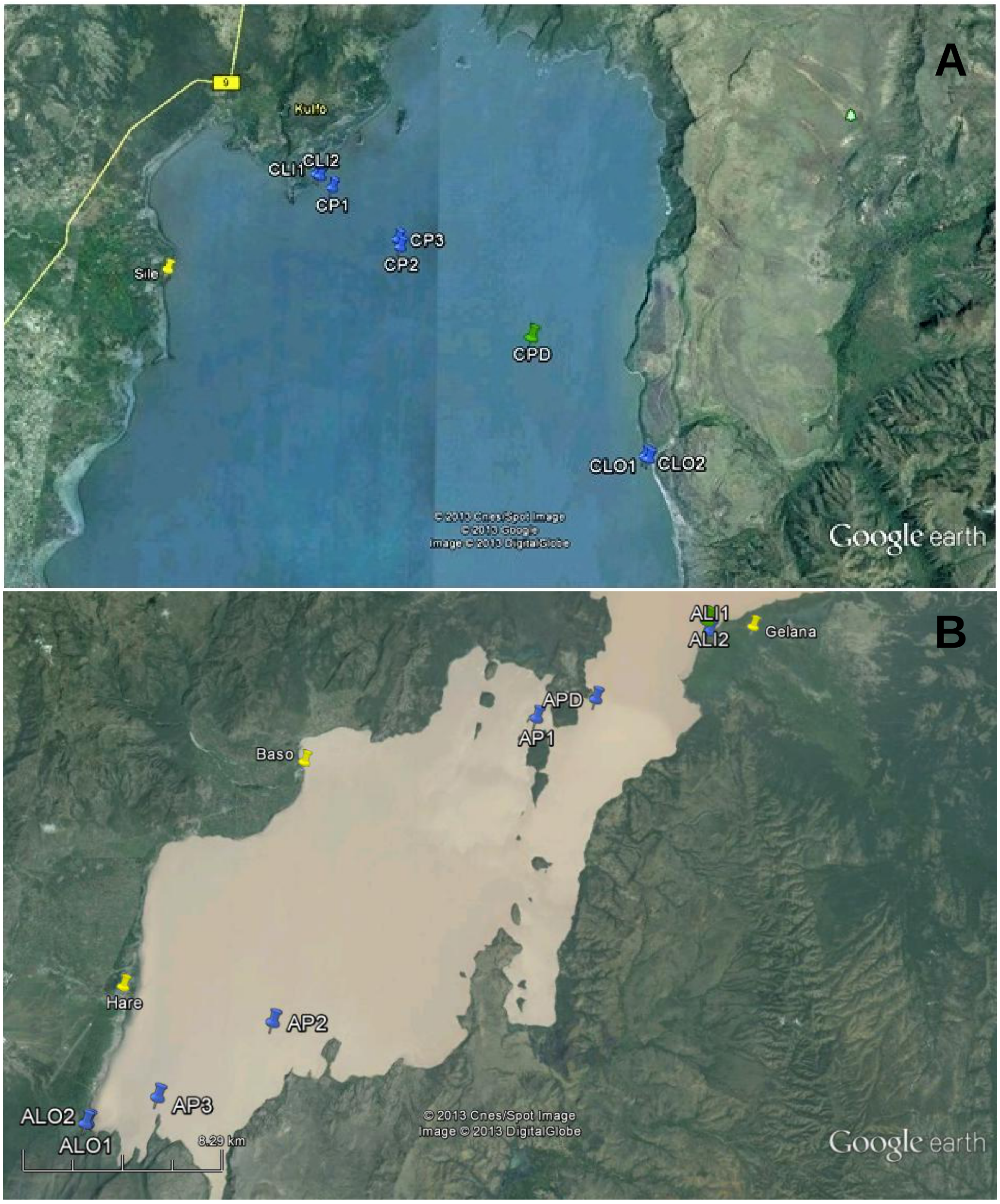
Appendix 1: Rainfall patterns

Appendix 1 A & B: A) Monthly total rainfall in Arba Minch since 1974-2012 demonstrating two wet, and two dry seasons. B) Monthly rainfall in 2012 (International Meteorological Station Region 63, 1974-2011) modified by: Fassil Eshetu Teferra & Arne Deriemaecker



Appendix 2: Locating the sample stations

Appendix 2 A & B: Transect lines and Sampling stations of Lake Chamo (A) and Abaya (B). Sample stations are identified by a four-character code. “C”/ “A” = Chamo or Abaya, “L” = littoral, “P”= pelagic, “D” = deep “I”= inflow and “O” = outflow, different numbers denote different sample stations.



Appendix 2C: Sample stations’ exact locations and distance from the first inflow-station

A

Sample station	Latituda	Longitude	Distance from CLI1 (m)
CLI1	5°55'10.44"N	37°33'32.47"E	0
CLI2	5°55'8.61"N	37°33'35.34"E	108
CP1	5°54'58.72"N	37°33'45.72"E	543
CP2	5°54'8.98"N	37°34'42.58"E	2711
CP3	5°54'15.35"N	37°34'40.44"E	2879
CPD	5°52'48.08"N	37°36'24.07"E	6848
CLO2	5°51'23.57"N	37°37'54.17"E	10666
CLO1	5°51'21.61"N	37°37'56.95"E	10776

B

Sample station	Latituda	Longitude	Distance from ALI1 (m)
ALI1	6°12'39.74"N	37°50'46.17"E	0
ALI2	6°12'4.16"N	37°50'48.56"E	1189
AP1	6°10'22.10"N	37°46'20.96"E	9148
AP2	6° 2'59.77"N	37°40'7.38"E	26657
AP3	6° 1'19.18"N	37°37'33.53"E	32158
APD	6°10'52.01"N	37°47'49.98"E	6524
ALO2	6° 0'46.07"N	37°35'59.90"E	34615
ALO1	6° 0'44.58"N	37°35'57.22"E	35018

Appendix 3: Environmental characteristics between and within lakes Abaya and Chamo

Appendix 3 A: Environmental variables between lakes, marked correlations are significant ($p < 0.050$)

Chamo > Abaya	Test	Transformation	Output
Daytime oxygen concentration	Kruskal Wallis ANOVA	/	p = 0.036
Chlorophyll-a	One-way ANOVA	/	SS = 56663.24, MS = 56663.24, F = 9,066, P < 0.001
Conductivity	Kruskal Wallis ANOVA	/	p = 0.012
pH	Kruskal Wallis ANOVA	/	p = 0.012
Phytopankton productivity	One-way ANOVA	/	p = 0.002
Salinity	Kruskal Wallis ANOVA	/	p = 0.011
TDS	Kruskal Wallis ANOVA	/	p = 0.012
Abaya > Chamo	Test	transformation	output
Ammonium	One-way ANOVA	/	SS = 0.06, MS = 0.06, F = 12.084, P = 0.004,
Nitrate	One-way ANOVA	log(x+1)	SS = 0.10, MS = 0.10, F = 8.664, p = 0.011
Turbidity	Kruskal-Wallis ANOVA	/	p = 0.009
Phosphate	Kruskal-Wallis ANOVA	/	p = 0.036
TSS	Kruskal-Wallis ANOVA	/	p = 0.046
Chamo vs. Abaya	Test	transformation	output
% Carbonate (Sediment)	Kruskal-Wallis ANOVA	/	p = 0.401
% Organic matter (Sediment)	Kruskal-Wallis ANOVA	/	p = 0.074
Euphotic depth	Kruskal-Wallis ANOVA	/	p = 0.142
Temperature	One-way ANOVA	/	SS = 0.092, MS = 0.092, F = 0.057, p = 0.815
Total nitrogen	Kruskal-Wallis ANOVA	/	p =1.000
Total phosphorous	Kruskal-Wallis ANOVA	/	p = 0.317

