Why are Lake Abaya and Lake Chamo so different? A limnological comparison of two neighboring major Ethiopian Rift Valley Lakes

Fassil E. Teffera[1,2 *], Pieter Lemmens[2*°], Arne Deriemaecker[2], Jozef Deckers[3], Hans Bauer[4], Feleke W. Gamo[1], Luc Brendonck[2] and Luc De Meester[2]

*shared first author

[1]Arba Minch University, Biology Department, P.O.Box 21, Arba Minch, , Ethiopia
[2]KU Leuven, Laboratory of Aquatic Ecology, Evolution & Conservation, Charles Deberiotstraat 32, 3000 Leuven, Belgium
[3]KU Leuven, Division of Soil and Water Management, Celestijnenlaan 200E, 3001 Leuven, Belgium
[4]University of Oxford, Wildlife Conservation Research Unit, Recanati-Kaplan Centre, Tubney, OX13 5QL, UK.

°Corresponding author: Pieter Lemmens, KU Leuven, Laboratory of Aquatic Ecology, Evolution and Conservation, Charles Deberiostraat 32, 3000 Leuven, Belgium, email: pieter.lemmens@kuleuven.be

Abstract

Lake Abaya and Lake Chamo are the two largest Ethiopian Rift Valley lakes; they are located close to each other, but have a strikingly different water transparency. We explain key differences in the structure and the functioning of the food web with variation in limnological variables and major pelagic food web compartments within and across both lakes. Data from a detailed comparative investigation of physical and chemical variables and zooplankton community characteristics during the wet and dry season from two consecutive years revealed major differences in key limnological variables between Lake Abaya and Lake Chamo. The most pronounced differences were related to water transparency and the amount of suspended solids in the water column. Lake Abaya is much more turbid, has lower phyto- and zooplankton biomass, and has considerably lower primary production than Lake Chamo. Based on our results, we infer that the profound differences in food web structure between both lakes probably result from differences in sediment load. Finally, our results indicate that conservation programs should focus on reducing sediment inflow from the catchments into the lakes.

Keywords: Lake Abaya, Lake Chamo, limnology, water transparency, suspended solids, primary production, phytoplankton, zooplankton.

Introduction

The Ethiopian Rift Valley comprises a set of seven iconic lakes (from North to South: Ziway, Abijata, Langano, Shala, Hawassa, Abaya and Chamo) and one large reservoir (Koka) (Ayenew & Legesse 2007). These lentic water bodies provide a variety of vital ecosystem services and are highly recognized for their unique and outstanding biological diversity (Baxter 2002; Zinabu et al. 2002). Despite their natural richness, the Ethiopian Rift Valley lakes are increasingly subjected to human demands, resulting in nutrient enrichment and profound siltation due to soil erosion in their catchments (Teffera et al. 2017; Willén et al. 2011). This has led to profound environment degradation that severely alters the socio-ecological integrity of the region (Ayenew 2007; Meshesha et al. 2012). At the global scale, excessive sediment loading remains a primary anthropogenic disturbance that is especially important for tropical water bodies (Donohue & Garcia Molinos 2009), and which can strongly undermine the provisioning of major ecosystem services such as water supply, fisheries and tourism (Pimentel et al. 1995). The Ethiopian Rift Valley lakes are currently recognized as among the most fragile inland waters on Earth (Ayenew & Legesse 2007).

Lake Abaya and Lake Chamo are the two largest Ethiopian Rift Valley lakes within the Main Ethiopian Rift (Belete et al. 2015). They are key determinants of the ecology of the region and have an exceptionally high socio-economic value since they provide multiple ecosystem services (Alemayehu & Raju 2015; Golubtsov & Habteselassie 2010; Kassawmar et al. 2011). Both lakes are also widely recognized for their important ecological richness (Ayenew & Legesse 2007). Although Lake Abaya and Lake Chamo are located in close proximity to each other and are only separated by an approximately 5 km wide ridge, they are characterized by a strikingly different water transparency and water color. Lake Abaya is very turbid and has a reddish color due to suspended red clay and colloidal ferric oxide, while Lake Chamo is considerably clearer and lacks red water coloration (Gebremariam 2007; Schröder 1984). Over the past decades, both lakes have been subjected to severe sediment run-off and eutrophication, which likely result from strong soil erosion due to deforestation in their catchments and intensified fertilizer application on the surrounding agricultural lands (Teffera et al. 2017). Earlier investigations indicate that the phytoplankton community in the turbid Lake Abaya is dominated by picoplankton, whereas cyanobacteria, including *Microcystis sp.*, are dominant in Lake Chamo (Belay & Wood 1982; Willén et al. 2011). A comparative study of eight Ethiopian freshwater lakes along a North-South gradient by Vijverberg et al. (2014) indicates that the zooplankton communities in Lake Abaya and Lake Chamo are dominated by copepods, while the overall density of cladocerans in both lakes is relatively low. Lake Chamo and Lake Abaya do not differ in overall fish community composition, but the fish density is considerably higher in Lake Chamo than in Lake Abaya (Lemmens et al. 2017). *Synodontis schall* (Bloch and Schneider) is the most abundant fish species in both lakes (Golubtsov & Habteselassie 2010; Lemmens et al. 2017; Vijverberg et al. 2012). Despite the high societal value of these two iconic lakes, the majority of studies conducted on Lake Abaya and Lake Chamo have largely focused on specific limnological variables as part of an overall comparison of the different Ethiopian Rift Valley Lakes. Detailed comprehensive limnological studies that include a broad range of physical, chemical and biological variables are currently lacking. Information from such studies is, however, urgently needed for the conservation of the biological diversity in the Rift Valley, as well as for a sustainable socio-economic development of the region.

