Some biotic and abiotic factors affect phytoplankton functional groups in Lake Hawassa, Ethiopia

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This is to certify that the thesis prepared by Getacher Beyene Estifanos, entitled: Some biotic and abiotic factors affect phytoplankton functional groups in Lake Hawassa, Ethiopia and submitted in partial fulfillment of the requirements for the degree of Master of Sciences (Aquatic Ecosystems and Environmental Management) complies with the regulations of the university and meets the accepted standards with respect to originality and quality.

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List of abbreviations

ANOVA	Analysis of variance
APHA	American Public Health Association
CANOCO	Canonical community ordination
CCA	Canonical correspondence analysis
CCME	Canadian Council of Ministers of the Environment
Chl-a	Chlorophyll-a
DCA	Detrended correspondence analysis
DO	Dissolved oxygen
EC	Electrical conductivity
EEA	European Environmental Agency
EPA	Environmental Protection Agency
FGs	Functional groups
FWB	Fresh weight biomass
MBFGs	Morphology-based functional groups
MZ	Macrophyte zone
NTU	Nephelometric turbidity unit
OW	Open water part
PA	Phenolphthalein alkalinity
RDA	Redundancy analysis
RFGs	Reynolds functional groups
RH	Referral hospital influent area
SD	Standard deviation
SPSS	Statistical package for social sciences
SRP	Soluble reactive phosphorus
TA	Total alkalinity
TDIN	Total dissolved inorganic nitrogen
TDS	Total dissolved solids
TP	Total phosphorus
TSI	Trophic status index
TSS	Total suspended solids
TW	Tikur Wuha inlet
USEPA	United States Environmental Protection Agency

VIF	Variance inflation factor
WHO	World Health Organization
Z_{eu}	Euphotic depth
Z_{SD}	Secchi depth

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Abstract

The water quality of Lake Hawassa has been deteriorated due to high influent load from various sources, including effluents of a hospital, industries, hotels, and agricultural runoff, which can induce changes in phytoplankton functional groups (FGs). The functional association of algae can also be affected by the dominant zooplankton and macrophytes coverage. FGs are groups of phytoplankton species with similar ecological requirements. The FGs approach has greater effectiveness than the taxonomic method in detecting the changes in phytoplankton assemblages in relation to the predominant environmental stressors. No previous study has however been conducted on the FGs in the lake. It was hypothesized that the introduction of pollutants through the various influents of the lake and the composition and abundance of the major zooplankton groups, and the presence of Echichloa pyramidalis (emergent macrophyte) influence the FGs. The main objective of this study was, therefore, to document scientific information on the variations of phytoplankton FGs in relation to these ecological factors in Lake Hawassa, Ethiopia. Sample collection and insitu measurements of physico-chemical parameters were made monthly (April to August in 2019) from four sites. Data analyses were performed using SPSS version 20 and CANOCO version 4.5. A total of 130 species of phytoplankton were identified and classified into 18 trait-based functional groups (RFGs) and 6 morphology-based functional groups (MBFGs). ***SN****,* ***M****,* ***P****,* ***J****, and* $\boldsymbol{L_O}$ *were the most dominant FGs contributing for 91.17% of the total fresh weight biomass of the RFGs.* ***III****,* ***IV****,* ***V****,* ***VI*** *and* ***VII,*** *which accounted 99.0035% of the total fresh weight biomass, were the most conspicuous MBFGs. RDA analysis indicated that the RFGs* ***SN****,* ***Lo****,* ***M****,* ***F****,* ***N****,* **J*****, P, MP*** *and* ***D*** *and the MBFGs* ***III****,* ***V****,* ***VII****,* ***IV*** *and* ***VII*** *were correlated significantly with electrical conductivity, DO, pH, TSS, turbidity, Secchi depth and total phosphorus (*$P \leq 0.004$*) revealing the overriding importance of these parameters in influencing the variation of the phytoplankton FGs in Lake Hawassa. The potentially toxigenic FGs were dominant at the Macrophyte zone due to their preference for shading and water column stability. Rotifers and cyclopoid copepods were the dominant zooplankton taxa with no significant impact on the FGs. The results of this study supported our hypothesis that the biotic (the macrophyte Echinochloa pyramidalis) and the human-induced abiotic (the influents associated) factors have significant impact on the phytoplankton FGs. But, further research is mandatory to better understand the underlying mechanisms governing their interactions. The current study can have practical importance to efforts directed towards improving the water quality of the lake and may also serve as base-line information for further studies.*

Keywords: *Influents, Lake Hawassa, macrophyte, phytoplankton functional groups, water quality, zooplankton*

1. Introduction

Phytoplankton are microscopic aquatic autotrophs adapted for suspension in the water column (Hötzel and Croome, 1999). They inhabit both marine and inland water systems. Among inland water systems, lakes are home for myriads of the planktonic autotrophs. Phytoplankton are the direct or indirect sources of food for both herbivorous and carnivorous organisms (e.g. fishes) thereby establishing the basis of the aquatic food web (Arrigo, 2005), which supports the fishery sectors (Baloloy *et al*., 2016). They are well known for their role in regulating the resource dynamics (mainly nutrients, light and DO) and the health of aquatic systems (Bellinger and Sigee, 2010).

The growth, reproduction, morphology and functional properties of phytoplankton, can be determined by the interactive effects of biological and physico-chemical parameters. Due to the dynamic nature of aquatic systems, the plankton groups dominating the systems can show variations with time depending on the physical structure of the system and availability of nutrients that selectively favor species-specific strategic adaptations (Reynolds, 1980). Phytoplankton can, therefore, provide early warning signals for the deterioration of water quality via their fast response to a wide range of stressors (Domingues and Galvão, 2007; Baloloy *et al*., 2016). Therefore, studying almost all aspects of phytoplankton is relevant for bio-monitoring of aquatic ecosystems.

In Ethiopia, the taxonomic composition of phytoplankton have been studied by many workers (e.g. Elizabeth Kebede and Amha Belay, 1994; Girma Tilahun, 2006; Tadesse Fetahi, 2010; Tadesse Fetahi and Seyoum Mengistou, 2014; Yeshiemebet Major, 2016). However, the taxonomic method of the plankton study is not sufficient to describe the perceived ecological functions (Padisák and Salmaso, 2007). In addition, the taxonomic unit can contain phytoplankton species that have different ecological and functional properties. Chlorophyceae (green algae), for instance, includes algal taxa characterized by very different structures body forms ranging from single picoplanktonic cells (Stockner and Antia, 1986) to long filaments and large colonies. Similarly, though some species appear relatively predictable, the vast majority of the species show no clear relationship with the environmental conditions (Kruk *et al*., 2011).

This may cause confusion when using phytoplankton as bio-indicators of water quality deterioration and for ecological assessment. In addition, the taxonomic study is not suitable for comparison among distant ecosystems with different species composition, while having similar functional characteristics (Salmaso *et al*., 2015). These problems would be avoided by classification of algae based on their functional properties as proposed by Reynolds (1980, 1984) with the aim to obtain a better understanding and possible generalization of the ecosystems' functioning.

Phytoplankton functional groups (FGs) consist of species with similar morphology, physiology, tolerances and sensitivities to different combinations of biological, physical, and chemical properties of aquatic ecosystems regardless of their phylogenetic categories (Reynolds *et al*., 2002; Demir *et al*., 2014). In contrast to long species lists of dominant taxonomical groups, FGs make it much easier to examine and compare the seasonal changes in various lake types and to evaluate the responses of phytoplankton to environmental conditions and changes (Weithoff *et al*., 2001; Kruk *et al*., 2002). The classification of planktonic algae based on their sensitivity to environmental constraints originated from the works of Tüxen (1955) and Braun-Blanquet (1964), who had developed the sorting methods of plants. However, the systems do not use formal phytosociological names, but alphanumeric codes are used to distinguish the FGs. In addition, the method is criticized for lacking a valid principle to be used as a base for robust advocacy of the functional grouping. In contrast, the findings of Reynolds and Irish (1997) and Kruk *et al*. (2002) seem to corroborate the validity of the functional grouping. Kruk *et al*. (2002) indicated that the functional classification of phytoplankton is comparable with statistical variations.

Algae forming a single functional group also have similar morphological features. Among these, surface area (s), volume (v) and maximum linear dimension (m) of phytoplankton are found to be powerful predictors of their optimum dynamic performance (Reynolds and Irish, 1997). In addition, morphological traits are relatively easy to measure and have clear relationships with the functional properties of phytoplankton (Reynolds, 1984; Kruk *et al*., 2010). Furthermore, separation of algae on the basis of their morphology coincides substantially with the distributions of the species among different types of habitat distinguished on the basis of light and nutrient levels (Reynolds, 1984, 1997). The morphology-based functional groups (MBFGs) approach clusters organisms into 7 groups (**Fig**. **1**) in terms of morphological traits independently from the organism's taxonomic affiliation (Kruk *et al*., 2010).

Separating of different phytoplankton taxa on the basis of specialist adaptations and requirements (such as having high affinity for phosphorus or carbon dioxide at low external concentrations, requiring skeletal silicon, or having a good light antenna) will help to predict the phytoplankton dynamics with good precision (Reynolds *et al*., 2002).

Different species of phytoplankton are known to react uniquely to environmental variations. The various responses of the different species of phytoplankton to environmental factors have been combined to build habitat templates (Reynolds, 1988). The habitat is considered as a template on which evolution shapes phytoplankton traits. The findings of Quéré *et al*. (2005) and Follows *et al*. (2007) have demonstrated that clustering species based on their functional traits can be used to summarize their response to environmental changes.

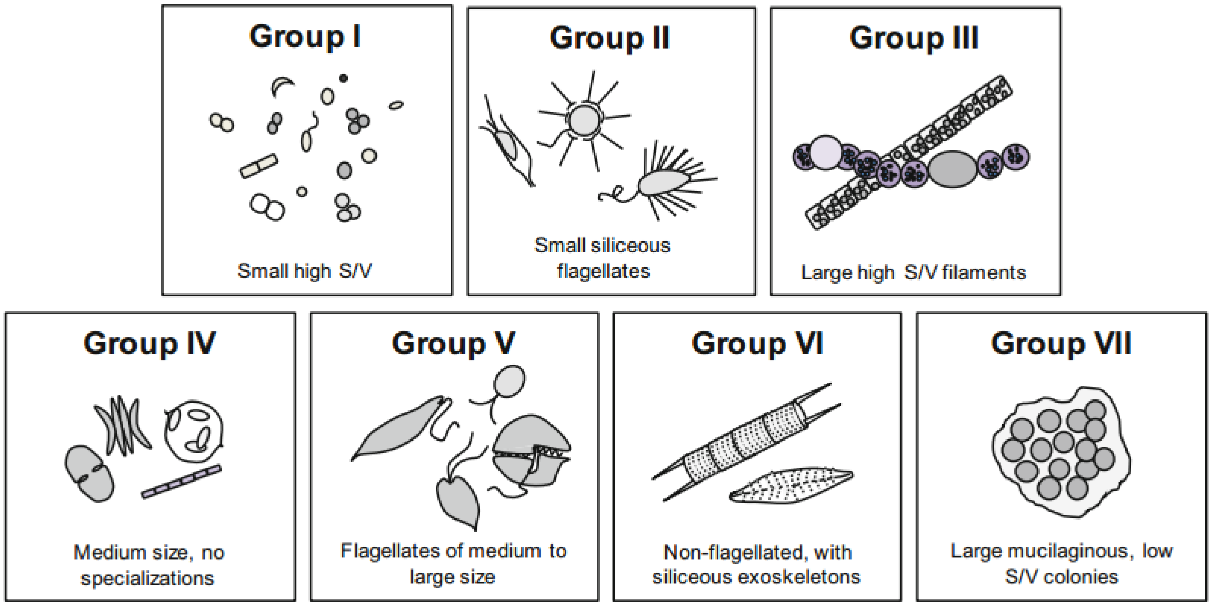


Figure 1. Schematic representation of the seven MBFGs with a brief description of their morphology. S = surface area, V = volume (Kruk *et al*., 2010).

Phytoplankton FGs have been extensively studied in temperate lakes. In contrast, only a few research works have been done in the tropical region (especially in Africa) concerning the subject. The usefulness of phytoplankton FGs as indicators of the environmental conditions was emphasized by Dantas *et al*. (2012) following their study on functional assemblages of algae in three reservoirs of northeastern Brazil. Bouvy *et al*. (2006) had studied the functional association of phytoplankton in Lake Guiers, Senegal and reported physical factors as the driving forces of phytoplankton succession. Huszar *et al*. (2006), Costa *et al.* (2009), Becker *et al.* (2013) and Souza *et al.* (2018) have confirmed the importance of studying algal FGs for better understanding of changes happening in aquatic ecosystems.

In Ethiopia, Mesfin Gebrehiwot *et al*. (2017) have studied the influence of emergent macrophytes on phytoplankton functional dynamics in Lake Ziway, Ethiopia. They have indicated the importance of uneven distribution of macrophytes in structuring the phytoplankton community via their effect on nutrient availability, water stability and zooplankton abundance. Fasil Degefu and Schagerl (2015) have also applied the functional approach in the study of the phytoplankton community of Lake Wonchi, Ethiopia, and found that mixing event and nutrient levels were the major determinants of functional dynamics in the lake. Atelomixis was indicated to be the key driver of phytoplankton assemblage in Ethiopian highland lake, Lake Hayq (Tadesse Fetahi *et al*., 2014). Adequate information on the phytoplankton dynamics and their key drivers is relevant to tackle the problem of eutrophication and the subsequent occurrence of algal bloom via an appropriate management measure.

The focus of the present study, Lake Hawassa, is considered to be the most exhaustively studied fresh water Lake of Ethiopia (Seyoum Mengistou, 1989; Elizabeth Kebede and Amha Belay, 1994; Girma Tilahun, 2006; Tadesse Fetahi, 2010; Tadesse Fetahi and Seyoum Mengistou, 2014; Getasew Amsalu, 2017). However, previous studies have not considered the functional association of phytoplankton in the lake. On the other hand, major drivers of phytoplankton FGs (e.g nutrients and other pollutants) have increased due to industrial, municipal, hospitals and hotel discharges. Therefore, there is a need to study the morpho-functional properties of the community of the water system and to establish relatively easy indicators. In this study, the spatial variability of phytoplankton FGs in relation to the major influents, zooplankton and macrophytes were determined. The toxin-producing cyanobacteria are the most important ecologically as they are associated with eutrophication. These taxa were also addressed in this study.