Appendix 3B: Environmental variables within both lakes in a horizontal transect, marked correlations are significant ($p < 0.050$) TDS = Total dissolved solids, [O] = daytime oxygen concentration

inflow vs. pelagic vs. outflow	Test	Transformation	Output
Chamo-Ammonium	Kruskal-Wallis ANOVA	/	p = 0.954
Chamo-Chlorophyll-a	Kruskal-Wallis ANOVA	/	p = 0.031
Chamo-Conductivity	Kruskal-Wallis ANOVA	/	p < 0.001
Chamo-[DO]	One-way ANOVA	/	SS = 8.547, MS = 4.273, F = 11.055, p < 0.001
Chamo-Nitrate	Kruskal-Wallis ANOVA	/	p = 0.078
Chamo-Orthophosphate	Kruskal-Wallis ANOVA	/	p = 0.569
Chamo-pH	Kruskal-Wallis ANOVA	/	p = 0.156
Chamo-Salinity	Kruskal-Wallis ANOVA	/	p < 0.001
Chamo-TDS	Kruskal-Wallis ANOVA	/	p < 0.001
Chamo-Turbidity	Kruskal-Wallis ANOVA	/	p < 0.001
Abaya-Chlorophyll-a	Kruskal-Wallis ANOVA	/	p = 0.258
Abaya-Conductivity	Kruskal-Wallis ANOVA	/	p = 0.448
Abaya-[DO]	One-way ANOVA	/	SS = 69.481, MS = 34.741, F = 21.543, p < 0.001
Abaya-pH	Kruskal-Wallis ANOVA	/	p = 0.275
Abaya-Salinity	Kruskal-Wallis ANOVA	/	p = 0.216
Abaya-TDS	One-way ANOVA	/	SS = 550.688, MS = 275.344, F = 7.548, p = 0.007
Abaya-Turbidity	Kruskal-Wallis ANOVA	/	p = 0.027

Appendix 3C: Environmental variables within both lakes over the pelagic water column, marked correlations are significant ($p < 0.050$) TDS = Total dissolved solids, [O] = daytime oxygen concentration

Surface vs Middle vs. Bottom	Test	Transformation	Output
Chamo-[DO]	Friedman ANOVA	/	p = 0.039
Chamo-Chlorophyll-a	Repeated measures ANOVA	log(x+1)	SS = 0.014, MS = 0.007, F = 7.942, p = 0.021
Chamo-Conductivity	Repeated measures ANOVA	/	SS = 37125454, MS = 37125454, F = 136672, p < 0.001
Chamo-Salinity	Friedman ANOVA	/	p = 0.717
Chamo-TDS	Friedman ANOVA	/	p = .867
Chamo-Temperature	Repeated measures ANOVA	/	SS = 2.645, MS = 1.323, F = 76.45, p <0.001
Chamo-Turbidity	Friedman ANOVA	/	p = 0.0497
Abaya-[DO]	Friedman ANOVA	/	p = 0.368
Abaya-Chlorophyll-a	Repeated measures ANOVA	log(x+1)	SS = 1916.752, MS = 958.376, F = 9.221, p = 0.015
Abaya-Conductivity	Friedman ANOVA	/	p = 0.627
Abaya-Salinity	Friedman ANOVA	/	p = 0.368
Abaya-TDS	Friedman ANOVA	/	p = 0.627
Abaya-Temperature	Repeated measures ANOVA	/	SS = 1.902, MS = 0.951, F = 7.87, p = 0.021,
Abaya-Turbidity	Friedman ANOVA	/	SS = 1180.626, MS = 590.313, F =4.691, p = 0.059
pH	Friedman ANOVA	/	p = 0.627

Appendix 3D: Environmental variables over the vertical profile of Chamo's pelagic deep station, marked correlations are significant ($p < 0.050$), TDS = Total dissolved solids, [O] = daytime oxygen concentration

Correlation with depth	Test	Output
CPD-Chlorophyll-a	Lineair regression	SS = 6200.415, MS = 6200.415, F = 29.114, p <0.001, slope = -7.676
CPD-conductivity	Spearman correlation:	r = -0.927, p < 0.050
CPD-[DO]	Lineair regression	SS = 4.116, MS = 4.116, F = 25.459, p <0.001, slope = -0.198
CPD-pH	Spearman correlation:	p > 0.050
CPD-Salinity	Lineair regression	SS = 0.0001, MS = 0.0001, F =3.13, p = 0.111
CPD-TDS	Spearman correlation:	r = -0.639276071, p < 0.050
CPD-Temperature	Lineair regression	SS = 0.001, MS = 0.001, F = 10.298, p = 0.011, slope = -0.004
CPD-Turbidity	Lineair regression	SS = 448.524, MS = 448.524, F =3.770, p = 0.084

Appendix 4: Long term data

Appendix 4A: Long term environmental variables 1: dates in yellow and blue are situated respectively in dry and wet season. “nda” = no data available, measurements divided by a dash are range values, the first and the second number are respectively minimum and maximum measurements.