The present study aims to fill this major knowledge gap by conducting a detailed comparative investigation of major physical and chemical variables and zooplankton community characteristics in Lake Abaya and Lake Chamo based on data collected during multiple field sampling campaigns over different seasons in two consecutive years. We specifically aim to unravel key differences in the structure and the functioning of the food web in both lakes by (1) testing for differences in limnological variables and major pelagic food web compartments (e.g. phytoplankton and zooplankton) between lakes, and (2) explore seasonal and spatial variation in major abiotic and biotic variables within and across lakes.

Material and methods

Study area

Lake Abaya (5°5’14N; 37°41’20”E) and Lake Chamo (5°50’59”; 37°33’54”E) are located in Southern Nations Nationalities and People’s Regional State of Ethiopia (Figure 1). Both lakes are naturally separated by only a 5 km wide ridge with a vertical offset of approximately 60 m (Awulachew 2006a; Belete et al. 2015). Lake Abaya and Lake Chamo both are relatively shallow (8-12 m) and polymictic throughout the year (Makin et al. 1975).

Both lakes do not share the same catchment. The catchment area of Lake Abaya is considerably larger compared to that of Lake Chamo (15219 km^2 and 1109 km^2, respectively). Likewise, the surface area of Lake Abaya is by far larger than that of Lake Chamo (1943 km^2 and 329 km^2, respectively) (Awulachew 2006a; Awulachew 2006b). The rivers Bilate, Gidabo and Galana are the main perennial rivers entering Lake Abaya, whereas Lake Chamo receives water from the rivers Kulfo, Sile and Elgo (Makin et al. 1975; Teklemariam 2005). The two lakes have a complex history of being hydrologically interconnected or disconnected from each other (Baxter 2002; Schutt & Thiemann 2006). Lake Abaya and Lake Chamo have been interconnected in the past, with water flowing from Lake Abaya into Lake Chamo via the Kulfo river, but the lakes were disconnected from 1980 (Tekelemariam & Wenclawiak 2004) until 2013 (Teffera et al. 2017).

The catchments of both lakes are characterized by a humid to hot semi-arid tropical climate with a bimodal rainfall pattern including two wet seasons (a first from end-March to mid-June, a second from mid-September to late November) and two dry seasons (a first from December to mid-March, a second from end-June to mid-September) (Makin et al. 1975; Wagesho 2014).

Most of the alluvial soils around Lake Abaya and Lake Chamo were formed from recently deposited material (Makin et al. 1975). The flood plains and the deltas of both lakes are fertile and hence have been under extensive agricultural cultivation over the last three decades.

Data collection

Major physical and chemical variables and zooplankton community characteristics were determined at eight locations in each lake along a transect from inflow to outflow during the dry (mid-March) and wet (end-May) seasons of 2013 and 2014; two locations close to the major tributary, four locations in the pelagic zone of which one at the deepest point of the lake, and two locations close to the outflow of the lake. In addition, phytoplankton productivity was quantified once at each location in both lakes during the dry season of 2012 (mid-August) using *in situ* stable isotope addition experiments (see below for more details).

Water from different depths (just below water surface, middle water column and just above lake bottom) was collected at each location in each lake using a Van Dorn water sampler (SEBA). Water from different depths was pooled and the combined water sample was used to determine water temperature, pH, electric conductivity, nutrient concentrations and phytoplankton biomass. Oxygen concentration was measured directly in the lake approximately 1 meter below water surface.

Water temperature, oxygen concentration, pH and conductivity were measured using a standard electrode (HACH, HQ40D). Subsamples from the pooled water sample were taken for the analysis of nutrient concentrations. Samples for the analysis of nitrate (NO_3^-) and phosphate (PO_4^{3-}) concentrations were filtered over a glass fiber filter (Whatman GF/F) in the field to remove small particles and phytoplankton. Nutrient samples were stored cool in the dark in the field and were kept frozen (-20°C) in the laboratory until further analysis. Phytoplankton biomass was estimated by *in situ* measurements of chlorophyll-*a* concentration in the pooled water sample using a hand-held fluorometer (AquaFluor™, Turner Designs, Sunnyvale, CA). Water transparency was measured using a Secchi-disc (diameter: 0.3 m).

In the laboratory, the concentration of total suspended solids in the water column was determined gravimetrically by filtering a known volume of lake water through a pre-weighted glass fiber filter (Whatman GF/C). Total nitrogen (TN) and total phosphorus (TP) concentrations were analyzed using a photometer (HACH DR/900) after alkaline persulphate digestion following Koroleff (1970). Samples for the measurement of NO_3^- and PO_4^{3-} concentrations were processed without digestion. The results of the nutrient analyses were validated by a parallel analysis of a subset of samples using an Auto Analyzer II (Technicon) (analyses performed at KU Leuven, Belgium).

Zooplankton communities were sampled depth integrating using a Schindler-Patalas trap (12 liter, 64 µm mesh size) collecting samples at 0.5 meter intervals from the water surface near to the lake bottom. Samples from different depths were combined into one pooled sample that was preserved in glucose saturated formaldehyde (4%). In the laboratory, cladocerans were identified to species level using Flössner (2000) and Korinek (1999), except for individuals belonging to the genus Diaphanosoma and Macrothrix for which the genus level was used. At least 300 adult cladocerans from each sample were counted. Copepods were identified as either belonging to the Cyclopoida or the Calanoida and counted. Cyclopoids were further classified to genus level following Boxshall and Halsey (2004). Zooplankton abundances were converted into biomasses using measured lake-specific mean body sizes of each species and published body size-dry weight regressions (Bottrell et al. 1976).