2. Statement of the Problem

Lake Hawassa is greatly important in supporting the livelihood of the local people via providing an ideal environment for fish production, water for consumption, recreation and moderation of the surrounding climate. In addition, the lake is inhabited by a variety of faunal and floral species that have both economic and ecological significance. Among the components of the aquatic flora, phytoplankton are known to play a central role in forming the food web's base of the lake and contributing immensely to overall ecological services of the lake. But, because of the increasing anthropogenic factors such as overexploitation and pollution, the lake is being subjected to undesirable changes with time. For instance, the influents from the Hawassa University Referral Hospital, Hawassa textile and ceramic factories, runoff from agricultural lands and Hawassa city can be considered as the major contributors. Consequently, the overall habitat quality of the water system is deteriorating with time at an alarming rate. Reduction in water quality of the lake can disturb the phytoplankton community structure thereby negatively affecting the normal functioning of the entire food web of the lake ecosystem. The study of phytoplankton based on the FGs has been tested for its effectiveness in detecting the change in phytoplankton assemblage in many lakes of various climatic regimes ranging from tropical to sub-polar regions (Izaguirre *et al*., 2012). In addition, Vörös *et al*. (2013) have indicated the existence of negative relationship between functional diversity of phytoplankton and trophic state of a lake revealing the greater efficiency of the functional approach in depicting any change in phytoplankton community structure in relation to environmental conditions. The predominant environmental stressor can also be predicted from the dominant algae with specific functional trait (Reynolds, 1998; Barrow, 2017). Therefore, studies on phytoplankton FGs have great importance in understanding the functioning of aquatic ecosystems.

Several studies have been conducted by many scholars regarding the plankton and water quality of Lake Hawassa. Studies made so far investigated phytoplankton primary production (Demeke Kifle and Amha Belay, 1990), species composition and biomass (Elizabeth Kebede and Amha Belay (1994) and size-structure of primary production and biomass (Girma Tilahun, 2006), zooplankton species composition (Seyoum Mengistou, 1989) and its long-term changes along with phytoplankton communities (Tadesse Fetahi and Seyoum Mengistou, 2014), the impact of the macrophyte *Potamogeton schweinfurthii* on natural phytoplankton communities (Getasew

Amsalu, 2017) and most recently, species composition and abundance of diatoms, and applicability of the European diatom indices for bio-monitoring purpose by Tarekegn Wondmagen *et al.* (2019). Scientific information on the phytoplankton FGs dynamics in Lake Hawassa is, however, not available. The water quality of the lake that determines the dominant phytoplankton FGs, may have, however, been deteriorating due to the direct effluent discharges from point sources and runoff from agricultural based catchments. To fill this knowledge gap, the spatial variations in phytoplankton FGs with respect to the major influents, zooplankton groups and emergent macrophyte (*Echinochloa pyramidalis*) was investigated in this study.

3. Hypothesis

Null hypothesis (H_0): The type and level of influents, the composition and abundance of major zooplankton groups, and emergent macrophyte (*Echinochloa pyramidalis*) coverage have no impact on the patchiness of phytoplankton FGs from both spatial and temporal perspective.

Test hypothesis (Ha): The level and type of influents and the composition and abundance of major zooplankton groups, and emergent macrophyte (*Echinochloa pyramidalis*) have impact on the spatial and temporal variations of phytoplankton FGs.

4. Significance of the Study

The results of this study could have practical application in water quality management of Lake Hawassa in an environmentally friendly way, while contributing indirectly to the improvement of fish production potential of the lake in a sustainable manner as assessment of phytoplankton population dynamics can provide information on water quality status of the lake and the amount of food available for zooplankton and fishes. In addition, since no studies have so far been made regarding the functional dynamics of phytoplankton in the lake, the results of this study can be used as base-line information for further studies. The findings of this sudy can also be used as an input for development of water quality monitoring systems via biological method in cost effective way.

5. General Objective: The overall objective of this study was to generate scientific information on factors affecting the variations of phytoplankton FGs in Lake Hawassa, Ethiopia, while contributing data towards the development of phytoplankton FGs model for water quality bio-monitoring purpose.

5.1. Specific objectives

- ➢ To determine the spatial and temporal variations of physico-chemical parameters
- ➢ To identify the species composition of phytoplankton, categorize them into FGs
- ➢ To determine the spatial and temporal variations of phytoplankton FGs
- ➢ To identify factors associated with the variations in FGs of the algae
- ➢ To assess the water quality of Lake Hawassa using the phytoplankton FGs and the level of physico-chemical parameters
- ➢ To determine the species composition, abundance and spatio-temporal variations of zooplankton in relation to phytoplankton FGs

5.1.1. Research questions

- ✓ How are the variations in the levels of physico-chemical parameters in space and time?
- ✓ To which FGs do the resident phytoplankton belong?
- ✓ Are there spatial and temporal changes in the phytoplankton FGs in relation to water quality parameters?
- ✓ How do the phytoplankton and zooplankton interact in this lake?
- ✓ What is the extent of physico-chemical water quality deterioration in Lake Hawassa and its relation to the phytoplankton FGs?

6. Limitation of the Study

The sampling frequency of the present study on plankton and the associated physico-chemical parameters was only one time per month due to financial constraints. In addition, sampling was carried out starting from the middle of the minor rainy season (April) and ending in the middle of the major rainy season (August). This may not be adequate to reveal the temporal dynamics of phytoplankton because their population density and taxonomic composition can show alteration drastically within a few days depending on the weather conditions and water quality parameters of the water system (Hötzel and Croome, 1999). Only four sampling sites were selected to represent the entire water body (Lake Hawassa). The results obtained from the analysis of these samples may not be sufficient to depict the water quality and the overall ecological status of the lake adequately.

7. Literature Review

7.1. Concept of phytoplankton functional assemblages

Classifying of organisms based on structural and functional characteristics and the use of phytoplankton (Teiling, 1955; Lepistö and Rosenström, 1998; Lepistö, 1999) for the purpose of ecological assessment have long history. In phyto-sociological approach, the phytoplankton associations are defined as groups of species that share common ecological attributes (Reynolds, 1980, 1984). Reynolds (1980) formed 14 species associations by identifying the patterns in a long series of phytoplankton data from a number of lakes using this approach. After a long-lasting effort, Reynolds *et al*. (2002) produced 31 entries of trait-mediated FGs. The approach has been further extended to include more than 45 assemblages that are identified by alpha-numerical codes (letters and numerals) according to their sensitivities and tolerances (Reynolds, 2006; Padisák *et al*., 2009). These comprised aggregates of organisms that happened to be at the same time and increased or decreased simultaneously in the water. The associations were considered as robust indicators of ecological affinities of phytoplankton (Reynolds, 2000). The scheme has been expanded to accommodate associations represented among a wider number of lakes (Reynolds, 1997; Padisák and Reynolds, 1998). Analysis of how changes generated by imposed environmental variations, either natural or deliberate management, reveals important aspects of the tolerances and susceptibilities of the normal community (Powell, 1995). Communities are more reliable indicators of the environmental condition than the presence and absence of a species as communities have larger spatial coverage and survive for a longer time so they can better reflect the habitat condition. Kruk *et al*. (2002) tested the discriminatory power of taxonomic affiliation and functional association and found that the functional method has greater discriminatory power.

7.2. Criteria for functional classification of phytoplankton or developing phytoplankton functional groups model

7.2.1. Cell size, morphology and physiology

Understanding the impacts of environmental factors on morphological features of phytoplankton is a crucial step in clarifying aquatic ecosystems functioning and improving assessment of human impacts (Litchman and Klausmeier, 2008; Kruk and Segura, 2012). The role of phytoplankton cells and many physiological processes depend on their morphology. Numerous morphological properties could be strategic, helping to explain phytoplankton differences and patterns under contrasting hydrodynamic conditions (Fraisse *et al.*, 2013). In natural environments, size and shape selection is strongly related to the variability of environmental factors. Morphological traits thus are very important in the determination of phytoplankton ecological function. The coexistence of differently sized phytoplankton organisms is the result of a morphological adaptive strategy in response to environmental changes (Roselli and Basset, 2015; Weithoff and Gaedke, 2016). Ecological classification systems usually employ size and other morphological characteristics of algae because the different strategies of various phytoplankton are strongly related to the differences in geometrical dimensions and shapes (Padisák and Salmaso, 2007). For instance, the sinking properties and motility, growth rates, efficiency of nutrients and light utilization, susceptibility to grazing and buoyancy regulation (Lehman, 1988) can be determined by the shape and size of the species. These elements, together with other functional traits including the requirement for specific resources (e.g., silica) and the ability to obtain alternative carbon and nutrient sources, represent strong factors that are able to select the best competitors under different environmental constraints (Weithoff, 2003). Motility of algae is dependent not only on the presence/ absence of flagella but also on the specific shape of the species considered. In addition, phytoplankton shape is important in determining the loss from settling and grazing pressure (Padisák *et al.*, 2003). Phytoplankton with flat and serrated shape tend to be less susceptible to sinking than the tapered-shaped ones. Algae develop spiny projection to deter predation. Considering phytoplankton geometry, smaller-sized phytoplankton are highly affected by grazing pressure than larger-sized algae. Therefore, morpho-functional variations among phytoplankton are useful in discriminating different taxa. Cyanobacteria are prokaryotes and exhibit defined morphological and physiological differences compared with the eukaryotic phytoplankton. Among these, the ability to regulate vertical position through the formation of gas-vesicles (aerotopes) and the ability to fix atmospheric nitrogen constitute a set of unique features of cyanoprokaryote (Whitton and Potts, 2000), which distinguish them from eukaryotic phytoplankton. On the other hand, diatoms are distinguished by their siliceous wall that makes them more vulnerable to sinking during stratification.

Different taxa may have the same or different functions in ecosystems according to specific traits (e.g., size). Cell size is considered to be a morphological master trait that influences reproduction, growth, metabolism, resource acquisition, and predator avoidance (Litchman and Klausmeier, 2008). Smaller algae have high SA:V ratio and higher nutrient acquiring potential than the lager phytoplankton that have low SA:V ratio. Large species, on the other hand, are believed to benefit from a pulsed nutrient supply because of their higher uptake and storage potential (Stolte and Riegman, 1996). Hence, smaller phytoplankton tends to be dominant in an oligotrophic lake, while larger phytoplankton are prominent in a productive (eutrophic) environment (Litchman and Klausmeier, 2008).

Planktothrix rubescens is a filamentous cyanobacterium that uses photosynthetically active radiation (PAR) with high efficiency due to its high SA:V ratio (Reynolds, 1997). On the other side, this species is photo-inhibited under conditions of high irradiance (Bartram and Chorus, 1999) and inhabits the metalimnion (Feuillade, 1994) where light intensity is relatively low. Larger phytoplankton (e.g. diatoms) are better adapted to turbulence. But, turbulence may cause physical damage to smaller phytoplankton (flagellates) and these small flagellates persistent under stratified conditions due to their swimming ability (Paredes and Montecino, 2011). Considering such size specific habitat conditions, ecosystems changes can be depicted from the size specific fluctuation. Diversity of phytoplankton size classes becomes greater under the intermediate trophic condition (Paredes and Montecino, 2011) expressing pattern in phytoplankton dynamics. Cell size also affects the colonization strategy of algae. Smaller algae, owing to their fast growth rate, are the first to appear in disturbed environments (Rojo and Rodriguez, 1994). So, system maturity can be predicted using the size class diversity. Small cells will be replaced by larger phytoplankton when resources become sufficient. Size diversity of plankton would be high at optimum conditions and low at higher disturbance levels (Grover, 1997; Reynolds, 1997). Consequently, ecosystem health and change in phytoplankton community structure can be assessed from variations in size composition. Abiotic factors including water movement, depth of photic zone, trophic state and nutrient concentration affect the pattern of variation of phytoplankton size structure on spatial and temporal scale. Geometric dimensional features are responsive to natural and anthropogenic pressure (Vadrucci *et al.*, 2013). Because of size dependencies of many biological processes, the analysis of the size structure of phytoplankton may, therefore, allow the formulation of testable hypotheses about general relationships with environmental factors (Rojo and Rodriguez, 1994).

7.3. Factors affecting the variability of phytoplankton functional group dynamics both in space and time

Phytoplankton species are known to develop morphological and physiological adaptive strategies that help them to thrive in particular environmental conditions (Reynolds, 2006). The functional assemblages and phytoplankton community dynamics can be determined by physical, chemical and biological factors (Tadesse Fetahi *et al.*, 2014; Baloloy *et al.*, 2016).

Light, temperature, stratification and mixing events are physical factors that have a considerable impact on phytoplankton survival, growth, and developments and on overall community structure and functioning. The chemical factors include nutrients, pH, salinity, DO, alkalinity and others. Among physical factors, the temperature has a determining effect on the level of other chemical and physical parameters.

7.3.1. Stratification and mixing, and depth of water systems

Temperature difference can be responsible for stratification and mixing. Stratification can be caused to come to an end as a result of cooling effect (temperature fall). When surface water temperature decreases to a lower level, the density of the upper part of the water column tends to increase and consequently sinks down to the bottom (Sherman *et al.*, 1978; Fassil Degefu and Schagerl, 2015). This leads to a mixing event that circulates materials from bottom to surface and vice versa. Higher intensity and frequency of turbulence are more likely to occur in shallow lakes than deeper lakes. The mixing in turn affects nutrient availability, light penetration, pH and DO level. The intensity, duration and frequency of stratification and mixing have regulating impact on survival of phytoplankton assemblages. Accordingly, a special mixing pattern called atelomixis was regarded as a key variable driving the phytoplankton assemblages thereby leading to the dominance of heavy plankton such as diatoms in the deep tropical lake, Lake Hayq (Tadesse Fetahi *et al.*, 2014).