Parameters	Dates	depth (m)	Abaya	Chamo	Units	Authors
Conductivity	1937	nda	758.2	nda	µS/Cm	Cannicci & Almagia (1947)
	Dec 1937- Feb. 1938	nda	747.05-845.09	nda	µS/Cm	Loffredo & Maldera
	10-11 Mar. 1938	nda	nda	1033.605	µS/Cm	Loffredo & Maldera
	23 May 1961	nda	1003.5	nda	µS/Cm	Talling & Talling, 1965
	Jan.-Feb. 1964	0.1-0.5	694.645	nda	µS/Cm	Wood & Talling, 1988
	Feb. 1964	0.1-0.5	nda	1226.5	µS/Cm	Wood & Talling, 1988
	Julyy 1966	0.1-0.5	1062.595	1115	µS/Cm	Belay & Wood, 1982
	Feb.1975	surface	1254.375	nda	µS/Cm	Klein, 1977
	June 1989	surface	nda	1350	µS/Cm	Zinabu & Taylor, 1997
	15 Mar. 1991	0-2m	nda	1320	µS/Cm	Kebede, Zinabu& Ahlgren, 1994
	15 Mar. 1991	4-5m	nda	1260	µS/Cm	Kebede, Zinabu& Ahlgren, 1994
	16 Mar. 1991	0-2m	925	nda	µS/Cm	Kebede, Zinabu& Ahlgren, 1994
	Mar. 1991	surface	nda	1320	µS/Cm	Zinabu & Taylor, 1997
	Nov. 1991	surface	nda	1428	µS/Cm	Zinabu & Taylor, 1997
	Aug. 1992	surface	nda	1100	µS/Cm	Zinabu & Taylor, 1997
	Jan. 1993	surface	nda	1200	µS/Cm	Zinabu & Taylor, 1997
	Feb. 1993	surface	nda	1326	µS/Cm	Zinabu & Taylor, 1997
	Okt. 1993	surface	nda	1350	µS/Cm	Zinabu & Taylor, 1997
	Sep. 1984	nda	800	1078	µS/Cm	Tudorancea & Zullini 1989
	1990-2000	surface	914.6	1535.7	µS/Cm	Zinabu, Chapman & Chapman, 2002
	1990-2000	surface	921(500–1075)	1568(1260–2310)	µS/Cm	Zinabu, Kebede & Desta, 2002
	Dec. 2002- Jan. 2004	surface	1030-1110	1810-1960	µS/Cm	Tecklemariam & Wenclawiac, 2004
	Sep.-Nov. 2003	near surfac	nda	1751	µS/Cm	Shumbulo, 2004
	Jan., Apr.-May 2004	near surfac	nda	1692	µS/Cm	Shumbulo, 2004
	Jan.-Apr. 2005	nda	nda	1910	µS/Cm	Tilahun & Alghren 2010
	Mar.-July, Sep. 2005	surface	1116.833333	1935	µS/Cm	Shumbulo & Assefa, ca. 2005
	Mar.-July 2008	surface	nda	1761.8	µS/Cm	Ugo, 2008
	Aug. 2012	0-0.5	1064.4375	nda	µS/Cm	Deriemaecker, 2013
	Aug-sept, 2012	0-0.5	nda	1806.25	µS/Cm	Deriemaecker, 2013
TDS	2002-2004	surface	911.1	1522.45	mg/l	Tecklemariam & Wenclawiac, 2004
	Mar.-July 2008	surface	nda	1181	mg/l	Ugo, 2008
	Aug. 2012	0-0.5	530.75	nda	mg/l	Deriemaecker, 2013
	Aug.-Sep. 2012	0-0.5	nda	898.9375	mg/l	Deriemaecker, 2013
Salinity	1937-1938	dnf	0.517	0.651	g/l	Loffredo & Maldura (1941)
	May 1961	nda	0.884	1.063	g/l	Talling & Talling, 1965
	Jan.-Feb. 1964	0.1-0.5	0.771	n.d.	g/l	Wood & Talling, 1988
	Feb. 1964	0.1-0.5	n.d.	1.099	g/l	Wood & Talling, 1988
	July 1966	dnf	0.868	0.945	g/l	Belay & Wood, 1982
	1976	nda	0.768	0.953	g/l	Damm & Edmond, 1984
	1978	dnf	0.72	1.000	g/l	Belay & Wood,1982
	15 Mar. 1991	0-2	0.9	nda	g/l	Kebede, Zinabu& Ahlgren, 1994
	16 Mar. 1991	0-2	nda	1.000	g/l	Kebede, Zinabu& Ahlgren, 1994
	1990-2000	surface	0.833	1.213	g/l	Zinabu, Chapman & Chapman, 2002
	Aug. 2012	0-0.5	0.5325	nda	g/l	Deriemaecker, 2013
	Aug.-Sep. 2012	0-0.5	nda	0.903	g/l	Deriemaecker, 2013

Teklemariam & Wenclawiac, 2004; Ugo, 2008; Wood & Talling, 1988; Talling & Talling, 1965; Klein, 1977; Zinabu & Taylor, 1997; Kebede, Zinabu& Ahlgren, 1994; Zinabu & Taylor, 1997; Tudorancea & Zullini, 1989; Zinabu, Chapman & Chapman, 2002; Zinabu, Kebede & Desta, 2002; Shumbulo, 2004; Tilahun & Alghren 2010; Shumbulo & Assefa, ca. 2005; modified by Arne Deriemaecker

Appendix 4B: Long term environmental variables 2: dates in yellow and blue are situated respectively in dry and wet season. "nda" = no data available, measurements divided by a dash are range values, the first and the second number are respectively minimum and maximum measurements.

Parameters	Dates	depth (m)	Abaya	Chamo	Units	Authors
Turbidity	2002-2004	surface	64-90	40-100	NTU	Tecklemariam & Wenclawiac, 2004
	July, Sep. 2005	nda	95.9 (92.2-99.5)	61 (55-67)	NTU	Shumbulo & Assefa, 2005
	Mar.-July 2008	surface	nda	54.9 (39-83)	NTU	Ugo, 2008
	Aug. 2012	0-0.4	115.46875	nda	NTU	Deriemaecker, 2013
	Aug.-Sep. 2012	0-0.5	nda	34.3925	NTU	Deriemaecker, 2013
TSS	Dec. 2002- Jan. 2004	surface	60-250	50-350	mg/l	Tecklemariam & Wenclawiac, 2004
	Mar.-July 2008	surface	nda	101.5 (18-375)	mg/l	Ugo, 2008
	Aug. 2012	0-0.5	81.12	nda	mg/l	Deriemaecker, 2013
	Aug.-Sep. 2012	0-0.5	nda	47.48809524	mg/l	Deriemaecker, 2013
Chl-a	July 1966	nda	69	89	µg/l	Belay & Wood,1982
	May 1979	nda	nda	73	µg/l	Belay & Wood,1982
	Jan. 1988	dna	7	170	µg/l	Kebede (unpublished)
	June 1989	surface	nda	262	µg/l	Zinabu & Taylor, 1997
	Aug. 1990	surface	nda	181	µg/l	Zinabu & Taylor, 1997
	15 Mar. 1991	0-2m	dna	44.2	µg/l	Kebede, Zinabu& Ahlgren, 1994
	15 Mar. 1991	4-5m	dna	34.6	µg/l	Kebede, Zinabu& Ahlgren, 1994
	16 Mar. 1991	0-2m	5	dna	µg/l	Kebede, Zinabu& Ahlgren, 1994
	16 Mar. 1991	5-6m	3.3	dna	µg/l	Kebede, Zinabu& Ahlgren, 1994
	Mar. 1991	surface	nda	45	µg/l	Zinabu & Taylor, 1997
	Nov. 1991	surface	nda	59	µg/l	Zinabu & Taylor, 1997
	Aug. 1992	surface	nda	123	µg/l	Zinabu & Taylor, 1997
	Jan. 1993	surface	nda	97	µg/l	Zinabu & Taylor, 1997
	Feb. 1993	surface	nda	86	µg/l	Zinabu & Taylor, 1997
	Okt. 1993	surface	nda	40	µg/l	Zinabu & Taylor, 1997
	1990-2000	surface	8.2 (0-33)	100.3 (6.4-267)	µg/l	Zinabu, Kebede & Desta, 2002
	Aug.-Dec. 2003	near surfac	nda	75	µg/l	Shumbulo, 2004
	Jan.-May 2004	near surfac	nda	72.46	µg/l	Shumbulo, 2004
	Jan.-Dec. 2005	nda	nda	29.9	µg/l	Tilahun & Alghren 2010
	Mar.-July 2008	surface	nda	50.9 (30.58-99.39)	µg/l	Ugo, 2008
	Aug. 2012	0-0.5	5.864685	nda	µg/l	Deriemaecker, 2013
	Aug.-Sep. 2012	0-0.5	nda	9.51109	µg/l	Deriemaecker, 2013
Secchi depth	Sep. 1984	surface	19	115	cm	Tudorancea & Zullini, 1989
	15 Mar. 1991	surface	43	nda	cm	Kebede, Zinabu & Ahlgren, 1994
	16 Mar. 1991	surface	nda	65	cm	Kebede, Zinabu & Ahlgren, 1994
	Aug.-Dec. 2003	near surfac	nda	33.7	cm	Shumbulo, 2004
	Jan.-May 2004	near surfac	nda	29.3	cm	Shumbulo, 2004
	2004-2005	surface	nf	35	cm	Tilahun, 2006
	Mar.-July, Sep. 2005	surface	14.5 (12-17)	nda	cm	Shumbulo & Assefa, ca. 2005
	Mar.-July 2005	surface	nda	27.8 (23.8-31)	cm	Shumbulo & Assefa, ca. 2005
	Jan.-Dec. 2005	nda	nda	35	cm	Tilahun & Alghren 2010
	Mar.-July 2008	surface	nda	19.4 (12-30)	cm	Ugo, 2008
	Aug. 2012	0-0.5	14.6	nda	cm	Deriemaecker, 2013
	Aug.-Sep. 2012	0-0.5	nda	34.6875	cm	Deriemaecker, 2013
Euph. depth	Aug.-Dec. 2003	surface...	nda	108	cm	Shumbulo, 2004
	Jan.- May 2004	surface...	nda	93.6	cm	Shumbulo, 2004
	Jan.-Dec. 2005	surface...	nda	109	cm	Tilahun & Alghren 2010
DO	Mar.-July 2008	surface	nda	6,3	mg/l	Ugo, 2008
	Aug. 2012	0-0.5	8.385	nda	mg/l	Deriemaecker, 2013
	Aug.-Sep. 2012	0-0.5	nda	8.899375	mg/l	Deriemaecker, 2013
pH	Jan.-Feb. 1964	0.1-0.5	8.9	nda	pH	Wood & Talling, 1988
	July 1966	nda	8.9	8.9	pH	Belay & Wood, 1982
	Feb. 1975	surface	8.75	nda	pH	Klein, 1976
	1976	nda	8.85	9.5	pH	Damm & Edmond, 1982
	Sep. 1984	nda	8.7	9.2	pH	Tudorancea & Zullini 1989
	15 Mar. 1991	0-2m	8.65	nda	pH	Kebede, Zinabu& Ahlgren, 1994
	16 Mar. 1991	0-2m	nda	8.9	pH	Kebede, Zinabu& Ahlgren, 1994
	1990-2000	surface	8.7 (7.8-9.3)	9.2 (8.6-9.6)	pH	Zinabu, Kebede & Desta, 2002
	Dec. 2002- Jan. 2004	surface	8.5-9.0	9-9.23	pH	Tecklemariam & Wenclawiac, 2004
	Aug.- Dec. 2003	near surfac	nda	9.03	pH	Shumbulo, 2004
	Jan.- May 2004	near surfac	nda	9.27	pH	Shumbulo, 2004
	Mar.-July Sep. 2005	surface	8.61 (8-8.92)	9.15 (8.8-9.4)	pH	Shumbulo & Assefa, ca. 2005
	Jan.-Dec. 2005	nda	nda	8.84	pH	Tilahun & Alghren 2010
	Mar.-July 2008	surface	nda	9.19	pH	Ugo, 2008 (zelf gemiddelde berekend)
	Aug. 2012	0-0.5	8.21875	nda	pH	Deriemaecker, 2013
	Aug.-Sep. 2012	0-0.5	nda	8.516666667	pH	Deriemaecker, 2013