Phytoplankton productivity was estimated during the dry season of 2012 by measuring carbon uptake rates at *in situ* light conditions at the surface using *in situ* stable isotope ^{13}C addition experiments following Bouillon et al. (2011). This approach provides a relative measure of primary production, but cannot be used to quantify daily areal primary production rates. At each location in each lake, two replicate bottles (500 ml, polycarbonate) with lake surface water were spiked with $NaH^{13}CO_3$ (500 µl, 99% ^{13}C) and immediately incubated 0.5m below water surface for 2 hours. Phytoplankton production was quantified as the carbon uptake over the incubation period (µg C L^{-1} h^{-1}) following Dauchez et al. (1995) after determination of the percentage of dissolved ^{13}C and the percentage of ^{13}C in the particulate organic material at the start (T_o) and the end (T_{end}) of the incubation. Carbon stable isotope ratios were analyzed with an elemental analyzer-isotope ratio mass spectrometer (Thermo Flash HT/EA with Delta V Advantage, Bremen, Germany) at KU Leuven.

Data analysis

The associations between physical and chemical variables and between multiple zooplankton taxa were visualized in relation to lake, season and habitat using ordination plots of Principal Component Analyses (PCA). Additional separate redundancy analyses (RDA) were applied to formally test for an overall effect of lake, season, habitat, and the interaction lake-habitat and lake-season on the entire set of physical and chemical variables variables and zooplankton community composition. The significance of RDA models was evaluated with 999 Monte Carlo permutations. Dependency of multiple observations from each lake was taken into account by restricting the permutations to blocks (see Table S1.)

In a second step, we used linear mixed models to test for differences between lakes and seasons for each physical and chemical variable and zooplankton community biomass separately. Lake and season were included as fixed factors in these analyses, while year and location nested within year were modelled as random factors to take into account temporal and spatial dependency of observations within each lake.

All data, except pH, were logarithmically transformed prior to statistical analysis in order to improve assumptions of normality. Statistical analyses were done in R (version 3.4.2; R

Development Core Team 2013) using the ‘vegan’ and the ‘lme4’ package (Oksanen et al. 2010).

Results

Environmental variables

Partial RDA analyses revealed a significant effect of lake, season and habitat on the entire set of investigated physical and chemical variables ($R^2_{adj.}$ = 41.1%, 12.2% and 21.9% respectively) (Table 1). In addition, the interaction between lake and habitat explained a considerable proportion of variation in limnological conditions ($R^2_{adj.}$ = 11.8%). Albeit statistically significant, the effect of the interaction lake-season was relatively small ($R^2_{adj.}$ = 4.1%). The first and the second PCA axis jointly explained 62.9% of the overall variation in limnological conditions (Figure 2A). The first axis explained 47.4% of the variation and clearly differentiated Lake Abaya from Lake Chamo. The concentration of total suspended solids (TSS), nitrate (NO_3^-) and phosphate (PO_4^{3-}) was higher in Lake Abaya than in Lake Chamo, whereas chlorophyll-*a* (Chl-*a*), pH, daytime oxygen concentration (DO) and water transparency were higher in Lake Chamo than in Lake Abaya. Interestingly, Chl-*a* was not associated with TN and TP, but instead showed a strong negative association with TSS. The first PCA axis also distinguished inflow habitats from pelagic and outflow habitats, with inflow locations in both lakes having relatively higher nutrient concentrations and TSS. The second axis explained 15.5% of the variation in environmental variables and mainly differentiated between the wet and dry season. TN and TP concentrations tended to be higher in the wet season compared to the dry season.

Linear mixed models revealed that TN and TP concentrations did overall not differ between lakes, and were significantly higher in both lakes during the wet season than during the dry season (Figure 3). NO_3^- concentrations tended to be higher in Lake Abaya than in Lake Chamo during the wet season. Similarly, PO_4^{3-} concentrations tended to be higher in Lake Abaya compared with Lake Chamo, especially during the dry season when PO_4^{3-} concentrations in Lake Chamo were relatively low. The amount of TSS was systematically higher in Lake Abaya than in Lake Chamo, and was in both lakes higher during the wet season. In contrast, phytoplankton biomass was considerably higher in Lake Chamo than in Lake Abaya during the dry season. Similarly, oxygen concentrations tended to be higher in Lake Chamo than in Lake Abaya. Water transparency, pH and zooplankton biomass were higher in Lake Chamo than in Lake Abaya during both the wet and dry season. Conductivity was higher in Lake Chamo than in Lake Abaya during the dry season, but varied considerably between sampling locations in Lake Chamo. Similarly, water transparency was higher in Chamo compared to Lake Abaya, but also varied strongly between sample locations in Lake Chamo. The high within-lake variability for conductivity and water transparency in Lake Chamo can largely be attributed to considerably lower values of both variables at inflow habitats compared to pelagic and outflow habitats (Figure S1.). Pelagic phytoplankton production was on average more than 10 times lower in Lake Abaya compared with Lake Chamo (mean and standard deviation for Lake Abaya and Lake Chamo: 33.4 µg C L^{-1} h^{-1}, 42.9 µg C L^{-1} h^{-1} and 456.0 µg C L^{-1} h^{-1}, 164.5 µg C L^{-1} h^{-1}, respectively; T-test: $t = -7.44$, $df = 18.7$, $p < 0.001$).