The study lake (Lake Hawassa) has been shown to experience two phases of stratification (Elizabeth Kebede and Amha Belay, 1994). Surface stratification (superficial stratification) from September to November (first phase) followed by complete mixing in December and a strong and deep-seated thermal stratification from January to May (second phase). Lake Hawassa experiences mixing event in the remaining months of the year (Elizabeth Kebede and Amha Belay, 1994). It is known that stratification negatively affects nutrient availability which influences the vertical distribution of phytoplankton. The complete mixing event in December may reverse this effect as it makes nutrients available to the surface plankton. Phytoplankton FGs that have little potential for resuspension such as *Cosmarium* and *Aulacoseira* species (diatoms) will occupy the plankton niche during the mixing event (Reynolds *et al.*, 2002).

7.3.2. Nutrient availability and temperature

In addition to mixing/stratification events, phytoplankton dominance in water bodies can be determined by nutrient availability, zooplankton and the interactive effects of other water quality parameters. Accordingly, different groups of phytoplankton may exist in diverse habitats depending on their functional affinity, sensitivity and tolerance. Under optimum conditions, they potentially operate successfully, but as the limiting conditions become more severe, the operational criteria select against less tolerant species (Reynolds *et al.*, 2002). Knowledge on sensitivities of the various FGs of cyanoprokaryota to the depth, stability and nutrient content of water columns, has been shown to have practical significance in the management of harmful algal blooms (Padisák and Reynolds, 1998; Huszar *et al.*, 2006). The limiting nutrient, especially during the time of water quality concern, can be determined either by chemical analysis or bioassay technique (Lee and Jones-Lee, 1998).

According to Lee and Jones-Lee (1998), P becomes a limiting nutrient to algal growth when the concentration of SRP is 0.002 mg L^{-1} or lower. These researchers also indicated that nitrogen would be limiting when the available nitrogen concentration is less than about 0.015 mg L^{-1}. Under some circumstances, both nutrients may present in growth-limiting amounts, and it could be a combination of these nutrients, which is limiting to maximum biomass development. In some water bodies, both nutrients may present in amounts greater than these limiting levels, in which case some factor other than nitrogen or phosphorus concentrations, such as light or a toxic substance, would limit maximum algal production. In addition, algal growth can also be dependent on the available nitrogen to phosphorus ratio. The algae will be nitrogen-limited when N:P ratio is < 7.5:1 and phosphorus limited at N:P ratio > 7.5:1 on mg L^{-1} basis (Lee and Jones-Lee, 1998). As some algae have similar demand for these two major nutrients (N and P) competition among them may occur when the resource is scarce.

Competition for limiting nutrients would be important as a selection factor in the determination of phytoplankton community composition (Sommer, 1989; Grover, 1997; Lagus, 2009). Phytoplankton assemblages that have different functional adaptations will continue to survive dominantly in such limiting conditions. *P. rubescens*, for example, is able to utilize organic forms of phosphorus due to the possession of alkaline phosphatase and survives in condition of PO_4^{3-} limitation (Feuillade, 1994). Sommer (1985) clustered algae into three categories according to their ability to utilize nutrients; affinity, velocity and storage specialists. Affinity specialists have little requirements for nutrients and are efficient users of low nutrient concentrations. A fluctuating nutrient supply should favor both velocity specialists (which are capable of rapid growth after nutrient pulses) and storage specialists (which are capable of luxury consumption), while a low and continuous nutrient supply would select for affinity specialists (Sommer 1985; Grover, 1991).

With rapid human population growth, increased anthropogenic nutrient enrichment of freshwater bodies is aggravating the problems of cultural eutrophication thereby stimulating the occurrence of harmful algal blooms. The increase in nutrient concentration of freshwater systems could induce a shift in the phytoplankton community towards dominance by toxic cyanobacteria (O'Neil *et al.*, 2012). Even nontoxic algal blooms can have a devastating impact on aquatic organisms including fish and invertebrates via causing oxygen depletion. In addition, high nutrient concentration can increase the heat absorbing potential of the waters systems and so, the water temperature. Natural communities of phytoplankton have been and will continue to be influenced by the increases in temperature as algal growth rates are strongly, but differentially, temperature dependent (Raven and Geider, 1988). High temperature provides a competitive advantage for harmful algae, e.g. *Microcystis aeruginosa* as it changes many of the characteristics of aquatic environments in a way that may be favorable for them. For instance, higher temperatures will decrease surface water viscosity that leads to sinking of larger, nonmotile phytoplankton with weak buoyancy regulation mechanisms (Paerl and Huisman, 2009; Wagner and Adrian, 2009). Furthermore, insular heating will increase the frequency, strength, and duration of stratification. This process will generally reduce the availability of nutrients in surface waters favoring cyanobacteria that regulate their buoyancy to obtain nutrients from deeper water, or that are diazotrophic. That is why cyanobacteria (e.g. *Anabaena or Dolichospermum* species) dominate phytoplankton assemblages in eutrophic, freshwater environments during the warmest periods of the year (O'Neil *et al.*, 2012). Stratification can also induce a shift in phytoplankton composition towards algal groups that have the ability to control their position in the water column e.g. flagellated *Euglena* species (Tadesse Fetahi, 2010).

The rise in temperature of an aquatic system can bring about fall in the level of CO_2 in the water systems via reducing its solubility and promoting its release to the atmosphere thereby resulting in raised pH level. This may cause primary production by most phytoplankton group to be carbon-limited. Cyanobacteria (**Fig. 2**) are known to outcompete eukaryotic algae under high pH and low CO_2 conditions because of having an efficient carbon concentrating mechanism and gas-filled vesicles (Oliver and Ganf, 2000; Qui and Gao, 2002). The gas vesicles will allow cyanobacteria to remain suspended in the upper part of the water column in close proximity to atmospheric CO_2 (Paerl and Huisman, 2009). Cyanobateria (e.g. *Anabaena)* are also known to possess the enzyme carbonic anhydrase that enables them to utilize bicarbonate as carbon source (Shiraiwa and Miyachi, 1985). But, the high pH condition alone may not be sufficient to support the dominance of cyanobacteria as they have greater adherence to high temperature. In general, the annual cycle of temperature and thermal stratification are considered as the major factor regulating the seasonal variation of phytoplankton (Grover and Chrzanowski, 2006).

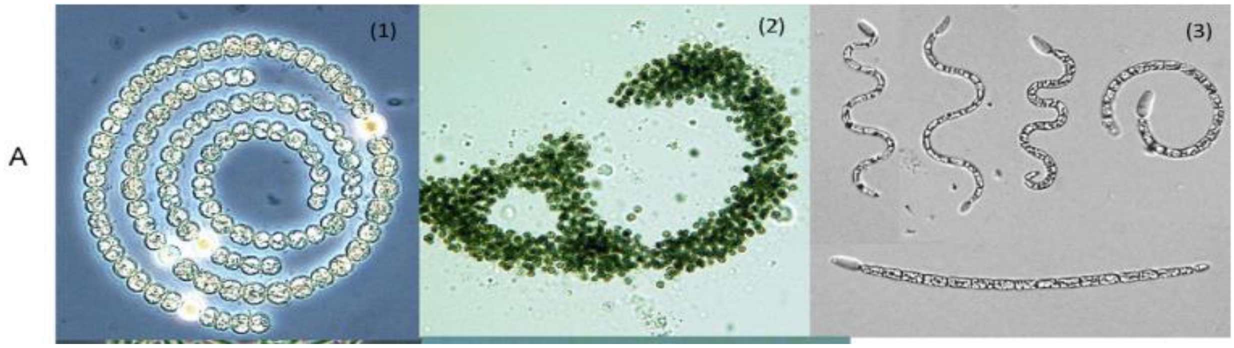


Figure 2. Representative cyanobacterial genera from freshwater: 1 = *Anabaena*, 2 = *Microcystis*, 3 = *Cylindrospermopsis* (O'Neil *et al*., 2012).

Dolichospermum (*Anabaena*) is a ubiquitous freshwater genus typically inhabiting lentic water bodies such as lakes and reservoirs. Some species of this genus produce toxins including microcystins, anatoxin-a and cylindrospermopsin, while others, principally *Anabaena circinalis*, produces saxitoxin. *A. circinalis* and *A. flos-aquae* are the commonly known harmful algal bloom-forming species of this genus. Toxin production by cyanobacteria is not universal in all species of blue green algae, instead, only those species that have the gene cluster responsible for toxin production can produce biotoxin (O'Neil *et al*., 2012). As a diazotroph, *Anabaena* grows better under low salinity condition (Engstro and Mikkonen, 2011) and has been functionally classified as tolerant of low nitrogen conditions, but sensitive to mixing and low light condition (Reynolds *et al*., 2002). It has physiological ability to outcompete non-nitrogen fixers (Wood *et al*., 2010) and even other diazotrophs such as *Aphanizomenon* in N-depleted waters (De-Nobel *et al*., 1997). *Anabaena* also has a strategic adaptation to perform better in the face of nutrient limitation. These include the ability to use organic form of nitrogen (Luo *et al*., 2010) and akinete formation (Olli *et al*., 2005) to survive longer when phosphorus is limiting.

The cyanobacterial genus *Cylindrospermopsis* (a solitary, filamentous diazotroph) and *Microcystis* (non-diazotrophic colonial genus) have the potential to form nuisance blooms and produce toxins. But, the biotoxin production is not universal in both genera. Toxic strains of *Cylindrospermopsis* and *Microcystis* have different functional adaptations. Toxin-producing *Cylindrospermopsis* (*C. raciborskii*) has been shown to have a competitive advantage at both low and high nitrogen levels, as they have flexible N-strategy. *Cylinderospermopsis* utilizes dissolved inorganic nitrogen when present and employs N_2-fixation at the time of depletion (Moisander *et al*., 2008). *Microcystis* species are sensitive to N and P limitation and will grow fast when both nutrients are sufficiently available. However, *Cylindrospermopsis* have a high affinity for both nutrients and not likely to be much affected by nutrient limitation (Padisák, 1997; Posselt *et al*., 2009). The observed difference in the functional adaptation of these cyanobacterial genera (*Anabaena*, *Cylindrospermopsis* and *Microcystis*) reveals the importance of the functional classification of phytoplankton to better understand the pattern of ecosystem dynamics in aquatic systems. In addition, the seasonal and spatial variations of phytoplankton seem to be better explained by their functional similarity than their taxonomic affinity.

7.3.3. Light

Litchman (1998) has assessed the effect of the temporal regime of light supply and light fluctuations on taxonomic composition, dominance patterns, dynamics of individual species, the total biomass of the community and its diversity. He found the presence of species specific responses to various light regimes. *Nitzschia* and *Fragilaria* and from among cyanobacteria, *Gloeocapsa* and *Oscillatoria* were reported to have higher densities under fluctuating light, while densities of *Asterionella*, *Cyclotella,* and *Navicula* either did not differ among light regimes or were lower under fluctuating light indicating the presence of co-occurring factors that influence these species and their tolerance to light fluctuation (Klemer and Barko, 1991). *Phormidium* and *Anabaena* growing at low average irradiance had higher densities under constant light (Litchman, 1998).

Diatoms were found to exhibit higher abundance and bio-volume when there is fluctuation in light supply at a low average irradiance level (Reynolds, 1994). Considering the size of phytoplankton, the large-size algae (*Cosmarium, Mougeotia,* and *Staurastrum*), are vulnerable to the competitive exclusion by fast growing groups (Reynolds, 1984; Huston, 1994) at a high irradiance level. At high light level, the fluctuation increases diversity. However, the phytoplankton community biomass is dependent only on the average irradiance level and not on its fluctuation (Tilman, 1996; Litchman, 1998). Cyanobacteria (that have high affinity for CO_2) and diatoms (low affinity for CO_2) under high pH have been shown to have high and low abundance in the presence of high average irradiance respectively (Shapiro, 1973; Talling, 1976). Both the absolute level and the degree of variability in light supply have a determining impact on diversity and abundance of phytoplankton species. Cyanobacteria and green algae dominated at low constant light and all high light conditions, while diatoms became prominent at average irradiance with fluctuation (Litchman, 1998). Compared to dinoflagellates, diatoms are known to have faster growth rates and grow faster under lower irradiance, cooler temperatures, and higher nutrient conditions (Irwin *et al.,* 2016). In multispecies community, fluctuations increased diversity at high irradiance but decreased diversity at low average irradiance (Litchman, 1998).

7.3.4. Trophic interaction (zooplankton and fish with phytoplankton)

Besides physical and chemical factors, feeding interactions also determine the resident phytoplankton assemblages. Zooplankton affect phytoplankton via their grazing effect and indirectly by their role in recycling nutrients (Grigorszky *et al*., 1998). The net effect of zooplankton on phytoplankton is known to be a function of the species composition of phytoplankton and zooplankton. For instance, *Anabaena spiroides* was found to be dominant in the presence of *Keratella* as it is too large to be consumed by this zooplankton.

Keratella consumes smaller-sized plankton like cryptomonads, chrysomonads, bacteria and a wide range of detritus (Bogdan and Gilbert, 1984; Hansson *et al.*, 1998) and favors the growth of larger-sized phytoplankton via their role as nutrient pump. *Keratella*, being unable to graze on the dominant filamentous cyanobacteria, had a net positive impact on their growth. Henry (1985) and Grigorszky *et al*. (1998) have reported that microzooplankton have the potential to recycle nutrients rapidly and support the growth of filamentous cyanobacteria (e.g. *Planktothrix rubescens*). Some clones of *P. rubescens* are able to produce microcystins to avoid grazing pressure of herbivorous zooplankton (Kurmayer and Jeüttner, 1999). On other hand, larger-sized zooplankton such as *Daphnia magna* have been shown to have significant grazing pressure on relatively larger-sized phytoplankton thereby negatively affecting the phytoplankton population (Grigorszky *et al*., 1998). In contrast, zooplankton can have a positive effect on phytoplankton community via their role in the nutrient cycle as they excrete SRP and ammonia (Tadesse Fetahi, 2010). In addition, trophic interaction of fish with plankton, particularly with large-sized plankton is known to have the potential to induce change in species composition of phytoplankton and trophic status of lake ecosystems.