Shumbulo, 2004; Tilahun & Alghren 2010; Wood & Talling, 1988; Zinabu, Kebede & Desta, 2002; Zinabu & Taylor, 1997; Kebede, Zinabu& Ahlgren, 1994; Ugo, 2008; Tudorancea & Zullini, 1989; Shumbulo & Assefa, ca. 2005; Teklemariam & Wenclawiac, 2004; Klein, 1976; modified by Arne Deriemaecker

Appendix 4C: Long term nutrient data, dates in yellow and blue are situated respectively in dry and wet season. “nda” = no data available, measurements divided by a dash are range values, the first and the second number are respectively minimum and maximum measurements.

Parameters	Dates	depth (m)	Abaya	Chamo	Units	Authors
Ammonia	Dec. 2002-Jan. 2004	surface	0.16-0.58	0.03-0.45	mg/l	Tecklemariam & Wenclawiac, 2004
	Mar.-July, Sep. 2005	nda	0.25*(0.13-0.5)*	nda	mg/l	Shumbulo & Assefa, ca. 2005
	Mar.-May, July, Sep. 2005	nda	nda	0.55*(0.05-0.8)*	mg/l	Shumbulo & Assefa, ca. 2005
	Mar.-July 2008	surface	nda	0.02 (0-0.06)	mg/l	Ugo, 2008
Ammonium	Sep. 1978	nda	nda	0.29	mg/l	Belay & Wood, 1982
	15 Mar. 1991	0-2 m	nda	0.0118	mg/l	Kebede, Zinabu & Ahlgren, 1994
	15 Mar. 1991	4-5m	nda	0.0279	mg/l	Kebede, Zinabu & Ahlgren, 1994
	16 Mar. 1991	0-2 m	0.0132	nda	mg/l	Kebede, Zinabu & Ahlgren, 1994
	16 Mar. 1991	5-6 m	0.0144	nda	mg/l	Kebede, Zinabu& Ahlgren, 1994
	Dec. 2002-Jan. 2004	surface	0.6-0.7	0.07-0.3	mg/l	Tecklemariam & Wenclawiac, 2004
	Aug.-Dec. 2003	near surfac	nda	0.577	mg/l	Shumbulo, 2004
	Aug.-Dec. 2003	near surfac	nda	0.6964	mg/l	Shumbulo, 2004
	Jan.-Dec. 2005	nda	nda	0.093	mg/l	Tilahun & Alghren 2010
	Aug. 2012	0-0.5	0.23	nda	mg/l	Deriemaecker, 2013
	Aug-Sept 2012	0-0.5	nda	0.14375	mg/l	Deriemaecker, 2013
Nitrite	Sep.1978	nda	nda	0.003	mg/l	Belay & Wood, 1982
	2002-2004	surface	0-0.05	0-0.02	mg/l	Tecklemariam & Wenclawiac, 2004
	Sep.-Dec. 2003	near surfac	nda	0.00375	mg/l	Shumbulo, 2004
	Jan.-May 2004	near surfac	nda	0.00285	mg/l	Shumbulo, 2004
	Mar.-July, Sep. 2005	nda	0.016 (0-0.071)	0.016 (0-0.058)	mg/l	Shumbulo & Assefa, ca. 2005
	Mar.-July 2008	surface	nda	0.015 (0-0.107)	mg/l	Ugo, 2008
Nitrate	Sep. 1978	nda	nda	0.02	mg/l	Belay & Wood, 1982
	May 1979	nda	nda	0.217-0.445	mg/l	Belay & Wood, 1982
	Dec. 2002-Jan. 2004	surface	0.6-1.8	0.7-3	mg/l	Tecklemariam & Wenclawiac, 2004
	Sep.-Dec. 2003	near surfac	nda	0.021	mg/l	Shumbulo, 2004
	Jan.-May 2004	near surfac	nda	0.024	mg/l	Shumbulo, 2004
	2003-2005	nda	nda	0.0033 (0.001-0.007)	mg/l	Tilahun, 2006
	Mar.-July, Sep. 2005	nda	0.45 (0.18-1)	0.59 (0.15-1.1)	mg/l	Shumbulo & Assefa, ca. 2005
	Jan.-Dec. 2005	nda	nda	0.00325	mg/l	Tilahun & Alghren 2010
	Mar.-July 2008	surface	nda	2.3 (0-7)	mg/l	Ugo, 2008
	Aug. 2012	0-0.5	0.86	nda	mg/l	Deriemaecker, 2013
	Aug-Sept, 2012	0-0.5	nda	0.040833333	mg/l	Deriemaecker, 2013
TN	Jan.-Dec. 2005	nda	nda	1.6	mg/l	Tilahun & Alghren 2010
	Aug. 2012	0-0.5	1.94	nda	mg/l	Deriemaecker, 2013
	Aug-Sept, 2012	0-0.5	nda	1.965	mg/l	Deriemaecker, 2013
	Sep. 1978	nda	nda	0.29	mg/l	Belay & Wood, 1982
SRP	Jan.-Feb. 1964	0.1-0.5	0.128	nda	mg/l	Wood & Talling, 1988
	Sep. 1978	nda	nda	0.2	mg/l	Belay & Wood, 1982
	15 Mar. 1991	0-2m	nda	0.0255	mg/l	Kebede, Zinabu& Ahlgren, 1994
	15 Mar. 1991	4-5m	nda	0.0294	mg/l	Kebede, Zinabu& Ahlgren, 1994
	16 Mar. 1991	0-2m	0.147	nda	mg/l	Kebede, Zinabu& Ahlgren, 1994
	16 Mar. 1991	5-6m	0.149	nda	mg/l	Kebede, Zinabu& Ahlgren, 1994
	1990-2000	surface	0.151(0.0772–0.284)	0.0294 (0.0064-0.082)	mg/l	Zinabu, Kebede & Desta, 2002
	2002-2004	surface	0-0.19	0-0.03	mg/l	Tecklemariam & Wenclawiac, 2004
	Aug.-Dec. 2003	near surfac	nda	0.05	mg/l	Shumbulo, 2004
	Jan.-May 2004	near surfac	nda	0.048	mg/l	Shumbulo, 2004
	Mar.-May Sep. 2005	nda	0.3*(0-0.8*)(x10^-3)	nda	mg/l	Shumbulo & Assefa, ca. 2005
	Mar.-May, July, Sep. 2005	nda	nda	1.5*(0-5.3*)*(x10^-3*)	mg/l	Shumbulo & Assefa, ca. 2005
	Jan.-Dec. 2005	nda	nda	0.118	mg/l	Tilahun & Alghren 2010