The same nine zooplankton taxa were found in both lakes over the entire set of samples. Nevertheless, RDA analysis revealed significant variation in zooplankton community composition between lakes, seasons and habitats (Table 1). Differences in zooplankton community were especially strong between lakes ($R^2_{adj.} = 94.2\%$), whereas season and habitat only explained a relative small proportion of variation ($R^2_{adj.} = 0.6\%$ and 7.2% respectively). Similarly, the interaction lake-season and lake-habitat had a significant, but small effect on zooplankton community composition ($R^2_{adj.} = 7.4\%$ and 7.9% respectively). The first axis of the PCA ordination plot comprised 78.9% of the compositional variation in zooplankton community and clearly differentiated Lake Abaya from Lake Chamo (Figure 2B). The second PCA axis explained 13.3% of the zooplankton compositional variation and was closely associated with differences between seasons and habitats. The majority of zooplankton taxa showed a positive association with Lake Chamo. In Lake Abaya, calanoid copepods and *Ceriodaphnia dubia* (Richard) tended to be slightly more abundant during the dry season.

The overall total zooplankton biomass was much higher in Lake Chamo than in Lake Abaya (overall average biomass in Lake Chamo and Lake Abaya 770.85 µg L^{-1} and 15.11 µg L^{-1}, respectively) (Table 2, Figure 3). Copepods were dominant in both lakes (77.61% and 71.51% of total zooplankton biomass in Lake Abaya and Lake Chamo respectively), with calanoid copepods being considerably more important in Lake Abaya than in Lake Chamo (36.60% and 1.52% of total zooplankton biomass respectively). *Moina micrura* (Kurz) was the most abundant cladoceran in both lakes. Other cladoceran taxa occurred only at relative low biomasses in both lakes (typically less than 6 % of total zooplankton biomass).

Discussion

Our study reveals profound differences in key limnological variables in two neighbouring major Ethiopian Rift Valley lakes. The most pronounced differences in physical and chemical characteristics between the two lakes relate to water transparency and the amount of suspended solids in the water column. Interestingly, total nutrient concentrations in Lake Abaya and Lake Chamo were very similar and did not distinguish the two lakes. Based on our results, we argue that differences in food web structure between both lakes result from lower primary production in Lake Abaya due to stronger light limitation in the water column as a result of a higher sediment load in this lake.

Our study indicates that the profound difference in water transparency between both lakes is largely caused by higher concentrations of suspended solids in Lake Abaya compared with

Lake Chamo. The higher turbidity of Lake Abaya likely has multiple explanations. First, Lake Abaya is much larger than Lake Chamo, which makes it more prone to wind-induced sediment resuspension (Scheffer 2004). Secondly, the much larger catchment area of Lake Abaya results in higher sediment input per unit lake area (Ekholm et al. 2000; Hecky et al. 2003). Third, deforestation and soil erosion in the main catchment of Lake Abaya has been extensive and occurred earlier than land degradation in the catchment of Lake Chamo (Makin et al. 1975; Schröder 1984). Importantly, the current turbid state of Lake Abaya is not its natural state. Historical data indicate that the lake shifted from a clear to a turbid state more than four decades ago due to profound land degradation in its main catchment (Teffera et al. 2017). Ethiopia is a country in full transition and the expansion of agricultural activities in the Ethiopian Rift Valley has increased pressure on its natural resources (Ayenew & Legesse 2007; Meshesha et al. 2012). The large scale conversion of the natural vegetation to cropland (Belay et al. 2015) has improved food security in Ethiopia (Belay & Abebaw 2004), but has also resulted in enhanced soil erosion and nutrient input (Ayenew & Legesse 2007). As a consequence, the majority of the Ethiopian Rift Valley lakes currently suffer from massive sediment input and eutrophication.

Water transparency also seems to determine food web structure in the two investigated lakes. Although both lakes are hypertrophic and have very similar total nutrient concentrations (with TN and TP concentrations typically >3.10 mg L^{-1} and >1.77 mg L^{-1}, respectively), phytoplankton biomass and productivity are considerably lower in Lake Abaya than in Lake Chamo. Similarly, other productivity related variables, such as oxygen concentration and pH, are lower in Lake Abaya compared to Lake Chamo. This is in line with earlier observations on the occurrence of periodic strong algae blooms in Lake Chamo and the absence of such blooms in Lake Abaya (Belay & Wood 1982). Given that Lake Abaya is turbid and Lake Chamo is relatively clear, these findings suggest that primary production in Lake Abaya is largely limited by light in the water column, rather than by nutrients. Indeed, the photic zone is considerably smaller in Lake Abaya than in Lake Chamo (0.7m and 1.6 m respectively, data not shown). This is consistent with the fact that freely available phosphorus tends to be lower in Lake Chamo compared to Lake Abaya. Similar to our findings, the currently low primary production in Lake Tana (Ethiopia) has also been linked to increased light limitation due to human induced sediment erosion from its catchment area (Dejen et al. 2017).