Tadesse Fetahi (2010) has reported that introduction of tilapia into Lake Hayq, Ethiopia has caused the replacement of larger-sized zooplankton community (the cladoceran *Daphnia magna)* by smaller copepods and rotifers. This has resulted in the rise of phytoplankton biomass and change in food web structure as fish selectively feed on larger zooplankton. In the absence of larger herbivorous zooplankton such as *Daphnia*, the larger-sized phytoplankton tend to grow extensively and form blooms that lead to reduction in species richness and diversity of phytoplankton due to stress associated with hypoxia. Among zooplankton, red pigmented cyclopoid copepods and red pigmented *Daphnia* were reported to be tolerant to anoxic condition

(Sell, 1998). Therefore, these zooplankton are predictable in eutrophic conditions as the case for cyanobacteria. In general, zooplankton could have impact on the dynamics of phytoplankton assemblage due to their selectivity for size, i.e. the larger zooplankton selectively feed on larger sized phytoplankton while the smaller zooplankton selectively feed on smaller phytoplankton. Tadesse Fetahi (2005) has analyzed the feeding interaction in Lake Hawassa and reported that *O. niloticus* is a major consumer of phytoplankton. The researcher also indicated that *Clarias gariepinus* is a piscivorous fish that feeds mainly on *O. niloticus* and *Labaeobarbus* species, while *L. intermedius* consumes *O. niloticus*. Thus, these fish species have regulating impact on the phytoplankton community dynamics of the lake.

7.3.5. Macrophyte coverage

Macrophytes are known to have a controlling impact on phytoplankton assemblages in lake ecosystems in many ways. Firstly, they compete for nutrients with phytoplankton and absorb nutrients extensively so that little will be left for use by phytoplankton. Secondly, macrophytes provide refuge for zooplankton favoring population loss of phytoplankton via grazing (e.g. Mesfin Gebrehiwot *et al*., 2017). The authors reported change in species composition of phytoplankton in relation to the distribution of macrophytes. They may create calm condition by precluding wind-induced mixing that selects for taxa that can remain buoyant in the water column such as flagellated taxa, taxa that have gas vacuoles, and taxa that form large colonies such as *Botrycoccus* and *Microcystis* (Barrow, 2017).

Macrophytes increase heterogeneity of Lake Habitat, resulting in higher biodiversity with the development of species-rich bacteria, periphyton, and metaphyton communities that also compete with phytoplankton for essential resources (Barrow, 2017). Lastly, macrophytes can restrict the availability of sufficient light causing growth of phytoplankton to be light-limited. In addition, macrophytes are known to produce allelopathic chemicals that inhibit algal growth. For instance, *P. schweinfurthii* produces allelopathic compounds that can inhibit the growth of phytoplankton (Getasew Amsalu, 2017) and macrophytes like *Elodea* are also known to produces hydrophilic compounds that hinder cyanobacterial growth (Erhard and Gross, 2006). Hence, they are useful to control algal bloom problems in freshwater lakes (Wang *et al*., 2013). All in all, macrophytes can inhibit phytoplankton growth through a variety of mechanisms and thus their presence can exert selective pressure on phytoplankton community structure.

7.4. Use of phytoplankton functional groups in bio-monitoring of aquatic ecosystems

Today, due to the ever-increasing trend in nutrient enrichment rate of various water bodies, particularly the freshwater lakes, there is a dramatic change occurring in aquatic ecosystems. This will negatively affect the ecological and anthropogenic significance of the water systems. The undesirable ecosystems change, which is driven by eutrophication events, can be inferred from the change in species composition and community structure of phytoplankton (EEA, 1999).

The algal communities respond to the alterations in water quality both quantitatively and qualitatively. In quantitative change, increased primary production and phytoplankton biomass will happen to lead to increased consumption of DO and occurrence of anoxic condition (Tadesse Fetahi, 2010). The qualitative changes involve a shift in taxonomic composition from heterogeneous to homogenous groups, with the nuisance and toxic algae becoming dominant. For instance, diversity of phytoplankton tend to decline following the event of eutrophication eventually leading to cyanobacterial dominance and toxin production (Chellappa *et al*., 2009). Measurement of water quality parameters via analysis of periodical water samples has been criticized for its insufficiency to capture temporal changes in the levels of the parameters, because the water quality parameters change rapidly and may not be well related to taxonomic variations (Gökçe, 2016). This will limit our knowledge of the association between the environmental conditions and biotic community structure. Grouping phytoplankton species based on their ecological adaptation will help to overcome this limitation. Thus, phytoplankton FGs can be used as bio-indicator of environmental conditions. This can be developed based on the specific ecological requirement of different algal assemblages for their growth and reproduction (Reynolds *et al*., 2002).

Bio-indicators can provide information on the biological conditions and water quality status of lake ecosystems in relation to anthropogenic and natural factors. In addition, they can help to detect the biologically meaningful level of pollutants, which will not be detectable through chemical analysis (Gökçe, 2016). Phytoplankton FGs can indicate both the spatial and temporal patterns of the high risk of blooms (Vila and Masó, 2004). Phytoplankton are used also as one of the key indicators by various EU directives in the assessment of eutrophication for the purpose of water quality management (Delvin *et al*., 2011). For example, Chl-a concentration and phytoplankton cell abundance are included in UK WFD (water framework directive) method of estuary water assessment (Devlin *et al*., 2007). In agreement with these methods, the inclusion of phytoplankton in any water quality monitoring action is vital because algae can affect the concentration of nutrients, DO and the level of other water quality parameters (Gökçe, 2016).

Functional association of algae is believed to have greater importance to bio-monitoring than other biota for a number of reasons including: they form the strong link between the abiotic and biotic components of the food web, algae are not efficient in their movement (especially diatoms), and hence they cannot migrate to avoid pollution and so must tolerate or disappear; algal communities are diverse and each species has its own tolerance, phytoplankton have a fast response to changes via their short life cycle (Gökçe, 2016). In addition, habitat quality specificity of the different members of phytoplankton is reflected in their distribution and occurrence in relation to the quality of water they live in (Bhatt, *et al*., 1999; Saha *et al*., 2000). They may therefore be considered as a reliable tool for bio-monitoring of water quality and to assess the pollution status of the aquatic ecosystems (Bordoloi and Baruah, 2014). Furthermore, phytoplankton FGs are useful to easily understand habitat conditions and the key factors regulating spatial and temporal dynamics of phytoplankton species in communities. The phytoplankton assemblage can also be used to trace trophic tendency of lakes and to make a valid prediction about the phytoplankton community structure which will help to make the correct decisions in lake ecosystems' management process (Reynolds *et al*., 2002).

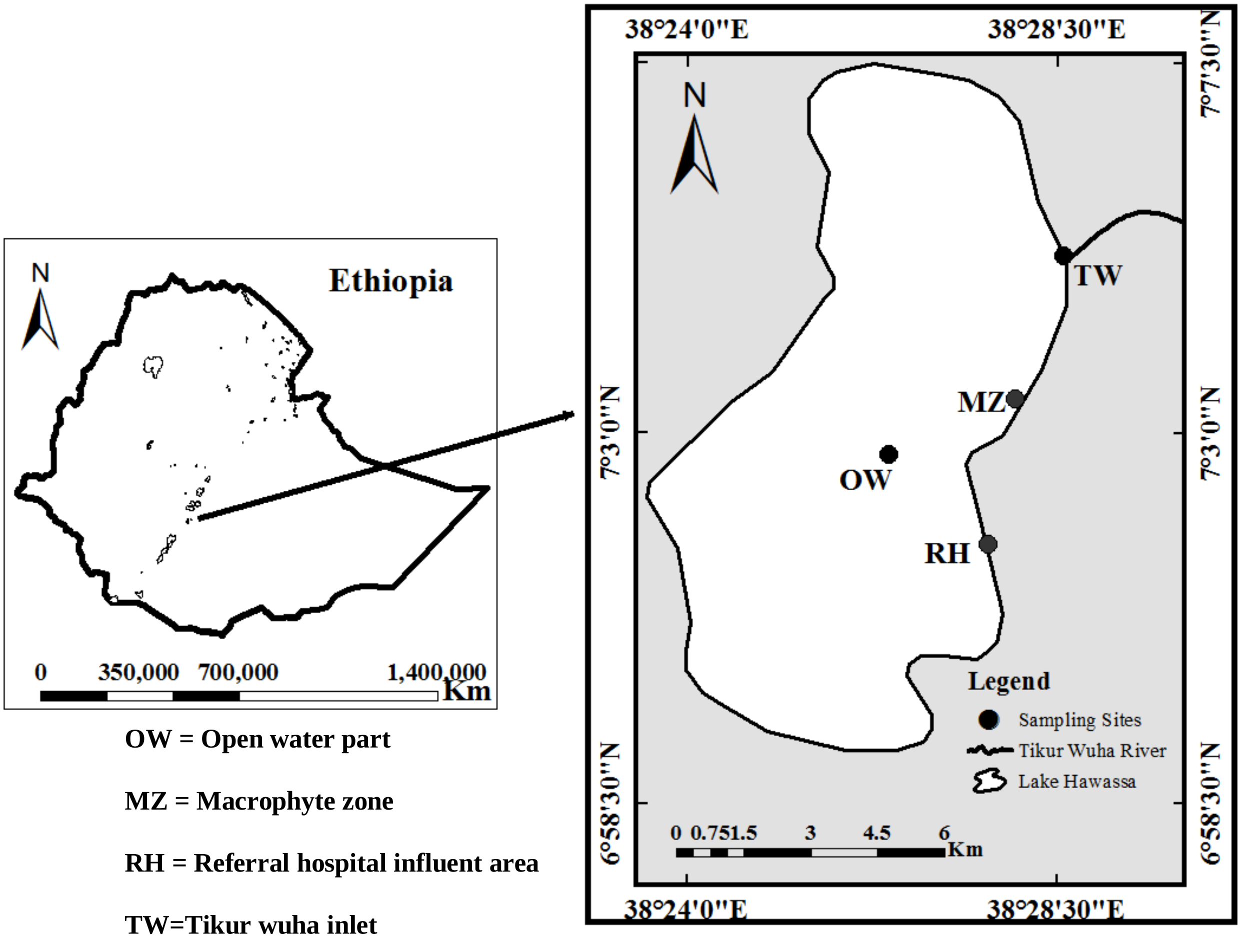
8. Materials and Methods

8.1. Description of the study area

8.1.1. Geographic features and catchment characteristics

Lake Hawassa (**Fig. 3**) is a rift valley lake of Ethiopia located at an altitude of 1785 m a.s.l within latitudinal and longitudinal ranges of 6˚40'45" - 7˚23'49"N, and 38˚18'34"- 38˚43'26"E respectively. This lake is believed to be tectonic in its origin and formed by tilted fault blocks. Lake Hawassa has closed nature with no surface outflow. It is stretched 16 km in the North East –South West and 6 km in North West-South East directions (Yemane Gebreegziabhier, 2004). The lake's surface area is 94.3km^2 (Elias Dadebo, 2000; Yemane Gebereegziabhier, 2004; Girma Tilahun and Ahlgren, 2010) with a maximum depth of 22 m and a mean depth of 11 m (Elias

Dadebo, 2000). The average annual inflow and outflow from Lake Hawassa are 1440mm and 570mm (underground flow), respectively (Abate Woldesenbet and Fitamo, 2015), and the total volume of the lake is 1.3 km^3 (Tenalem Ayenew, 1998).



OW = Open water part

MZ = Macrophyte zone

RH = Referral hospital influent area

TW=Tikur wuha inlet

Figure 3. Map of Lake Hawassa, Ethiopia.

The lake is primarily fed by the Tikur Wuha River. The catchment area of the lake is 1250 km^2 and is characterized mainly by flat-lying topography with scattered small hills. Elevation of the rift escarpments and rims in the east and west of the watershed ranges from 2000 to 2940 m a.s.l. It is known that the uplands on either side of the flat lowlands are deforested and denudated (Yemane Gebreegziabhier, 2004). The steeply sloping and deforested uplands are likely to produce high runoff over the lowlands shortly after individual storms. In addition, the lake is surrounded by steeply sloping areas on its eastern side, which have poor vegetation cover that increases the probability of high nutrient enrichment and siltation of the lake from the upper catchments.

The lake is surrounded by farm lands and Hawassa city from its eastern side. The intensive cultivation of the surroundings of the lake and atmospheric deposition of particulate matter may cause pollution of the lake. In addition, Lake Hawassa is affected by pollutants of industrial origin as it receives effluents of a brewery, soft drink factory, Hawassa Textile Factory and Tabor Ceramic Factory (Tadesse Fetahi, 2010; Yosef Tekle-Giorgis *et al*., 2016). Furthermore, wastes from the Referral Hospital of Hawassa University and municipal sewage, recreational activities, the presence of poor land use management practices (Tadesse Fetahi, 2010; Yosef Tekle-Giorgis *et al*., 2016), washing activities using soap, disposal of fish remains from soup preparation and flatting of fish flesh are amongst the anthropogenic factors driving the change in water quality of the lake. The lake area experiences a dry, sub-humid climate and receives a mean annual rainfall of about 1091 mm and has a mean annual air temperature of 19.8 ºC (Yosef Tekle-Giorgis *et al*., 2016). Lake Hawassa's watershed has extended period of wet season (March-October) with mean monthly rainfall varying from 85 to 133 mm. Lake Hawassa mixes during the main rainy months and in December (Yosef Tekle-Giorgis *et al*., 2016).

8.1.2. Major biota of Lake Hawassa (macrophytes, fishes and invertebrates)

The fish fauna of Lake Hawasa consists of Nile tilapia (*Oreochromis niloticus)* (Linnaeus), African catfish (*Clarias gariepinus*) *(*Burchell), Yellowfish (*Labeobarbus intermedius intermedius*) (Rüppell) and Common barbs (*Barbus paludinosus*) (Boulenger) (Demeke Admasu, 1996; Fishbase, 2010). *O. niloticus* is commercially the most important fish species (Yosef Tekle-Giorgis *et al*., 2016), consumes more diverse food items including benthic organisms and zooplankton at its juvenile stage while the adults feed mainly on phytoplankton (Tadesse Fetahi, 2005). African catfish is the top predator in the lake feeding on *O. niloticus*, *Labeobarbus* and *Garra* species. The yellow fish consumes macrophyte fruits and *O. niloticus* (Tadesse Fetahi, 2005).