	Mar.-July 2008	surface	nda	0.74 (0.04-2.98)	mg/l	Ugo, 2008
	Aug. 2012	0-0.5	0.46	nda	mg/l	Deriemaecker, 2013
	Aug.-Sep. 2012	0-0.5	nda	0.371666667	mg/l	Deriemaecker, 2013
TP	15 Mar. 1991	0-2 m	nda	0.135	mg/l	Kebede, Zinabu& Ahlgren, 1994
	15 Mar. 1991	4-5m	nda	0.165	mg/l	Kebede, Zinabu& Ahlgren, 1994
	16 Mar. 1991	0-2 m	0.237	nda	mg/l	Kebede, Zinabu& Ahlgren, 1994
	16 Mar. 1991	5-6 m	0.216	nda	mg/l	Kebede, Zinabu& Ahlgren, 1994
	Aug.-Dec. 2003	near surfac	nda	0.087	mg/l	Shumbulo, 2004
	Jan.-May 2004	near surfac	nda	0.093	mg/l	Shumbulo, 2004
	2003-2005	nda	nda	0.1179 (0.104-0.144)	mg/l	Tilahun, 2006
	Mar.-May, July, Sep. 2005	nda	3.9*(2.7-5.1)*(x10^-3)	5.02*(2.2-6)*(x10^-3)	mg/l	Shumbulo & Assefa, ca. 2005
	Jan.-Dec. 2005	nda	nda	0.182	mg/l	Tilahun & Alghren 2010
	Aug. 2012	0-0.5	1.44	nda	mg/l	Deriemaecker, 2013
	Aug.-Sep. 2012	0-0.5	nda	1.495	mg/l	Deriemaecker, 2013

Teklemariam & Wenclawiac, 2004; Shumbulo & Assefa, ca. 2005; Ugo, 2008; Shumbulo, 2004; Kebede, Zinabu& Ahlgren, 1994, Tilahun & Alghren 2010; Talling & Talling, 1965; Wood & Talling, 1988 and Zinabu, Kebede & Desta, 2002; modified by Arne Deriemaecker

Appendix 5: Zooplankton characteristics between both lakes

Appendix 5A: Abundance and relative abundance differences between the lakes, significant differences are marked in red. “x” = variable in question, “R.”= Relative.

Chamo > Abaya	Test	Transformation	Output
Abuncande(all taxa)	Kruskal-Wallis ANOVA	/	$p < 0.001$
Abundance(C. cornuta)	Kruskal-Wallis ANOVA	/	$p < 0.001$
Abundance(Cladocera)	Kruskal-Wallis ANOVA	/	$p < 0.002$
Abundance(Copepoda)	Kruskal-Wallis ANOVA	/	$p < 0.003$
Abundance(D. australiensis)	One-way ANOVA	$x^{0.5}$	MS = 2.101, SS = 2.101, F = 5.718, p = 0.027
Abundance(D. barbata)	Kruskal-Wallis ANOVA	/	p = 0.004
Abundance(M. mongolica)	Kruskal-Wallis ANOVA	/	p = 0.001
Abundance(Mesocyclops. spp.)	Kruskal-Wallis ANOVA	/	$p < 0.001$
Abundance(nauplii)	One-way ANOVA	log(x+1)	MS = 2.264, SS = 2.264, F = 10.236, p = 0.005
Abundance(Rotifera)	Kruskal-Wallis ANOVA	/	$p < 0.001$
R. Abundance(C. cornuta)	Kruskal-Wallis ANOVA	/	$p < 0.001$
R. Abundance(D. barbata)	Kruskal-Wallis ANOVA	/	p = 0.036
R. Abundance(Mesocyclops spp.)	One-way ANOVA	/	SS = 0.256, MS = 0.256 F = 4.661, p = 0.043
Chamo < Abaya	**Test**	**Transformation**	**Output**
Abundance(C. laticaudata)	Kruskal-Wallis ANOVA	/	p = 0.009
Abundance(Calanoida)	Kruskal-Wallis ANOVA	/	$p < 0.001$
R. Abundance(C. laticaudata)	Kruskal-Wallis ANOVA	/	p = 0.005
R. Abundance(Calanoida)	Kruskal-Wallis ANOVA	/	$p < 0.001$
R. Abundance(nauplii)	One-way ANOVA	$x^{0.5}$	SS = MS = ,F = 5.676, p = 0.027
Chamo vs. Abaya	**Test**	**Transformation**	**Output**
Abundance(D. magna)	Kruskal-Wallis ANOVA	/	p = 0.163
Abundance(juv. Cladocera)	Kruskal-Wallis ANOVA	/	p = 0.243
Abundance(Leydigia)	Kruskal-Wallis ANOVA	/	p = 0.310
Abundance(M. spinosa)	Kruskal-Wallis ANOVA	/	p = 0.632
R. Abundance(Cladocera)	Kruskal-Wallis ANOVA	/	p = 0.107
R. Abundance(Copepoda)	Kruskal-Wallis ANOVA	/	p = 0.974
R. Abundance(D. australiensis)	Kruskal-Wallis ANOVA	/	p = 0.178
R. Abundance(D. magna)	Kruskal-Wallis ANOVA	/	p = 0.708
R. Abundance(juv. Cladocera)	Kruskal-Wallis ANOVA	/	p = 0.133
R. Abundance(Leydigia)	Kruskal-Wallis ANOVA	/	p = 0.317
R. Abundance(M. mongolica)	Kruskal-Wallis ANOVA	/	p = 0.009
R. Abundance(M. spinosa)	Kruskal-Wallis ANOVA	/	p = 0.971
R. Abundance(Rotifera)	Kruskal-Wallis ANOVA	/	p = 0.071
pelagic Chamo vs pelagic Abaya	**Test**	**Transformation**	**Output**
R. Abundance(D. barbata)	One-way ANOVA	/	SS = 0.002, MS = 0.002, F = 44.552, $p < 0.001$
R. Abundance(D. magna)	One-way ANOVA	/	SS = 0.0003, MS = 0.0003, F = 5.133, p = 0.064
R. Abundance(D. australiensis)	One-way ANOVA	/	SS = 0.002, MS = 0.002, F = 7.346, p = 0.035