Water turbidity seems to be an important determinant of zooplankton community characteristics in the investigated lakes. The much lower water transparency in Lake Abaya due to high sediment load and the resulting low primary production very likely explain the lower zooplankton biomass in Lake Abaya compared with Lake Chamo (approximately 50 times). A negative relation between zooplankton density and water turbidity has previously also been observed in Lake Tana (Dejen et al. 2004). Low phytoplankton production leads to low food availability for herbivorous zooplankton. In addition, high turbidity might also have profound direct negative effects on zooplankton by interfering with their filter capacity (Kirk & Gilbert 1990). This might explain the strong dominance of selective herbivorous calanoid copepods in Lake Abaya. Similarly, we argue that the relative high abundance of *Moina micrura* in the investigated lakes is at least partly related to water turbidity as the genus *Moina* is known to be tolerant for high turbidity (Hart 1988; Lougheed & Chow-Fraser 1998). The observed strong dominance of copepods and relative low abundance of cladocerans in both investigated lakes is in line with earlier findings of Vijverberg et al. (2014). Low primary production and low zooplankton biomass might explain the overall lower fish density in Lake Abaya than in Lake Chamo as previously observed by Lemmens et al. (2017). Similar observations have also been made in other Ethiopian lakes. For example, Dejen et al., (2017) link the strong decline in fish density in Lake Tana to increased turbidity that results in low primary production. Enhanced sediment load has also been linked the overall decline in fish species richness in the Ethiopian Rift Valley lakes (Vijverberg et al. 2012). Problems related to enhanced sediment load are not only restricted to Ethiopian lakes, but have also resulted in profound food web alterations in multiple other tropical lakes. For example, human induced increases in sediment load in Lake Baringo (Kenya) resulted in the disappearance of aquatic vegetation, a strong reduction in primary production and a profound change in fish community composition (Aloo 2002).

The differences in some physical and chemical variables between seasons and habitats within each lake suggest that the inflow of water and sediment from the main catchments is important. The higher amount of suspended solids and the higher concentrations of nutrients during the wet season compared with the dry season in both lakes might be indicative of the importance of sediment run-off and inflow of nutrients from the catchment area due to erosion, especially during the wet season when rainfall in the region is high and the tributaries bring large volumes of water to the lakes. Inflow of sediments from the tributaries also explains the lower water transparency at inflow habitats of both lakes. The lower phytoplankton biomass in Lake Chamo during the wet season likely results from temporal light limitation due to increased suspended solid content in the water column.

In conclusion, our comparative analysis of the limnological characteristics of Lake Abaya and Lake Chamo revealed several major differences between these two major Ethiopian Rift Valley lakes. The two lakes differ substantially in water transparency and the amount of suspended solids. Lake Abaya is highly turbid, which in turn leads to lower primary production, lower phytoplankton and lower zooplankton biomass in this lake. Unfortunately, Lake Chamo is changing dramatically since the lake has become increasingly turbid over the latest decades (Teffera et al. 2017). Our study shows how this might change the limnological conditions and the food web structure of this lake. Many tropical lakes are currently subjected to a rapidly increasing sediment load as a result of land use intensification in their catchments. This has a strong impact on the functioning of these lakes, and has major implications for the conservation of global aquatic biodiversity (Donohue & Garcia Molinos 2009). Our study stresses the urgent need for catchment wide management programs that protect the ecological integrity of lentic waterbodies. Despite the prominent role of the Ethiopian Rift Valley in the maintenance of biological diversity and economic sustainability, little has been done to protect the Ethiopian Rift Valley lakes in general. Restoration programs should focus on reducing soil erosion from the catchment areas. In addition, the lakes and their surroundings need more effective protection.

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FIGURES

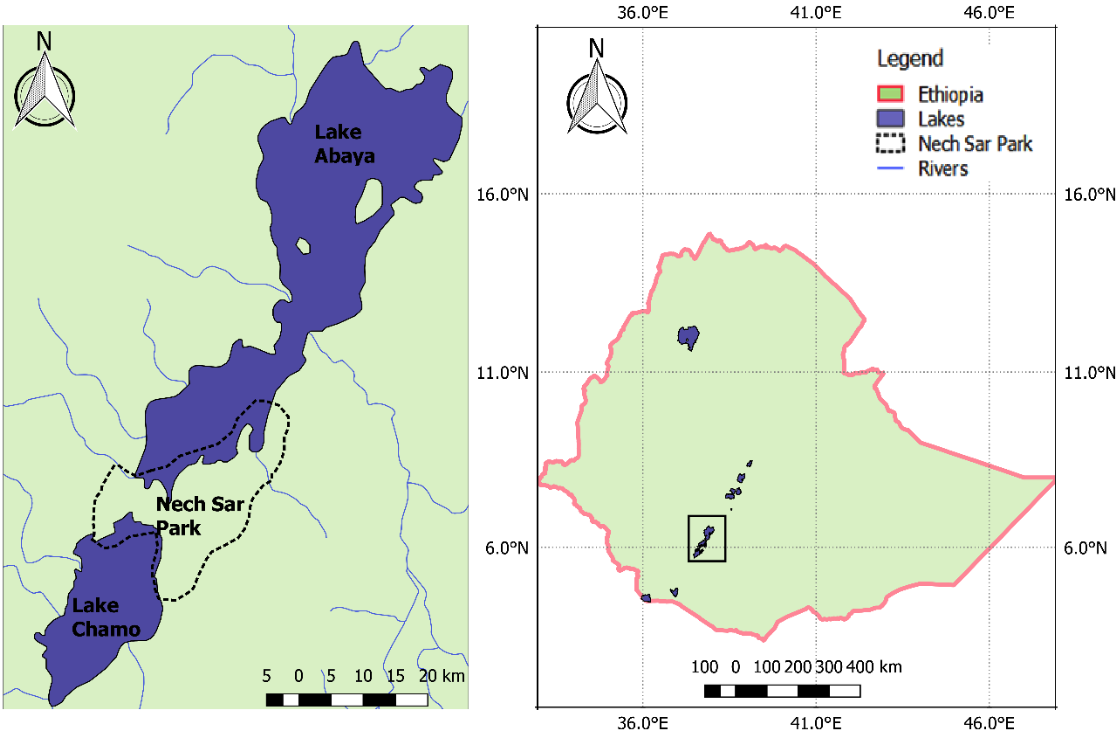

Figure 1. Outline map of Ethiopia with a detailed view on Lake Abaya and Lake Chamo (shape file downloaded from www.maplibrary.org).