The shoreline of Lake Hawassa has extensive macrophyte vegetation consisting of *Paspalidium germinatum, Potamogeton schweinfurthi, Typha latifolia, T. angustifolia* (Demeke Kifle and Amha Belay, 1990) and *Nymphaea* species (Girma Tilahun, 2006). The dominant microflora of the lake consists of green algae, blue-green algae and diatoms (Elizabeth Kebede and Amha Belay, 1994; Girma Tilahun, 2006).

Zooplankton of the lake includes copepods (*Mesocycolops* and *Thermocyclops* species*)*, cladocerans (*Diaphanosoma excisum*) and rotifers (*Brachionus and Keratella* species) as the common zooplankters (Seyoum Mengistou, 1989). The herbivorous zooplankton (*Diaphanosoma, Thermocyclops* and copepodites) in Lake Hawassa are inefficient grazers of phytoplankton especially for the filamentous and other large sized forms (Tadesse Fetahi and Seyoum, Mengistou, 2014). Recently, rotifers were reported as the most abundant zooplankton, followed by cyclopoid copepods and cladocerans (Tadesse Fetahi, 2010).

8.1.3. Water chemistry

The pH of the water in Lake Hawassa ranges from 8.3 to 9.0 giving the lake its alkaline nature. The chemical composition of Lake Hawassa shows variation with time. Sodium and chloride are the dominant cation and anion, respectively (**Table 1**).

Table 1. Water quality parameters measured previously in Lake Hawassa, Ethiopia.

Parameters	Recorded values with sources in parentheses	Parameters	Recorded values with sources in parentheses
Na^+ (meq L^{-1})	7.1 (a)	pH	8.3-9 (b)
		EC(µS cm^{-1})	730-825≫
K^+ (meq L^{-1})	0.7 ≫	Chl-a(µg L^{-1})	4-58 ≫
		SiO_2(mg L^{-1})	42.6 ≫ 37.6 (c)
Ca^{2+} (meq L^{-1})	0.5 ≫		
Mg^{2+} (meq L^{-1})	0.5 ≫	SRP (µg L^{-1})	5-45 (d) 22-45 (b)
SO_4^{2-} (meq L^{-1})	0.2 ≫		
Cl^- (meq/l)	0.8 ≫	NO_3^- (µg L^{-1})	25-165 (d), 7-100 (b) 2.5(c).
Alkalinity (meq L^{-1})	7.33-10.52 (b)	NH_3+NH_4^+(µg L^{-1})	5.7 (b), 118 (c).

A = (Zinabu Gebre-Mariam *et al*., 2002), b = (Elizabeth Kebede and Amha Belay, 1994) C = (Girma Tilahun and Ahlgren, 2010), d = (Demeke Kifle and Amha Belay, 1990), SRP = soluble reactive phosphorus

8.2. Sampling protocol

Since there was spatial heterogeneity in the level of anthropogenic pressure on the lake, representative sampling sites were determined during the preliminary study after being cognizant of wind direction, presence/absence and nature of point source pollutants etc. Four sampling sites were selected. These were the Referral Hospital influent area (RH), the Tikur Wuha inlet (TW), Open Water part (OW) and Emergent Macrophyte coverage zone (MZ) that are located at least at 2.5 kilometers away from one another (having high spatial independence). The exact location of each sampling site was recorded using GPS and the total depth was measured using ecosounder (**Table 2**). *In-situ* measurements of physico-chemical parameters, collection of samples for the analysis of water quality parameters and the plankton were made once-a-month from April to August in 2019 at each site. Macrophyte sample was collected in August from MZ.

Table 2. The selected sampling sites in Lake Hawassa, Ethiopia.

Sampling sites	GPS	Altitude above sea level	Ranges of depth
Tikur Wuaha inlet (TW)	N 07^{o}05'17" E 038^{o}28'43.2"	1680 m	0.7-2 m
Referral Hospital influent site (RH)	N 07^{o}01'39" E 038^{o}27'45.6"	1683 m	1-2.6 m
Open Water part (OW)	N 07^{o}02'44.16" E 038^{o}26'58.44"	1678 m	14-19 m
Macrophyte Zone (MZ)	N 07^{o}03'24.6" E 038^{o}27'59.4"	1681 m.	3.2-3.6 m

8.2.1. *In-situ* measurement of physico-chemical parameters

Secchi depth (Z_{SD}) was estimated using a 20 cm diameter Secchi disk according to APHA (1999). Temperature and DO were measured using multi-parameter probe (HQ40d model) at one meter interval to determine the presence/absence of thermal stratification (Bartram and Ballance, 1996). Conductivity (EC) and pH, and turbidity were measured at each sampling site using a multi-parameter probe (HQ40d model) and turbidimeter (OakatonT-100 model) respectively. The EC values obtained from field measurement at temperatures above or below 25 ^{o}C were corrected to the values at the standard temperature (25 ℃) using the equation of Miller *et al.* (1988) as follows.

$\frac{ks}{k} = \frac{1}{1+0.0191(T-25)}$ From this KS = $EC_{25\,^{o}C}$, K = EC_T. Hence, $EC_{25\,^{o}C} = \frac{EC_T}{1+0.0191(T-25)}$ where KS = specific conductance at 25 °C which is equal to the corrected EC at 25 °C

K = EC_T = the EC values at a temperature T

The euphotic depth (Z_{eu}) were calculated from Z_{SD} reading using mathematical relationship: $Zeu \approx 2.7 * Z_{SD}$ (Padisák and Salmaso, 2007).

8.2.2. Sample collection

Since no stratification was detected throughout the entire study period, subsurface water samples (up to 10 cm from the surface) were taken for quantitative analysis of phytoplankton from the four sites (TW, RH, MZ and OW). Phytoplankton samples were also collected via vertical and horizontal towing of plankton net (15 µm mesh size) for qualitative analysis. The phytoplankton samples were placed in polyethylene terephthalate bottles and preserved with Lugol's solution until they took a weak tea color (Hötzel and Croome, 1999) and stored under dark condition. Concurrently, water samples for the analysis of water quality parameters (total phosphorus = TP, soluble reactive phosphorus = SRP, nitrate = NO_3^-, Chlorophyll-a, ammonia = NH_3+NH_4^+, molybdate reactive silica = SiO_2, total dissolved solids = TDS, total suspended solids = TSS, and alkalinity) were also gathered from each sampling site following the procedure used for the collection of phytoplankton samples for quantitaive analysis. The samples were stored in polyethylene terephthalate bottles of 2 liter capacity for each sampling site separately and placed in an ice box.

Zooplankton sampling were carried out at one time per month from the same established sampling sites by vertical hauling of 70 µm mesh size plankton net from different depths (m): 0.12-0.42 (at TW), 0.42-2 (at RH), 2.62-3.02 (at MZ) and 11-12 (at OW) during day light hours for enumeration. For identification purpose zooplankton samples were collected via vertical and horizontal towing of 30 µm and 70 µm mesh size nets to capture the smaller and large sized zooplankton respectively. Zooplankton samples were decanted into polyethylene terephthalate bottles and preserved with 4% formalin immediately after collection. Macrophyte sampling was done from the Macrophyte zone by plucking the predominant macrophyte carefully and then pressed.

Finally, all samples were transported to the limnology laboratory of Addis Ababa University and the water samples were stored in a refrigerator at 4℃ until further analysis.

8.3. Laboratory analysis of samples

8.3.1. Quantification of physico-chemical parameters

TSS was estimated as dry weight of seston filtered onto a glass fiber filter paper (GF/F) pre-dried at 105 ^{o}C and subsequently dried with seston at the same temperature and calculated using the following formula (APHA, 1999):

$$\text{TSS (mg L}^{-1}\text{)} = \frac{(\mathbf{W_2} - \mathbf{W_1}) \text{ X } \mathbf{1000}}{\mathbf{V}}$$

where:

$\mathbf{W_1}$ = Weight of dried clean filter paper (mg)

$\mathbf{W_2}$ = Weight of dried clean filter paper with seston (mg)

V = Volume of water sample used which was 100 ml for TW and 200 ml for the remaining sites. TDS was determined by oven drying 100 ml of filtered water in in a pre-dried erlenmyer flask.

Phenolphtalein alkalinity (PA) and Total alkalinity (TA) were determined by titration of 100 ml of water samples with 0.1N HCl to a pH of 8.3 and 4.5, respectively using phenophtalein indicator (for PA) and bromocresol green-methyl red mixed indicator solution (for TA) within a few hours after sample collection according to Wetzel and Likens (2001). The levels of predominant ions (HCO_3^-, CO_3^{2-} and OH^-) were calculated from the alkalinity values according to APHA (1999). Concentrations of inorganic nutrients were determined following the procedures outlined in APHA (1999). The samples used for the analyses of all nutrients except TP were filtered through glass fiber filter (GF/F). NO_3^- was analyzed by the sodium salicylate method, while ammonia was determined by the phenate method. Total dissolved inorganic nitrogen (TDIN) was considered as the sum of ammonia and nitrate assuming that contribution of nitrite is relatively insignificant. TP after persulfate digestion and SRP were analyzed by the ascorbic acid method. Molybdate-reactive silica (SiO_2) was determined by the molybdosilicate method.

8.3.2. Chlorophyll-a (Chl-a) analysis

An appropriate volume (140-200 ml) of samples was filtered using GF/F at low vacuum pressure (no more than 500 mmHg) (Sartory, 1982) as soon as possible. The filter papers containing algal seston were folded in half with seston inside and wrapped using aluminum foil and placed in a test tube. Then, a small volume of 90% acetone was added and stored in dark condition for overnight at 4°C to facilitate extraction of the pigment (APHA, 1999). The filters in the test tubes were ground using a glass rod. The tips of the glass rod and the inner surface of the test tubes used for grinding were rinsed with extraction solvent and the washes were transferred to a centrifuge tube. The extracts were centrifuged at 3000 rpm for 10 minutes to avoid the interference of suspended solids. The absorbance of pigment extracts was measured at 665 and 750 nm before and after acidification with 0.1 ml of 0.1N HCl (APHA, 1999). Following acidification the readings were taken after 90 seconds as suggested by APHA (1999).

The concentration of Chl-a was then calculated as follows using the absorbance values at 665 and 750nm before and after acidification.

$$[\text{Chl-a}, \mu g\ L^{-1}] = \frac{26.73\,(665b-750b)-(665a-750a)*ve}{Vf*Z} \quad \text{(Lorenzen, 1967)}$$

where 665b and 750b are absorbance at 665nm and 750nm before acidification respectively, while 665a and 750a are absorbance at 665 and 750 nm after acidification, respectively. Ve = Volume of extract in ml, Vf = Volume of sample filtered in litre, Z= Path length of the cuvette (1cm)

8.3. 3. Qualitative and quantitative analysis of plankton

8.3.3.1. Identification of phytoplankton

The phytoplankton samples were examined at different magnification levels under an inverted microscope and the encountered taxa were identified to genus / species level using various taxonomic literatures (e.g. Hecky and Kling, 1987; Hindák, 1992; Krammer *et al.*, 2002; Komárek and Komárková-Legnerová, 2003; Cronberg and Annadotter, 2006; František, 2006; Arguelles *et al.*, 2014; Lone, 2014). Algal division to which phytoplankton were assigned with names of taxonomic authors were according to Guiry and Guiry (2013).

8.3.3.2. Enumeration of phytoplankton

For achieving a random distribution of algal cells in the counting chambers during counting, preserved samples, sedimentation chambers and all equipment to be used for enumeration purpose were acclimatized to the same (room) temperature for at least 12 hours (Brierley *et al.*, 2007). 1000 ml of samples were taken and sedimented in measuring cylinders of one liter capacity. The samples were allowed to stand for a period equivalent to a sedimentation rate of 6 hrs per cm height of the sedimentation chamber under dark condition (Hötzel and Croome, 1999). After sedimentation, the top 90% of the volume of the total samples were carefully siphoned off without disturbing the settled algae.

After shaking the sedimented algae gently, a subsample of 1 ml was taken with Pasteur pipette and poured onto the counting chamber (Sedgewick-Rafter cell) placed under an inverted microscope (APHA, 1995). After allowing the aliquot to stand for 30 seconds, cell counts were made at a magnification of 400X for all algal units with counting error of 10.33% at 95% confidence limit (Lund *et al.*, 1958). At least 30 randomly selected grids were counted within the chamber so that 90 to 95% of the species present are included in the count (Hötzel and Croome, 1999). For filamentous algae, the number of cells per filament was determined for 30 filaments and the mean number of cells per filament was calculated. Likewise, the number of cells per colony was first determined for 30 colonies and then the mean number of cells per colony was calculated (Brierley *et al.*, 2007). The average numbers of cells per filament or colony were multiplied by the number of filaments or colonies to estimate the abundance of filamentous or colonial taxa. Estimation of phytoplankton abundance in cells ml^{-1} was made using the following formula (Hötzel and Croome, 1999).

$C = \frac{\mathrm{N\,x1000\,mm^3}}{\mathrm{AxDxGxCF}}$ where N = number of cells counted, A = Area of grid in mm^2, D = depth of grid in mm and G = number of grids counted. As total volume of water sample (TVS) used = 1000 ml = 1 liter, volume of concentrate (VC) = 10% TVS = 100 ml and concentration factor (CF) = $\frac{\mathrm{TVS}}{\mathrm{VC}}$

8.3.3.3. Phytoplankton bio-volume

Bio-volumes of major taxa of phytoplankton (with > 1% contribution to total abundance) were estimated based on approximation of the shape of the cells to appropriate geometric configurations (Hillebrand *et al.*, 1999; Sun and Liu, 2003; Vadrucci, *et al.*, 2013). First, a micrometer in Microscope Manager Software was calibrated with stage micrometer. According to the approximated geometric shape, measurements of the required cell dimensions (length, width, and diameter) were then made at a suitable magnification using the calibrated micrometer (Vadrucci *et al.*, 2013).