Appendix 5B: Biomass and relative biomass differences between the lakes, significant differences are marked in red. “x” = variable in question, “R.”= Relative.

Chamo > Abaya	Test	Transformation	Output
Biomass(All taxa)	Kruskal-Wallis ANOVA	/	p < 0.001
Biomass(C. cornuta)	Kruskal-Wallis ANOVA	/	p < 0.001
Biomass(Cladocera)	Kruskal-Wallis ANOVA	/	p < 0.001
Biomass(Copepoda)	Kruskal-Wallis ANOVA	/	p < 0.001
Biomass(D. australiensis)	Kruskal-Wallis ANOVA	/	p = 0.028
Biomass(D. barbata)	Kruskal-Wallis ANOVA	/	p = 0.012
Biomass(M. mongolica)	Kruskal-Wallis ANOVA	/	p < 0.001
Biomass(Mesocyclops spp.)	Kruskal-Wallis ANOVA	/	p < 0.001
R. Biomass(C. cornuta)	Kruskal-Wallis ANOVA	/	p < 0.001
R. Biomass(Mesocyclops spp.)	Kruskal-Wallis ANOVA	/	p < 0.001
Chamo < Abaya	Test	Transformation	Output
Biomass(C. laticaudata)	Kruskal-Wallis ANOVA	/	p = 0.002
Biomass(Calanoids)	Kruskal-Wallis ANOVA	/	p < 0.001
R. Biomass(Calanoida)	Kruskal-Wallis ANOVA	/	p < 0.001
R. BiomassC. (laticaudata)	Kruskal-Wallis ANOVA	/	p = 0.002
Chamo vs. Abaya	Test	Transformation	Output
Biomass(D. magna)	Kruskal-Wallis ANOVA	/	p = 0.475
Biomass(Leydigia)	Kruskal-Wallis ANOVA	/	p = 0.317
Biomass(M. spinosa)	Kruskal-Wallis ANOVA	/	p = 0.517
R. Biomass(Cladocera)	Kruskal-Wallis ANOVA	/	p = 0.790
R. Biomass(Copepoda)	Kruskal-Wallis ANOVA	/	p = 0.094
R. Biomass(D. australiensis)	Kruskal-Wallis ANOVA	/	p = 0.309
R. Biomass(D. barbata)	Kruskal-Wallis ANOVA	/	p = 0.089
R. Biomass(Leydigia)	Kruskal-Wallis ANOVA	/	p = 0.317
R. Biomass(M. mongolica)	Kruskal-Wallis ANOVA	/	p = 0.279
R. Biomass(M. spinosa)	Kruskal-Wallis ANOVA	/	p = 0.790
R. Biomass(Mesocyclops spp.)	Kruskal-Wallis ANOVA	/	p = 0.563
pelagic Chamo > pelagic Abaya	Test	Transformation	Output
R. Biomass(D. barbata)	Kruskal-Wallis ANOVA	/	p = 0.021
pelagic Chamo < pelagic Abaya	Test	Transformation	Output
R. Biomass(D. australiensis)	Kruskal-Wallis ANOVA	/	p = 0.021
R. Biomass(D. magna)	Kruskal-Wallis ANOVA	/	p = 0.024

Appendix 5C: Body-size differences between the lakes, significant differences are marked in red. “R.”= Relative.

Chamo > Abaya	Test	Transformation	Output
Body-size(D. australiensis)	One-way ANOVA	/	SS = 0.130, MS = 0.130, F = 10.178 p = 0.005
Chamo < Abaya	Test	Transformation	Output
Body-size(D. magna)	One-way ANOVA	/	SS = 0.432, MS = 0.432, F = 6.782, p = 0.025
Chamo vs. Abaya	Test	Transformation	Output
Body-size(C. cornuta)	Kruskal-Wallis ANOVA	/	p = 0.533
Body-size(D. barbata)	Kruskal-Wallis ANOVA	/	p = 0.077
Body-size(M. mongolica)	Kruskal-Wallis ANOVA	/	p = 0.870
Body-size(M. spinosa)	Kruskal-Wallis ANOVA	/	p = 0.451
Body-size(Mesocyclops spp.)	Kruskal-Wallis ANOVA	/	p = 0.094

Appendix 6: Zooplankton characteristics within each lake in a horizontal transect

Appendix 6A: Lake Chamo: zooplankton characteristics between three subhabitats (i.e. pelagic, vegetated littoral and littoral). Significant differences are marked in red, “x” = variable in question.