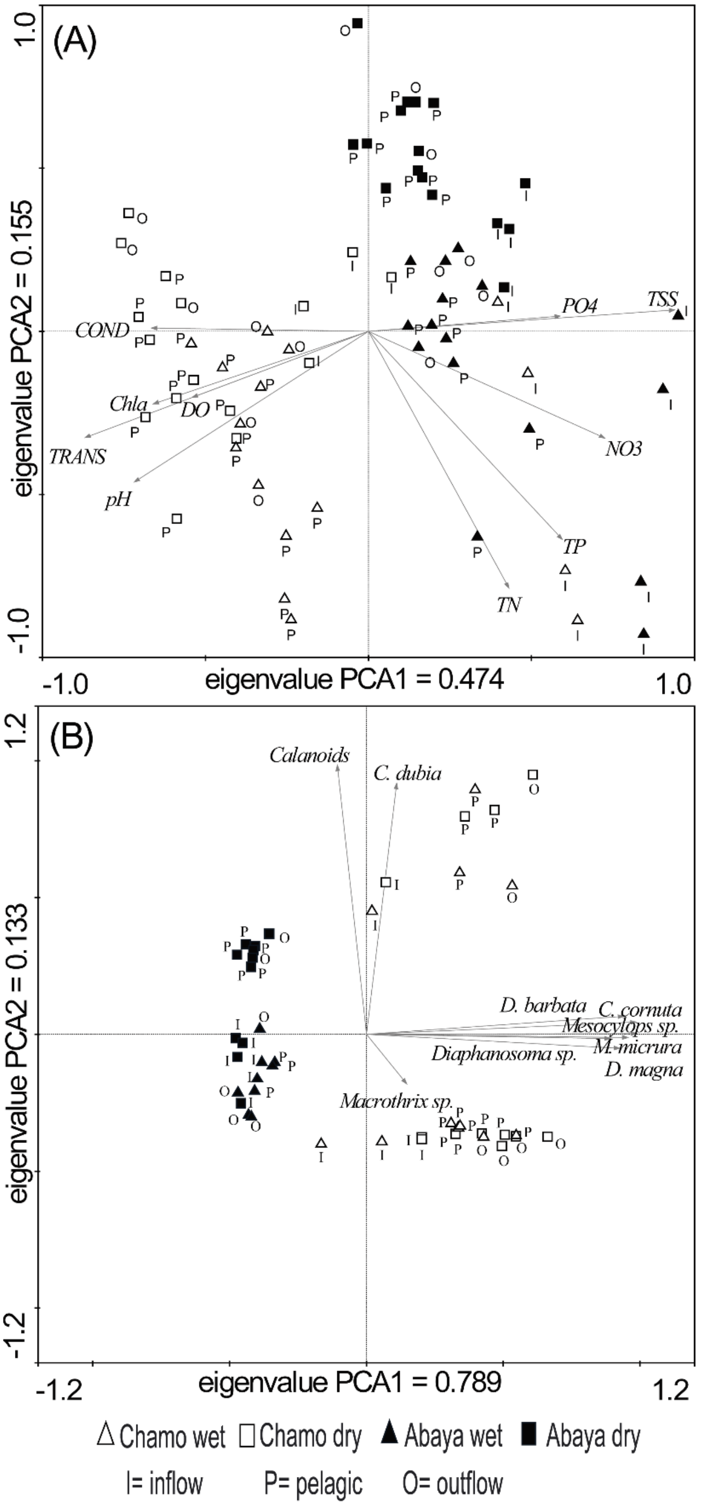

Figure 2. Biplots of Principal Component Analyses (PCA) showing (A) the associations between environmental variables and (B) zooplankton taxa in Lake Abaya and Lake Chamo as collected at different locations (inflow, pelagic, outflow) in the wet and dry season of 2013 and 2014. COND = conductivity, TRANS = water transparency, TSS = total suspended solids, PO4 = phosphate, NO3 = nitrate, TN = total nitrogen, TP = Total phosphorus, DO = dissolved oxygen concentration, and chla = chlorophyll-*a* concentration. *D. barbata* = *Daphnia barbata*

(Weltner), *C. cornuta* = *Ceriodaphnia cornuta* (Sars), *M. micrura* = *Moina micrura* (Kurz*), D. magna* = *Daphnia magna* (Straus).