The average cell dimensions were determined for each species by measuring the cell dimension of at least 30 individual units depending on their variability (Hotzel and croome, 1999). The average volume for each species was determined by entering the mean values of the appropriate cell dimensions of the species into the formula of the geometrical shape that is closest to the cell's shape. Then, the total algal volume (Vt) in $\mu m^3 L^{-1}$ was obtained by summing the multiple products of the mean volume of the individual cell considered and the number of cells counted for each species (APHA, 1995). $Vt = \sum_{i=1}^{n}(Ni \times Vi)$

Where

Ni = the number individual cells of i^{th} species counted L^{-1}

Vi = the average volume of cells of i^{th} species

For taxa with more complex shape (e.g some *staurastrum* and *staurodesmus* species) that does not resemble a specific geometric shape, the bio-volume were estimated by partitioning the algal unit part into combination of different geometric shapes (e.g. cone, cylinder) and summing the resulting volumes. All those species that contributes for more than 1% of the total bio-volume were considered for further analysis.

Furthermore, by assuming the specific density of phytoplankton cells as $1 \text{ g cm}^{-3} = 1 \text{ mg mm}^{-3}$ (Huszar *et al.*, 2006), the bio-volume measurements were converted to phytoplankton biomass in mg L^{-1}.

8.3.3.4. Functional classification of phytoplankton and water quality assessment

The different taxa of the identified phytoplankton were classified into trait-separated functional groups (RFGs) relying on their ecological affinity (Reynolds *et al.*, 2002; Padisák *et al.*, 2009) as well as into morphology-based functional groups (MBFGs) depending on their morphological features (Kruk *et al.*, 2010; Kruk and Segura, 2012). The biomass corresponding to each MBFG and RFG was also calculated for the numerical analyses. The functional diversity of phytoplankton were determined using Shannon diversity indices. Shannon diversity indices were calculated based on bio-volume.

$Hf = -\sum Pi\ln(pi)$ (Vörös *et al.*, 2013)

Where pi is the relative contribution of each functional group to the total biomass. The water quality status of Lake Hawssa was assessed based on the phytoplankton FGs (based on their composition and diversity) and based on the level of physico-chemical parameters at the different sites.

8.3.3.5. Zooplankton identification and counting

Each zooplankton sample was mixed and 10 ml aliquot was taken with a measuring cylinder and decanted into a gridded glass chamber placed under a compound microscope. The 10 ml subsample was taken because it was found to be suitable for identification and enumeration considering the size of the counting chamber and the density of zooplankton in the subsample. The zooplankton taxa were identified based on Koste (1978), Defaye (1988), and Fernando (2002). At least 100 individuals of the dominant taxa were counted randomly at a magnification of 100X. Zooplankton abundance was computed according to De-Bernardi (1984) and Edmomdson and Winberg (1971).

$$\text{Individual m}^{-3} = \frac{(n*gf*k)}{V}$$

Where: n = the total number of zooplankton counts

gf = grid factor

k = subsampling factor

V = the amount of water filtered by the sampling net in m^3. The volume of water filtered by the sampling net was estimated using the formula; $V = \pi r^2 d$ where r = the radius of the sampling net used (m), d = the depth of vertical haul (m).

8.3.4. Identification of macrophyte

The dominant macrophyte from the pressed sample was identified using identification key (Edwards *et al.*, 1995) and with the help of experts.

8.4. Data analysis

Spatial variations of physico-chemical and biological parameters were analyzed using one way ANOVA in SPSS (version 20) as the data satisfied the homogeneity of variance test in SPSS. Differences in fresh weight biomass of RFGs and MBFGs among sites were compared by

Kruskal–Wallis tets One Way ANOVA (k samples) due to the heterogeneity of variances. Multivariate analysis was performed using CANOCO Version 4.5 (Ter Braak and Smilauer, 2002). Detrended Correspondence Analysis (DCA) was performed for each functional approach, to determine whether the linear (Redundancy Analysis-RDA) or unimodal ordination method (Canonical Correspondence Analysis-CCA) would be more appropriate. All gradient lengths were short (< 3.0), indicating a linear response of the species to environmental variables. Therefore, RDA was selected (Lepš and Šmilauer, 2003) to evaluate the relationship between FGs and environmental variables.

The significance of environmental variables to elucidate the variability of species data in RDA was tested using Monte Carlo simulations with default unrestricted permutations (α = 0.05). Well correlated explanatory variables with variance inflation factor (**VIF**) more than 20 were removed from the analysis to reduce redundancy and increase the stability of the regression model as recommended by Ter Braak (1987). In the process, only one variable was removed at a time and the analysis was recomputed since the VIF of every variable depends on all the others. Q-Q plot in SPSS was applied to see whether the data were normally distributed or not. When the data were not normally distributed the log (X + 1) transformation of the environmental variables and Hellinger transformation of biomass data were applied (Legendre and Gallagher, 2001) prior to the ordination analysis. Trophic status index of the lake was calculated using the formula proposed by Lamparelli (2004) for tropical lakes (**Appendix 1A**). Finally, Sigma plot of version 10 was used for graphical presentation of results.

9. Results and Discussion

9.1. Spatial and monthly variations of physico-chemical parameters and Chl-a

There were variations in the levels of physico-chemical parameters among sites (**Table 3**). Secchi depth (Z_{SD}) and euphotic depth (Zeu) were relatively high in OW and MZ sites while very low in TW sites. Conversely, high TSS and turbidity were recorded at TW followed by those at RH. Generally, higher levels of nutrients were recorded at TW and RH sites.

Table 3. The levels of the measured physico-chemical parameters and Chl-a at all sampling sites (SD = standard deviation).

	Sampling sites			
	TW	RH	OW	MZ
Parameters	Mean ± SD (n = 5, df = 4)	Mean ± SD (n = 5, df = 4)	Mean ± SD (n = 5, df = 4)	Mean ± SD (n = 5, df = 4)
Z_{SD} (m)	0.21 ± 0.097	0.574 ± 0.189	0.822 ± 0.095	0.785 ± 0.151
Z_{eu} (m)	0.57 ± 0.262	1.55 ± 0.51	2.22 ± 0.255	2.12 ± 0.40
Turbidity (NTU)	77.98 ± 56.88	22.79 ± 10.57	10.88 ± 2.13	11.23 ± 2.34
TSS (mg L^{-1})	91.49 ± 49.83	34 ± 35.6	22.1 ± 28.2	11 ± 5.1
Temperature (^{o}C)	25.94 ± 1.8	24.02 ± 1.52	23.76 ± 1.62	24.15 ± 1.93
DO (mg L^{-1})	3.2880 ± 1.20	5.33 ± 1.59	6.57 ± 0.65	6.62 ± 0.93
TDS (mg L^{-1})	466.7 ± 654.86	410.7 ± 240.58	464.86 ± 247.16	504.2 ± 233.54
EC (µS cm^{-1})	312.73 ± 126.6	857.5 ± 93.3	851.23 ± 105.9	793.94 ± 25.7
PA (meq L^{-1})	0	0.96 ± 0.73	1.36 ± 0.59	1.52 ± 0.67
TA (meq L^{-1})	2.4 ± 1.54	3.66 ± 1.73	4.84 ± 3.19	2.58 ± 0.58
pH	7.6 ± 0.570	9.02 ± 0.124	9.13 ± 0.08	9.03 ± 0.23
SRP (µg L^{-1})	151.1 ± 154.87	38.37 ± 50.99	37.5 ± 23.55	34.28 ± 18.73
TP (µg L^{-1})	456.96 ± 181.44	256.28 ± 113.55	157.4 ± 84.09	133.6 ± 53.26
Ammonia (µg L^{-1})	141.1 ± 92.3	275.81 ± 155.7	207.3 ± 88.22	194.34 ± 115.7
Nitrate (µg L^{-1})	31.7 ± 11.31	18.8 ± 14.55	21.3 ± 31.41	17.09 ± 23.8
SiO_2 (mg L^{-1})	71.93 ± 13.79	69.79 ± 17.5	76.2 ± 34.57	74.48 ± 22.32
Chl-a (µg L^{-1})	14.91 ± 10.83	34.012 ± 20.14	29.95 ± 18.65	32 ± 16.31

Even though there were variations in the mean levels of all physico-chemical parameters among sites, statistically significant variations were observed only in some parameters including Z_{SD}, DO, pH, turbidity, nutrients and EC (**Table 4**).

The levels of turbidity and nutrients (**Table 4**) showed spatial variations with the highest levels at TW. The continuous introduction of suspended and dissolved substances from the catchment area (e.g. point sources: Hawassa textile factory and nonpoint sources; agricultural lands) with the inflowing river may have made a large contribution to the elevated turbidity and nutrients levels at TW site. High turbidity and nutrients levels were also recorded at RH site than those of OW and MZ though the differences were not significant ($P > 0.05$). Particulates such as clay and silt from shoreline erosion or resuspended bottom sediments and organic detritus from wastewater discharge of Hawassa University Referral Hospital were likely sources of the high turbidity and nutrients levels observed at RH. On the other hand, the high clarity of the water and relatively low levels of nutrients at MZ and OW sites can be due to the filtering effect of the macrophyte and the dilution effect of increased water level (on TSS and TDS present) respectively. Horppila and Nurminen (2001) also indicated that emergent macrophytes could reduce sediment resuspension thereby decreasing turbidity and TSS content of near-surface waters.

Transparency of the water at all sites of Lake Hawassa was generally higher than the transparency of Lake Ziway (Getachew Beneberu and Seyoum Mengistou, 2009; Girma Tilahun and Ahlgren, 2010; Mesfin Gebrehiwot *et al*., 2017), Lake Chamo (Girma Tilahun and Ahlgren, 2010), lakes Abaya and Chamo (Fassil Eshetu, 2016) and Koka Reservoir (Yeshiemebet major, 2016) due to the greater depth and the smaller area of Lake Hawassa. Lakes Ziway, Abaya and Chamo have much higher surface area and shallower depth and consequently these lakes tend to receive more input than Lake Hawassa. Generally, lakes those have small surface area and greater depth exhibit higher water quality than those that have larger surface area and shallow depth (Limgis, 2001). A general trend of frequent mixing that may have increased the internal nutrient loads and so as the turbidity was discussed in lakes Chamo and Ziway by Girma Tilahun (2006) due to their shallowness. Davies-Colley (1988) also reported that the mixing depth of lakes tends to increase with surface area. On the other hand, the Secchi depth of Lake Hawassa is much shallower than the two narrow deep highland lakes of Ethiopia: Lake Hayq (Tadesse Fetahi, 2010) and Lake Wonchi (Fasil Degefu *et al*., 2014).

The trends of spatial variations in levels of DO and pH were similar to that of the Z_{SD}. Accordingly, the levels of pH and DO were significantly lower at TW sites (**Table 4**) than the other sites which could be due to reduced photosynthetic production of DO and increased consumption of the available DO in dark condition. The resulting lower photosynthetic removal of CO_2 may result in a lower pH level. Biological processes (e.g. photosynthesis and respiration) as well as turbulence and aeration are known to influence pH by varying the concentration of dissolved carbon dioxide (CCME, 2003). The relatively high pH level at the remaining sites may have resulted from greater photosynthetic removal of CO_2 (Talling, 2010). The pH of Lake Hawassa is generally higher than those of Lake Ziway (Mesfin Gebrehiwot *et al.*, 2017) but comparable with the pH levels reported previously for Lake Chamo (Eyasu Shumbulo, 2004).

The presence of light limitation for algal growth due to the turbid condition was also revealed by the low level of Chl-a at TW than other sites though the difference was not significant statistically. The dominance of large-sized phytoplankton may be the other reason for the observed low level of Chl-a at TW as large cells generally are known to contain lower amount of Chl-a per unit volume than the small forms (Malone 1980; Felip and Catalan, 2000).

The levels of nutrients, pH and Chl-a at OW site were higher than the results reported in previous studies made by Demeke Kifle and Amha Belay (1990), Elizabeth Kebede *et al.* (1994), Elizabeth Kebede and Amha Belay (1994), Zinabu Gebre-Mariam *et al*. (2002) and Girma Tilahun and Ahlgren (2010). The elevated levels of the parameters recorded in the present study may resulted from the more diverse and intensive anthropogenic activities in the lake's area. But, a much higher level of TP was reported from other rift valley lakes (lakes Abaya and Chamo) by Fassil Eshetu (2016).

Although the level of TDS at TW was high, the EC value was significantly low compared to those of the other sites (**Table 4**). This can be due to the complex interactions of ions that reduce their mobility. Miller *et al*. (1988) had indicated that the conductivity of an aqueous solution is determined not only by concentration and charge, but also by the mobility of the dissolved ions.

Such irregular relationships between conductivity measurements and total ionic concentrations (TDS) were also observed in studies made in Lake Ziway (Girma Tilahun, 1988), and lakes Abijata and Langano (Kassahun Wodajo, 1982), lakes Abaya, Abijata, Chamo and Shalla (Zinabu Gebre-Mariam *et al*., 2002). Sources of such irregularities could be the difference in contribution of different ions to conductivity and the contribution per unit concentration may change with salinity (Wood and Talling, 1988). At the remaining study sites, the mean EC value was high as the TDS value. Both the mean (**Table 3**) and upper boundary value of the range (793-1040 µS cm^{-1}) of EC at OW were considerably higher than those reported previously by Zinabu Gebre-Mariam *et al*. (2002; 780-965, 846 µS cm^{-1}) and Girma Tilahun and Ahlgren (2010; 844 µS cm^{-1}).

Table 4. The variations of physico-chemical parameters between TW, and RH, OW and MZ in Lake Hawassa based on the difference in the mean levels of the parameters (α = 0.05).

Dependent Variable	(I) Sites	(J) Sites	Mean Difference (I-J)	Std. Error	Sig.
DO	TW	RH	-2.038	0.728	0.056
		OW	-3.28140	0.728	0.002
		MZ	-3.336	0.728	0.002
EC	TW	RH	-544.794	60.519	<0.001
		OW	-538.503	60.519	<0.001
		MZ	-481.210	60.519	<0.001
pH	TW	RH	-1.415	0.198	<0.001
		OW	-1.534	0.198	<0.001
		MZ	-1.427	0.198	<0.001
Turbidity	TW	RH	55.189	18.324	0.037
		OW	67.096	18.324	0.01
		MZ	66.704	18.324	0.011
Z_{SD}	TW	RH	-.363	0.088	0.004
		OW	-.611	0.088	<0.001
		MZ	-.574	0.088	<0.001
Zeu (m)	TW	RH	-0.98118	0.237	0.004
		OW	-1.65170	0.237	<0.001
		MZ	-1.55088	0.237	<0.001
TSS	TW	RH	57.486	21.383	0.069
		OW	69.386	21.383	0.024
		MZ	80.486	21.383	0.008
TP	TW	RH	200.68	74.649	0.069
		OW	299.560	74.649	0.005
		MZ	323.360	74.649	0.003

In contrast to the suggestion of Wood and Talling (1988), inflow of groundwater with considerably high ion concentration would be a more probable explanation for the long-term increase in EC.