pelagic vs. vegetated- vs. littoral	Test	Transformation	Output
Abundance(D. barbata)	One-way ANOVA	/	SS = 252.621, MS = 126.311, F = 8.543, p = 0.010
Abundance(juv. Cladocera)	Kruskal-Wallis ANOVA	/	p = 0.523
Abundance(Leydigia sp.)	Kruskal-Wallis ANOVA	/	p = 0.263
Abundance(All taxa)	Kruskal-Wallis ANOVA	/	p = 0.215
Abundance(C. cornuta)	Kruskal-Wallis ANOVA	/	p = 0.1605
Abundance(C. laticaudata)	Kruskal-Wallis ANOVA	/	p = 0.416
Abundance(Cladocera)	Kruskal-Wallis ANOVA	/	p = 0.273
Abundance(Copepoda)	Kruskal-Wallis ANOVA	/	p = 0.215
Abundance(D. australiensis)	Kruskal-Wallis ANOVA	/	p = 0.1036
Abundance(D. magna)	One-way ANOVA	(x)05	SS = 3.725, MS = 1.862, F = 11.547, p = 0.004
Abundance(M. mongolica)	One-way ANOVA	/	SS = 4785.3, MS = 2392.7, F = 38.309, p < 0.001
Abundance(M. spinosa)	Kruskal-Wallis ANOVA	/	p = 0.7101
Abundance(Mesocyclops spp.)	Kruskal-Wallis ANOVA	/	p = 0.233
Abundance(nauplii)	One-way ANOVA	/	SS = 9309,6, MS =4654.8, F = 31.222, p <0.001
Abundance(Rotifera)	Kruskal-Wallis ANOVA	/	p = 0.523
Biomass (D. barbata)	One-way ANOVA	/	SS = 2304.7, MS = 1152.3, F = 15.551, p = 0.002
Biomass (D. magna)	Kruskal-Wallis ANOVA	/	p = 0.015
Biomass(All taxa)	Kruskal-Wallis ANOVA	/	p = 0.149
Biomass(C. cornuta)	Kruskal-Wallis ANOVA	/	p = 0.175
Biomass(C. laticaudata)	Kruskal-Wallis ANOVA	/	p =1.000
Biomass(Calanoida)	Kruskal-Wallis ANOVA	/	p =1.000
Biomass(Cladocera)	Kruskal-Wallis ANOVA	/	p = 0.462
Biomass(Copepoda)	Kruskal-Wallis ANOVA	/	p = 0.110
Biomass(D. australiensis)	Kruskal-Wallis ANOVA	/	p = 0.038
Biomass(M. mongolica)	Kruskal-Wallis ANOVA	/	p = 0.241
Biomass(M. spinosa)	Kruskal-Wallis ANOVA	/	p = 0.676
Biomass(Mesocyclops spp.)	Kruskal-Wallis ANOVA	/	p = 0.110
Body-size(All taxa)	Kruskal-Wallis ANOVA	/	p = 0.0406
Body-size(C. cornuta)	One-way ANOVA	/	SS = 0.003, MS = 0.001, F = 5.092, p = 0.037
Body-size(Cladocera)	Kruskal-Wallis ANOVA	/	SS = 0.026, MS = 0.013, F = 4.482, p = 0.049
Body-size(Copepoda)	Kruskal-Wallis ANOVA	/	SS = 0,090, MS = 0,045, F = 8.458, p = 0.011
Body-size(M. mongolica)	Kruskal-Wallis ANOVA	/	p = 0.184
Body-size(Mesocyclops spp.)	One-way ANOVA	/	SS = 0,090, MS = 0,045, F = 8.458, p = 0.011

Appendix 6B: Lake Abaya: Zooplankton characteristics between three subhabitats (i.e. pelagic, vegetated littoral and littoral). Significant differences are marked in red, “x” = variable in question.

pelagic vs. vegetated- vs. littoral	Test	Transforma	Output
Abundance(All taxa)	One-way ANO	/	SS = 793,953, MS = 396,976, F =6.182, p = 0.024
Abundance(C. cornuta)	Kruskal-Wallis	/	p = 0.372
Abundance(C. laticaudata)	One-way ANO	log(x+1)	SS = 0.022, MS = 0.011, F = 22.390, p < 0.001
Abundance(Calanoida)	One-way ANO	log(x+1)	SS = 0.364, MS = 0.182, F = 6.632, p = 0.020
Abundance(Cladocera)	One-way ANO	/	SS = 16.835, MS = 8.418, F = 6.286, p = 0.023
Abundance(Copepod nauplii)	One-way ANO	/	SS = 182.798, MS = 91.399, F = 19.888, p < 0.001
Abundance(Copepoda)	One-way ANO	/	SS = 549.677, MS = 274.838, F = 7.400, p = 0.015
Abundance(D. australiensis)	One-way ANO	/	SS = 1.287, MS = 0.644, F = 7.410, p = 0.015
Abundance(D. barbata)	One-way ANO	/	SS = 0.026, MS = 0.013, F = 11.349, p = 0.005
Abundance(D. magna)	Kruskal-Wallis	/	p = 0.016
Abundance(juv. Cladocara)	Kruskal-Wallis	/	p = 0.234
Abundance(Leydigia sp. sp.)	Kruskal-Wallis	/	p =1.000
Abundance(M. mongolica)	Kruskal-Wallis	/	p = 0.371
Abundance(M.spinosa)	Kruskal-Wallis	/	p = 0.082
Abundance(Mesocyclops spp.)	One-way ANOVA		SS = 56.197, MS = 28.099, F = 2.531, p = 0.141
Abundance(Rotifera)	Kruskal-Wallis	/	p = 0.027
Biomass(All taxa)	One-way ANO	/	SS = 1018.975, MS = 509.487, F = 5.434, p = 0.032
Biomass(C. cornuta)	Kruskal-Wallis	/	p = 0.161
Biomass(C. laticaudata)	One-way ANO	x0.5	SS = 0.697, MS = 0.348, F = 10.094, p = 0.006
Biomass(Calanoida)	Kruskal-Wallis	/	p = 0.080
Biomass(Cladocera)	One-way ANO	/	SS = 356.084, MS = 178.042, F = 1.,369, p = 0.004
Biomass(Copepoda)	One-way ANO	/	p = 0.095
Biomass(D. australiensis)	One-way ANO	/	SS = 2.965, MS = 1.482, F = 5.660, p = 0.029
Biomass(D. australiensis)	Kruskal-Wallis	/	p = 0.049
Biomass(D. barbata)	One-way ANO	/	SS = 0.398, MS = 0.199, F = 5.014, p = 0.039
Biomass(D. magna)	One-way ANO	/	SS = 102.531, MS = 51.265, F = 12.803, p = 0.003
Biomass(Leydigia sp.)	Kruskal-Wallis	/	p =1.000
Biomass(M. mongolica)	Kruskal-Wallis	/	p = 0.087
Biomass(M. spinosa)	Kruskal-Wallis	/	p = 0.041
Biomass(Mesocyclops spp.)	Kruskal-Wallis	/	p = 0.230
Body-size(C. cornuta)	One-way ANO	/	SS = 0.022, MS = 0.011, F = 6.346, p = 0.022
Body-size(Calanoida)	Kruskal-Wallis	/	p = 0.273
Body-size(D. australiensis)	Kruskal-Wallis	/	p = 0.931
Body-size(M. mongolica)	Kruskal-Wallis	/	p = 0.493
Body-size(Mesocyclops spp.)	Kruskal-Wallis	/	p = 0.273

Appendix 7: Zooplankton characteristics over the pelagic water column

Appendix 7A: Lake Chamo: Abundance, biomass and body-size differences in the pelagic water column, between all depths (i.e. 0-2m, 2-4m, 4-6m, 6-8m and 8-10m), Significant differences are marked in red, "x" = variable in question.