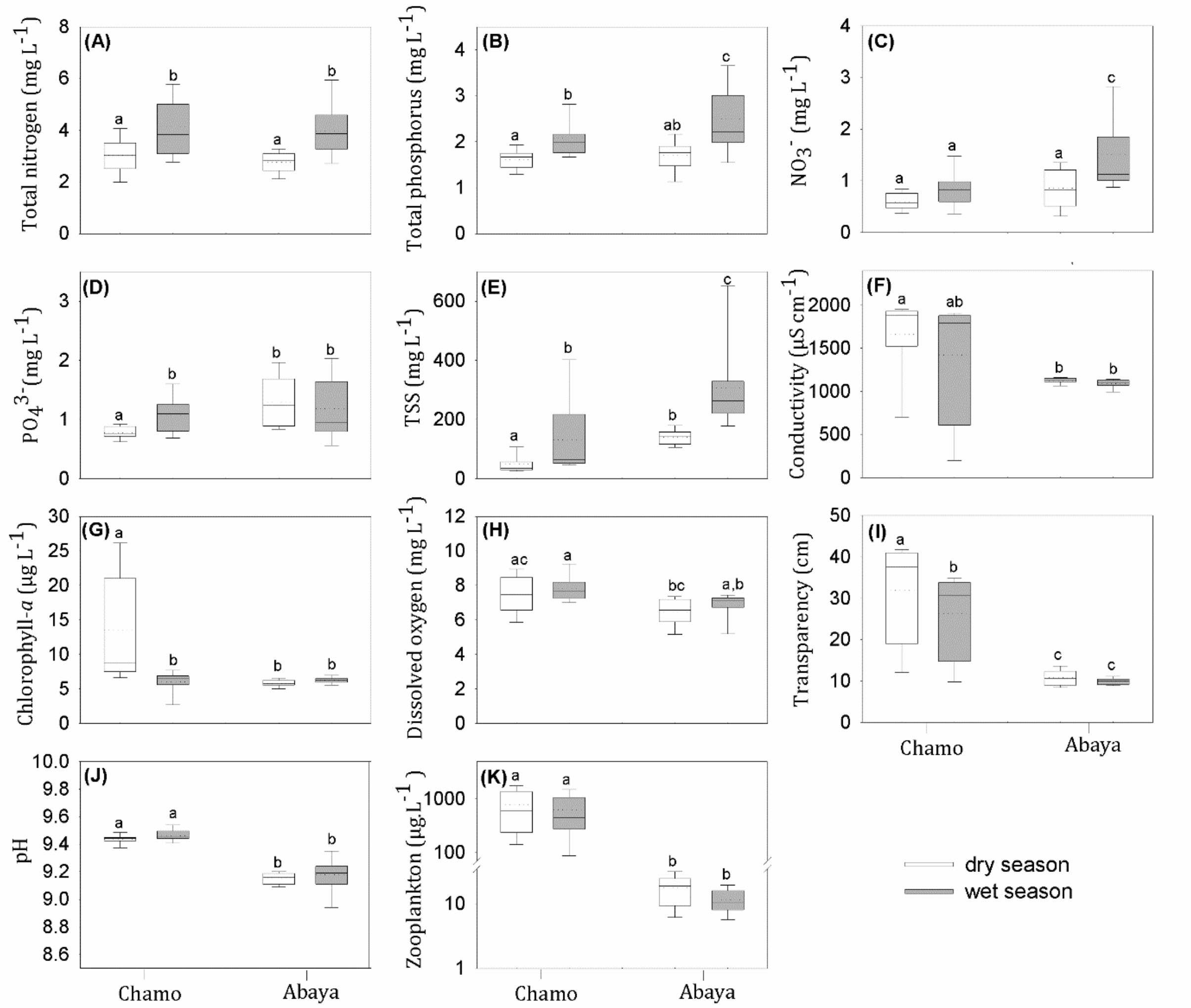

Figure 3. Boxplots with the median (solid line) and the mean (dotted line) values for each limnological variable and zooplankton community biomass in Lake Abaya and Lake Chamo in the dry and wet season. Boxes and error bars represent the 25th and 75th and the 10th and the 90th percentile respectively. (A) total nitrogen, (B) total phosphorus, (C) nitrate, (D) phosphate, (E) total suspended solids, (F) conductivity, (G) chlorophyll-*a*, (H) daytime oxygen concentration, (I) water transparency, (J) pH, and (K) total zooplankton biomass. Boxes without letters in common (a, b, c) differ significantly from each after pairwise post-hoc comparison (Tukey, P<0.05).

TABLES

Table 1. Results of partial RDA analyses testing for the effect of lake, season, habitat and their interactions on the entire set of limnological variables and zooplankton community composition as quantified in our field campaigns. Significant effects ($p < 0.05$) are shown in bold

		$R^2_{adj.}$	df	F	P
limnologial variables					
	lake	41.1%	1	78.8	**0.001**
	season	12.2%	1	36.12	**0.001**
	habitat	21.9%	1	23.47	**0.001**
	lake*season	4.1%	5	2.76	**0.003**
	lake*habitat	11.8%	2	18.9	**0.001**
zooplankton community					
	lake	94.2%	1	151.15	**0.001**
	season	0.6%	1	2.49	**0.049**
	habitat	7.2%	1	9.59	**0.001**
	lake*season	7.4%	6	4.16	**0.001**
	lake*habitat	7.9%	3	9.23	**0.001**

Table 2. Summary results of Linear Mixed Models testing for the effect of lake, season and their interaction on measured limnological variables and total zooplankton community biomass. Significant effects ($p < 0.05$) are shown in bold.