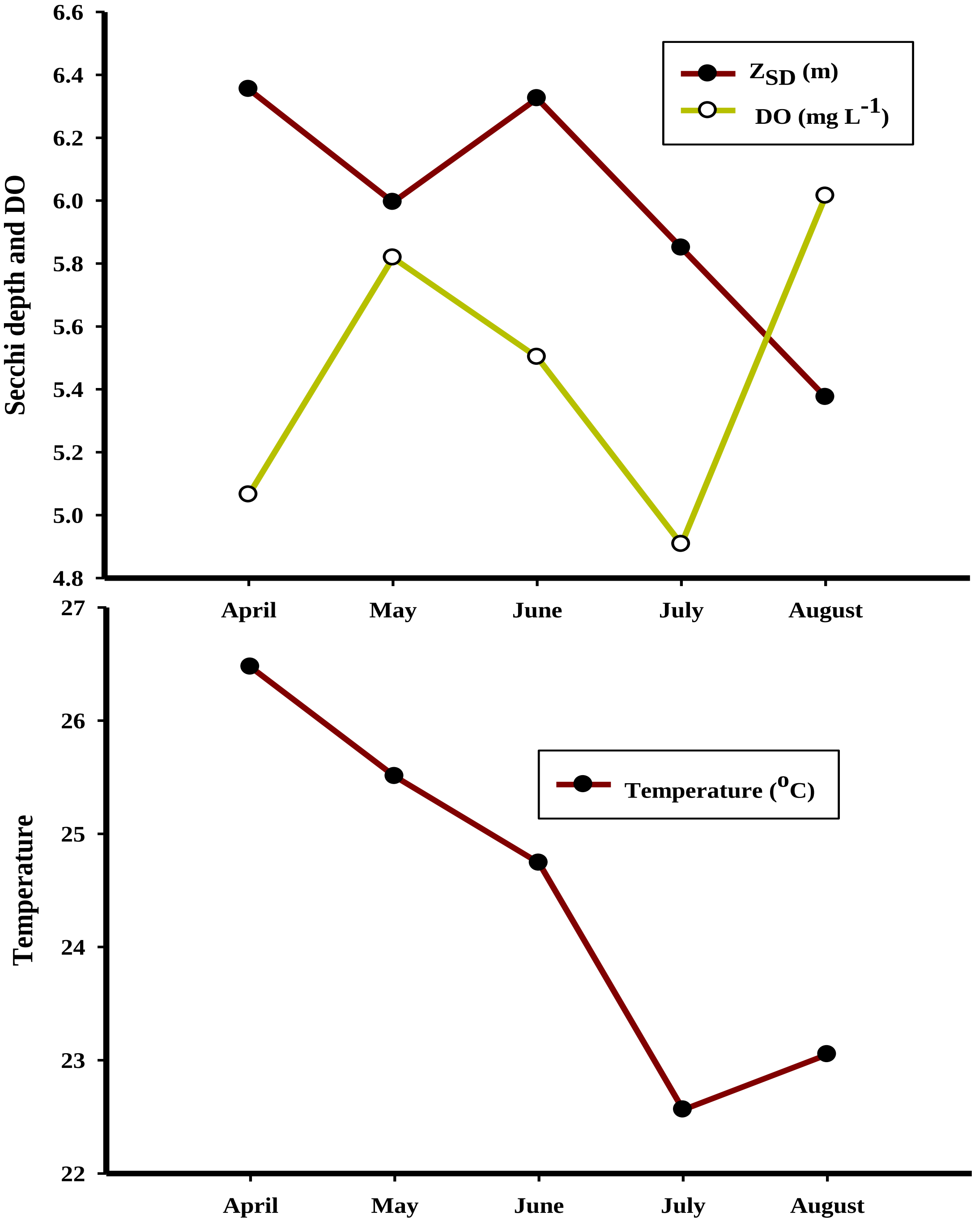
The increased concentration of nutrients might have also made some contribution to the increment in the EC value at the OW site. However, compared to some other rift valley lakes of Ethiopia such as lakes Abaya, Abijata, Chamo, Langano and Shalla (Zinabu Gebre-Mariam, 2002) and Lake Chamo (Eyasu Shumbulo, 2004), the EC value was lower due to relatively lower concentrations of ions although it is still higher than Lake Ziway.

The water transparency was similar during all the sampling months with a decreasing trend towards August (**Appendix 2A**). Turbidity (152 NTU) was high in August due to the high levels of TSS (36 mg L^{-1}), Chlorophyll-a (42 µg L^{-1}) and TDS (558 mg L^{-1}). A decreasing trend in water temperature was observed from April (26.47 ℃) to July (22.56 ^{o}C). The sampling day was sunny in April but cloudy in July and consequently, solar heating and cloud cover, respectively, caused the temperature variations in these months. There were monthly variations in the levels of DO and EC in Lake Hawassa. The mean concentration of DO (6.01 mg L^{-1}) was higher in August (**Fig. 4**) than those of other sampling months, which can be related to the increased photosynthetic production by phytoplankton as can be inferred from the peak Chl-a level (42 µg L^{-1}) of this month. EC followed a pattern, with the maximum value in August, similar to that of DO. The increased input of dissolved ions indicated by the elevated TDS level (558 mg L^{-1}) might has accounted for the increased level of EC in this month as the conductivity of an aqueous solution is related to the concentration of its constituent ions (Miller *et al*., 1988).

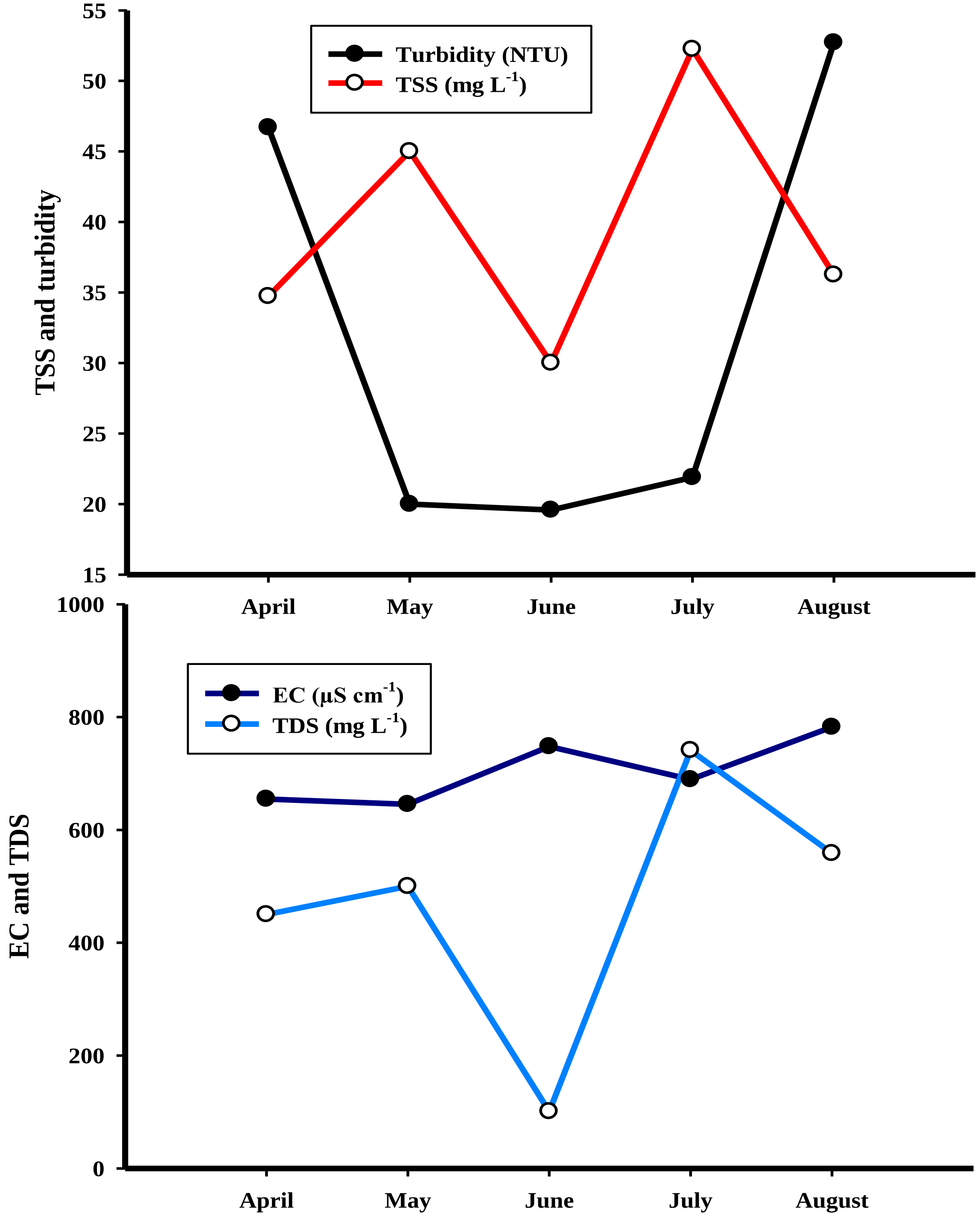
Monthly variations in the levels of alkalinity and pH were recorded (**Appendix 2**). Alkalinity was highest in May mainly due to high concentration of bicarbonate ions (with some carbonates) as revealed by the observed pH, which was only slightly higher than 8.3. A similar level of alkalinity was recorded in the remaining months. The highest level of alkalinity in May can be the result of an increased concentration of carbonate and bicarbonate ions as a result of leaching from the catchment area. Carbonates of calcium and magnesium can enter water systems as a result of naturally occurring processes like sedimentary rock erosion and seepage, runoff from soils (Health Canada, 2017). The increased release of ions from bottom to the upper water column as a result of the vertical mixing event in May in contrary to superficial stratification in April (**Appendix 2B**) could have also contributed for the elevated level of alkalinity in May. pH level was high (8.6-8.9) in all sampling months, which can be related to the existence of high photosynthetic activity in the lake as the assimilation of carbon dioxide during photosynthesis is ultimately responsible for the increase in pH. The highest pH level was observed in June. Higher pH values observed in lakes can be associated with the interactive effects of physico-chemical and biological conditions on carbon dioxide, carbonate-bicarbonate equilibrium (Patil *et al.*, 2012).

Phosphate concentration varied between 6.4 and 131 µg L^{-1}, with peaks in May followed by August (**Fig. 4**). The maximum level of SRP in May can be due to the mixing event (**Appendix 2**). At the OW site, hypoxic condition prevailed below 9 m depth in April (**Appendix 2C**), after which the lake experienced nearly complete vertical mixing in the remaining sampling months. This reflects the presence of high oxidative oxygen consumption in the deeper part of the water column in April. The high level of SRP in May can, therefore be, related to this phenomenon as a vertical mixing event brings the nutrients from bottom to surface. Vertical re-distribution, associated with de-stratification and change in phytoplankton uptake is likely to affect concentrations of nutrients and major ions (Zinabu Gebre-Mariam, 2002). Generally, an increasing trend in the concentration of nutrients was observed from April to August (**Appendix 2D**). Increased accumulation of nitrogen and phosphorus rich influents into the lake from various origins can be the reason for the increasing trend of nutrients. In comparison, elevated level of nutrients was reported by Zinabu Gebre-Mariam (2002) in seven rift valley lakes (lakes Abaya, Abijata, Chamo, Hawassa, Langano, Shalla and Ziway) during the rainy months as the result of mixing events that re-distribute nutrients to the surface water, and inputs from runoff.

Increasing trend in the concentration of Chl-a was recorded from April to August (**Appendix 2D**), which was associated with the similar temporal trend of the nutrients levels (**Fig. 4**). This trend is consistent with the findings of Demeke Kifle and Amha Belay (1990) that indicated an increased concentration of Chl-a during the wet season (between May and August) in the same lake. Elizabeth Kebede and Amha Belay (1994) also reported an increase in the concentration of Chl-a from June to the end of July, which corresponds to the mixing periods of the lake.