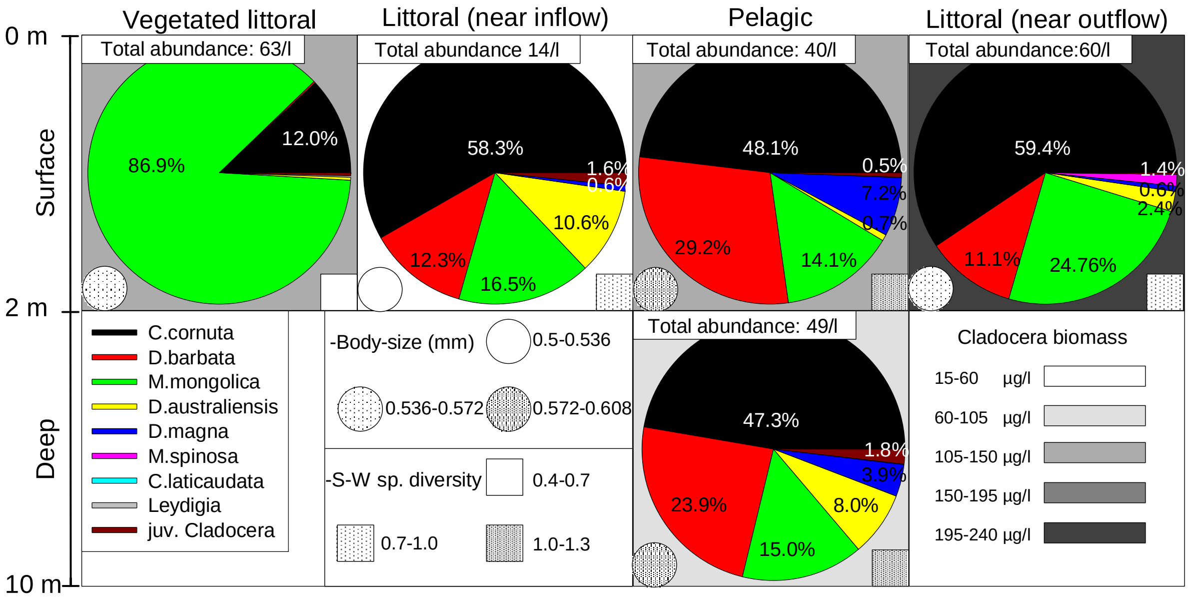
Pelagic water column (all depths)	Test	Transformation	Output
Abundance(C. cornuta)	Friedman ANOVA	/	p = 0.711
Abundance(D. barbata)	Friedman ANOVA	/	p = 0.760
Abundance(M. mongolica)	Friedman ANOVA	/	p = 0.663
Abundance(D. australiensis)	Friedman ANOVA	/	p = 0.102
Abundance(D. magna)	Friedman ANOVA	/	p = 0.615
Abundance(M. spinosa)	Friedman ANOVA	/	p = 0.652
Abundance(C. laticaudata)	Friedman ANOVA	/	p = 0.406
Abundance(Mesocyclops spp.)	Friedman ANOVA	/	p = 0.938
Abundance(juv. Cladocara)	Friedman ANOVA	/	p = 0.339
Abundance(copepod nauplii)	Friedman ANOVA	/	p = 0.102
Abundance(Rotifera)	Friedman ANOVA	/	p = 0.483
Abundance(All taxa)	Friedman ANOVA	/	p = 0.760
Biomass(D. australiensis)	Repeated measures ANOVA	/	SS = 1.407, MS = 0.352, F = 4.402, p = 0.036
Biomass(C. cornuta)	Friedman ANOVA	/	p = 0.809
Biomass(D. barbata)	Friedman ANOVA	/	p = 0.663
Biomass(M. mongolica)	Friedman ANOVA	/	p = 0.0533
Biomass(D. magna)	Friedman ANOVA	/	p = 0.569
Biomass(M. spinosa)	Friedman ANOVA	/	p = 0.558
Biomass(Mesocyclops spp.)	Friedman ANOVA	/	p = 0.856
Biomass(All taxa)	Friedman ANOVA	/	p = 0.992
Body-size(C. cornuta)	Friedman ANOVA	/	p = 0.231
Body-size(D. barbata)	Friedman ANOVA	/	p = 0.406
Body-size(M. mongolica)	Friedman ANOVA	/	p = 0.856
Body-size(D. australiensis)	Friedman ANOVA	/	p = 0.711
Body-size(D. magna)	Friedman ANOVA	/	p = 0.406
Body-size(Mesocyclops spp.)	Friedman ANOVA	/	p = 0.406

Appendix 7B: Lake Abaya: Abundance, biomass and body-size differences in the pelagic water column, between all depths (i.e. 0-2m, 2-4m, 4-6m, 6-8m and 8-10m). Significant differences are marked in red, "x" = variable in question.

Pelagic water column (all depths)	Test	Transformation	Output
Abundance(All taxa)	Repeated measures ANOVA	/	SS = 1.321, MS = 0.330, F = 8.045, p = 0.002
Abundance(copepod nauplii)	Repeated measures ANOVA	log(x+1)	SS = 1,351, MS = 0,338, F= 46.431, p < 0.001
Abundance(C. cornuta)	Friedman ANOVA	/	p = 0.270
Abundance(D. barbata)	Friedman ANOVA	/	p = 0.076
Abundance(M. mongolica)	Friedman ANOVA	/	p = 0.072
Abundance(D. australiensis)	Friedman ANOVA	/	p = 0.056
Abundance(D. magna)	Friedman ANOVA	/	p = 0.0720
Abundance(C. laticaudata)	Friedman ANOVA	/	p = 0.115
Abundance(Mesocyclops spp.)	Friedman ANOVA	/	p = 0.147
Abundance(Calanoida)	Friedman ANOVA	/	p = 0.330
Abundance(juv. Cladocara)	Friedman ANOVA	/	p = 0.246
Abundance(Rotifera)	Friedman ANOVA	/	p = 0.663
Biomass(D. australiensis)	Friedman ANOVA	/	p = 0.016
Biomass(M. mongolica)	Friedman ANOVA	/	p = 0.032
Biomass(D. magna)	Repeated measure ANOVA	log(x+1)	SS = 1.910, MS = 0.478, F = 12.275, p < 0.001
Biomass(C. cornuta)	Friedman ANOVA	/	p = 0.406
Biomass(D. barbata)	Friedman ANOVA	/	p = 0.185
Biomass(C. laticaudata)	Friedman ANOVA	/	p = 0.185
Biomass(Mesocyclops spp.)	Friedman ANOVA	/	p = 0.085
Biomass(Calanoida)	Friedman ANOVA	/	p = 0.287
Biomass(All taxa)	Friedman ANOVA	/	p = 0.287
Body-size(C. cornuta)	Friedman ANOVA	/	p = 0.464
Body-size(M. mongolica)	Friedman ANOVA	/	p = 0.433
Body-size(D. australiensis)	Friedman ANOVA	/	p = 0.189
Body-size(D. magna)	Friedman ANOVA	/	p = 0.525
Body-size(Mesocyclops spp.)	Friedman ANOVA	/	p = 0.213
Body-size(Calanoida)	Friedman ANOVA	/	p = 0.995

Appendix 8: Visualisation of the cladoceran community in both lakes

Appendix 8A Abundance distribution of cladocerans in Lake Chamo (dry season, transect from inflow (Kulfo River) to outflow), the pie charts give the percentages of each taxon in a particular habitat (i.e. vegetated littoral, inflow, pelagic, outflow and pelagic deep (2-10m). Depths, beneath two meter, are taken together as no significant differences were found between them (RESULTS 3.3.3). Total cladoceran biomass, average cladoceran body-size and Shannon-Wiener diversity over all taxa are also included.



Appendix 8B: Abundance distribution of cladocerans in Lake Abaya (dry season, transect from inflow (Gelana River) to outflow), the pie charts give the percentages of each taxon in a particular habitat (i.e. vegetated littoral, inflow, pelagic, outflow and pelagic deep (2-10m). Depths, beneath two meter, are taken together as no significant differences were found between them (RESULTS 3.3.3). Total cladoceran biomass, average cladoceran body-size and Shannon-Wiener diversity over all taxa are also included.