		estimate	std. Error	df	t-value	P
total nitrogen	Intercept	0.574	0.032	3.3	17.68	**<0.001**
	lake	0.024	0.033	21.5	0.74	0.470
	season	0.112	0.021	45.0	5.42	**<0.001**
	lake*season	-0.010	0.029	45.0	-0.34	0.734
total phosphorus	Intercept	0.428	0.024	3.2	17.93	**<0.001**
	lake	-0.013	0.024	25.0	-0.52	0.610
	season	0.106	0.018	45.0	5.99	**<0.001**
	lake*season	-0.038	0.025	45.0	-1.50	0.141
NO_3^-	Intercept	0.261	0.040	2.4	6.50	**0.014**
	lake	-0.058	0.036	19.0	-1.63	0.120
	season	0.125	0.019	45.0	6.53	**<0.001**
	lake*season	-0.067	0.027	45.0	-2.47	**0.017**
PO_4^{3-}	Intercept	0.354	0.021	22.9	16.58	**<0.001**
	lake	-0.105	0.030	22.9	-3.47	**0.002**
	season	-0.027	0.020	46.0	-1.34	0.188
	lake*season	0.090	0.029	46.0	3.12	**0.003**
total suspended solids	Intercept	2.142	0.077	16.0	27.73	**<0.001**
	lake	-0.506	0.109	16.0	-4.63	**<0.001**
	season	0.310	0.039	46.0	7.91	**<0.001**
	lake*season	0.009	0.055	46.0	0.16	0.867
conductivity	Intercept	3.052	0.075	16.2	40.71	**<0.001**
	lake	0.147	0.106	16.2	1.39	0.184
	season	-0.015	0.040	46.0	-0.36	0.718
	lake*season	-0.155	0.056	46.0	-2.74	**0.009**
chlorophyll a	Intercept	0.834	0.057	1.8	14.75	**0.006**
	lake	0.273	0.046	32.6	5.97	**<0.001**
	season	0.026	0.040	45.0	0.65	0.522
	lake*season	-0.300	0.056	45.0	-5.32	**<0.001**
dissolved oxygen	Intercept	0.872	0.016	12.4	53.89	**0.001**
	lake	0.054	0.021	20.1	2.54	**0.020**
	season	0.021	0.012	45.0	1.70	0.096
	lake*season	-0.001	0.018	45.0	-0.04	0.967
water transparency	Intercept	1.066	0.054	15.4	19.66	**<0.001**
	lake	0.416	0.075	14.7	5.56	**<0.001**
	season	-0.029	0.017	45.0	-1.75	0.086
	lake*season	-0.053	0.023	45.0	-2.28	**0.027**

pH	Intercept	9.152	0.021	9.0	437.98	**<0.001**
	lake	0.286	0.027	30.0	10.49	**<0.001**
	season	0.028	0.023	45.0	1.24	0.220
	lake*season	-0.003	0.032	45.0	-0.09	0.923
zooplankton biomass	Intercept	-0.318	0.911	26.4	-0.35	0.729
	lake	3.484	0.519	38.0	6.71	**<0.001**
	season	-0.312	0.544	38.0	-0.57	0.570
	lake*season	0.010	0.334	38.0	0.03	0.977

SUPPLEMENTARY INFORMATION

Table S1. Overview of the explanatory variables, covariates and the restriction of permutations in the different redundancy analyses testing for the effect of lake, season, habitat and the interaction lake-habitat and lake-season on the entire set of limnological variables and zooplankton community composition.

explanatory variables	covariates (as dummy variables)	permutation restricted to
lake	dummies of all year-habitat-season combinations	all covariates
season	dummies of all year-season combinations	all covariates
habitat	dummies of lake-habitat combinations	all covariates
lake*season	lake, season, habitat	habitat
lake*habitat	lake, habitat, all year-season combinations	all year-season combinations

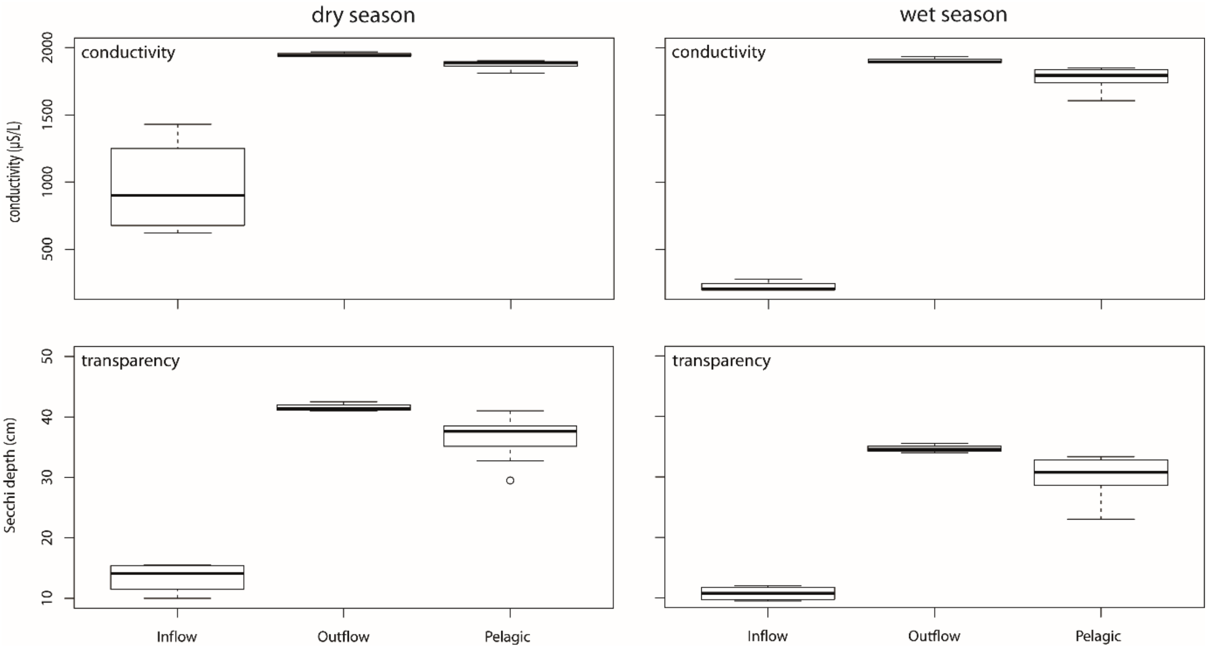

Figure S1. Boxplots showing the median conductivity and water transparency (upper and lower panels respectively) in Lake Chamo for the dry and wet season (left and right panels respectively) separately at the inflow, outflow and pelagic sampling habitats. Boxes and error bars represent the 25th and the 75th, and the 10th and the 90th percentile respectively. Dots depict outliers.