Secchi depth and DO
6.6
6.4
6.2
6.0
5.8
5.6
5.4
5.2
5.0
4.8
Z_{SD} (m)
DO (mg L^{-1})
April
May
June
July
August
Temperature
27
26
25
24
23
22
Temperature (^{o}C)
April
May
June
July
August



Turbidity (NTU)
TSS (mg L-1)
TSS and turbidity
55
50
45
40
35
30
25
20
15
April
May
June
July
August
EC (µS cm-1)
TDS (mg L-1)
EC and TDS
1000
800
600
400
200
0
April
May
June
July
August

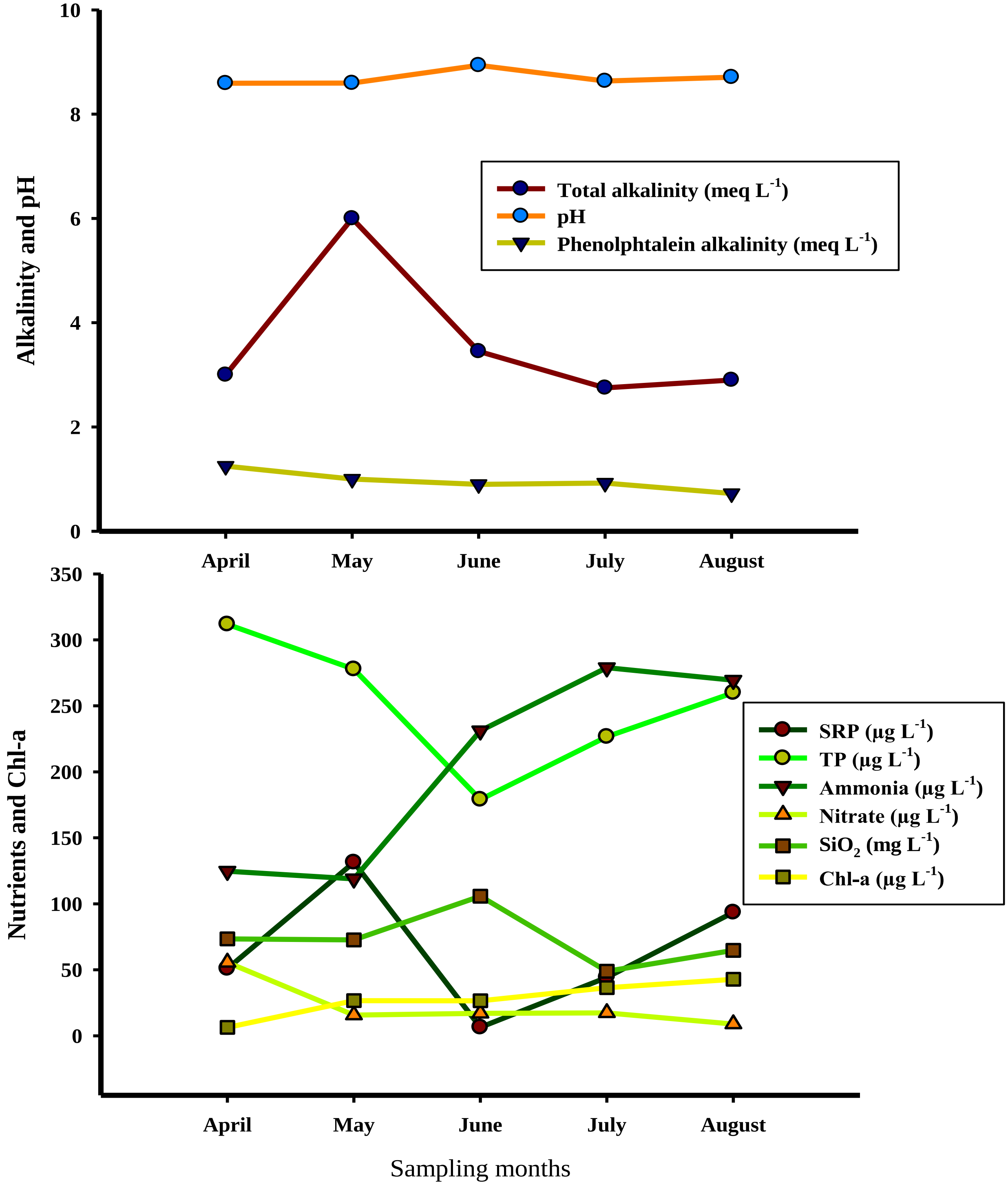


Figure 4. Temporal variations in the levels of physico-chemical parameters and Chl-a in Lake Hawassa, Ethiopia.

9.2. Taxonomic composition of phytoplankton

A total of 130 species of phytoplankton belonging to seven taxonomic groups such as *Bacillariophyta* (diatoms, 35), *Chlorophyta* (green algae, 33), *Cyanophyta* (blue-green algae or cyanobacteria, 28), *Charophyta* (charophytes, 13), *Euglenophyta* (euglenoids, 17), *Dinophyta* (dinoflagellates, 3) and *Cryptophyta* (cryptophytes, 1) were identified (**Table 5**). Diatoms were the most diverse accounting for 27.3% of the total species number followed by green algae and cyanobacteria, which accounted for 25.08% and 21.88% of the total number of species present respectively. Desmids contributed for 10.16%, while euglenoids comprised 12.5% of the total species encountered. Dinoflagellates and cryptophytes, which contributed only 2.3% and 0.78% of the total species number, respectively, were the rarest taxa. 46 species, which are indicated by an asterisk* (**Table 5),** are newly reported for the lake. The present results are comparable to those of the previous reports documented by Elizabeth Kebede and Amha Belay (1994) and Girma Tilahun (2006) except that diatoms were found to be slightly dominant over the green algae. The difference in the scheme of classification followed in the previous (Christensen, 1962), and present (Guiry and Guiry, 2013) studies may have caused the small difference in the percentage contribution of some taxa as the desmids *Cosmarium, Staurodesmus* and *Staurastrum* species were all included in *Chlorophyta* according to Christensen, (1962), while these same taxa were assigned to *Charophyta* according to Guiry and Guiry (2013).

As most desmids are restricted to freshwaters with low total ions, the reduced representation in Lake Hawassa can be due to high ionic concentrations and alkalinity of the lake as suggested by Elizabeth Kebede and Amha Belay (1994). However, according to Elizabeth Kebede and Willén (1998) occurrence of desmids in Lake Hawassa is more frequent than in the other rift valley lakes such as lakes Ziway, Shalla, Metahara, Langano, Chitu, Chamo, Abijata and Abaya, and Koka Reservoir.

All species encountered in this study were distributed throughout all sampling sites indicating the absence of spatial variation in species composition of phytoplankton. Consistent with the findings of Elizabeth Kebede and Amha Belay (1994), *Nitzschia* and *Botryococcus* species were found to be prominent phytoplankton species in the lake though *Cylindrospermopsis* and *Microcystis* (**Appendix 2E**) were by far the most dominant, contrary to the dominance of *Lyngbya nyassie* reported previously by Elizabeth Kebede and Amha Belay (1994). Similarly, the conspicuous occurrence of *Cylindrospermopsis and Microcystis* species was also reported from Lake Ziway (Mesfin Gebrehiwot *et al*., 2017), Koka Reservoir (Yeshiemebet Major, 2016) and Lake Kuriftu (Zelalem Dessalegn and Demeke Kifle, 2014). The dominance of *Nitzschia*, *Aulacoseira granulata* and *Microcystis* species was also reported from Lake Tana (Adane Melaku, 2017), Lake Chamo (Eyasu Shumbulo, 2004) and Lake Victoria (Lung'ayia *et al*., 2000).

Only the three taxonomic groups, namely *Bacillariophyta* (13.78%), *Chlorophyta* (11.14%), and *Cyanophyta* (74.4%) made significant percentage contribution to the total phytoplankton abundance of the lake. All the remaining taxa were relatively rare with combined percentage contribution of only 0.68% of the total phytoplankton abundance. The relative contribution of the major taxonomic groups to the total phytoplankton abundance recorded in the present study is similar to those documented in the earlier reports by Elizabeth Kebede and Amha Belay (1994), Tadesse Fetahi (2010) and Tadesse Fetahi and Seyoum Mengistou (2014) from the same lake.

Despite having the largest percentage share of the total phytoplankton counts, the contribution of cyanobacteria (24.16%) to the total fresh weight biomass was much lower than that of diatoms (69.61%) due to the larger size of the latter. The dominance of total phytoplankton biomass by diatoms was also reported from Lake Chamo by Girma Tilahun (2006).

Table 5. List of phytoplankton species identified in samples from Lake Hawassa and categorized into 7 phyla according to Guiry and Guiry (2013). The taxa recorded for the first time from the study lake are marked with an asterisk*.

Cyanophyta	***Bacillariophyta***
Microcystis aeruginosa (Kützing) Kützing	_Aulacoseira granulata_ (Ehrenberg) Simonsen
M. flosaquae (Wittrock) Kirchner	_Aulacoseira distans_ (Ehrenberg) Simonsen
M. panniformis Komárek _et al._	_Aulacoseira_ species
M. wesenberg	*_Pinnularia microstauron_ (Ehrenberg) Cleve
M. botrys (Teiling)	*_P. gibba_ (Ehrenberg) Ehrenberg
_M._species	_Caloneis alpestris_ (Grunow) Cleve
Chroococcus dispersus (Keissler) Lemmermann	_Navicula neoventricosa_ Hustedt
C. limneticus Lemmermann	*_N. brekkaensis_ Petersen
*_C. minor_ (Kützing) Nägeli	_N. pupula_ (Kützing)
C. minutus (Kützing) Nägeli	*_Achnanthes bioretii_ (Germain)
C.turgidus (Kützing) Nägeli	_A. lanceolata_ (Brébisson ex Kützing)
*_Aphanothcece minutissima_ Nägeli	*_A. exilis_ (Kützing)
A.clathrata West	*_Diatoma hyemalis_ (Roth) Heiberg
Cylindrospermopsis catemaco (Komárková-Legnerová and Tavera)	_Asterionella formosa_ Hassall
C.curvispora (Watanabe)	*_Epithemia argus_ (Ehrenberg) Kützing
C.raciborskii (Woloszynska) Seenayya and Subba	*_Elerbeckia arenaria_
Aphanizomenon aphanizomenoides (Forti) Hortobágyi and Komárek	_Nitzschia dissipata_ (Kützing) Rabenhorst
*_Oscillatoria curviceps_ (Agardh ex Gomont)	_N.linearis_ (Smith)
Planktothrix species Anagnostidis and Komárek	_Cymbella_ species
*_Komvophoron constrictum_ (Szafer) Anagnostidis and Komárek	_Gomphonema_ species
Spirulina species	*_G.telegraphicum_ Kützing
Coelospharium minutissimum Lemmermann	*_amphora subcutiuscula_
Merismopedia (Meyen).	_Cyclotella radiosa_(Grunow) Lemmermann
M. tenuissima Lemmermann	*_C. meneghiniana_ (Kützing)
M. punctata Meyen	_Stephanodiscus_ species
M. glauca (Ehrenberg) Kützing	*_Ceratoneis arcus_ (Ehrenberg) Kützing
Aphanocapsa species	*_Frustulia romboides_
Cyanodictyon species Pascher	*_Fragilaria biceps_ Ehrenberg
Cryptophyta	_F. construens_ (Ehrenberg) Grunow
Cryptomonas ovata Ehrenberg	_F. nana_ (Meister) Lange-Bertalot
Dinophyta	_Synedra ulna_ (Nitzsch) Ehrenberg
*_Peridinium cinctum_ (Müller) Ehrenberg	_Surirella linearis_ Smith
Peridinium lomnickii (Woloszynska)	*_S. ovalis_ Brébisson
Gymnodinium species	*_Amphora_ species
Chlorophyta	*_Cocconeis placentula_ Ehrenberg
Botryococcus brauni (Kützing)	***Charophyta***
B.terribilis Komárek and Marvan	_Staurastrum tetracerum_ (Ralfs ex ralfs)
B. fernandoi Komárek and Marvan	*_S. avicula_ (Brebisson)
_B._ species	_S. paradoxum_ (Meyen ex Ralfs)
Coelastrum reticulatum (Dangeard) Senn	*_S. muticum_ (Brebisson ex Ralfs)
C.sphaericum (Corda) ex Ralfs	*_Staurodesmus crassus_ (West and West) Florin
	*_S. indenticus_
	Cosmarium depressum (Nägeli) Lundel

*_C.cambricum_ (Archer)
_C._species
Golenkinia radiata (Chodat)
Ankistrodesmus babraianus
A. falcatus (Corda) Ralfs)
*_A. spiralis_ (Turner) Lemmermann
Kirchneriella obesa (West) West and G.S. West
Pediastrum duplex (Meyen)
P. boryanum (Turpin) Meneghini
P. simplex Meyen
P. tetras (Ehrenberg) Ralfs
Scenedesmus acuminatus (Legherheim) Chodat
*_S. arcuatus_ (Lemmerman)
S. acutus (Meyen)
*_S. bijugatus_ Kützing
S. dimorphus (Turpin) Kützing
S. quadricauda (Turpin) Brébbisson
Tetraëdron minimum (Braun) Hansgirg
T. triangulare (Korshikov)
T. caudatum (Corda) Hansgirg
*_Monoraphidium griffithii_ (Berkeley) Komárková-Legnerová
*_Volvox carteri_ (Stein)
Pandorina morum (Müller) Bory
*_Spirogyra_ species
Oocystis lacustris (Chodat)
O.marsoni (Lemmerman)
Crucigenia tetrapedia (Kirchner) Kuntze

C. contractum (Kirchner)
*_C. subprotumidum_ (Nordstedt)
*_C.sphaericum_
*_Closterium dianae_ (Ehrenberg ex Ralf)
C. limneticus
Euastrum bidentatum (Nägeli)
Euglenophyta
Euglena acus (Ehrenberg)
*_E. obtusa_ (Schmitz)
*_E. caudata_ (Hübner)
*_E. virids_ (Müller)
_E._ species
*_Lipocinclis ovum_ (Ehrenberg) Lemmermann
*_L. fusiformis_ (Carter) Lemmermann
Phacus longicauda (Ehrenberg) Dujardin
P. pleuronectes (Müller) Nitzsch, Dujardin
*_P. alatus_ (Pochmann)
*_P. tropicalis_
P. orbicularis Hübner
Trachelomonas species
T. aspera (Cunha)
*_T. volvocinia_ (Ehrenberg)
*_T. bacillifera_ (Playfair)
*_Monomorphina pyrum_ (Ehrenberg) MereschKowsky

9.3. Trait-separated and morphology-based phytoplankton functional groups and their variations in space and time

Qualitatively, the identified taxa were classified into 17 trait-based functional groups (RFGs) and 6 morphology-based functional groups of algae (MBFGs). The lists of RFGs and MBFGs with their typical representatives are given in **Table 6** and **Table 7** respectively. From the total of 17 RFGs, only the 11 RFGs (**D**, **F**, **J**, **Lo**, **M**, **N**, **P**, **SN**, **K**, **W1** and **W2**), which contributed for more than 1 percent of total fresh weight biomass of the RFGs were considered for further analysis. **D**, **J**, K, **Lo**, **M**, **N**, **P**, **SN and W2** were the dominant RFGs accounting for 95.24% of the total phytoplankton biomass. **P** constituted 54.9% of the total biomass followed by **SN** (14.65%), **M** (7.32%), **Lo** (4.89%), **J** (3.23%), **K** (2.99%), **W2** (2.97%, **N** (2.17%) and **D** (2.12%). These results are comparable with those of Mesfin Gebrehiwot *et al.* (2017). Mesfin Gebrehiwot *et al*. (2017) found the RFGs **S2–SN**, **J**, **P**, **M**, **L_O and W1-W2** to be the most important FGs in Lake Ziway, a water body located in the same rift valley as the current study lake.

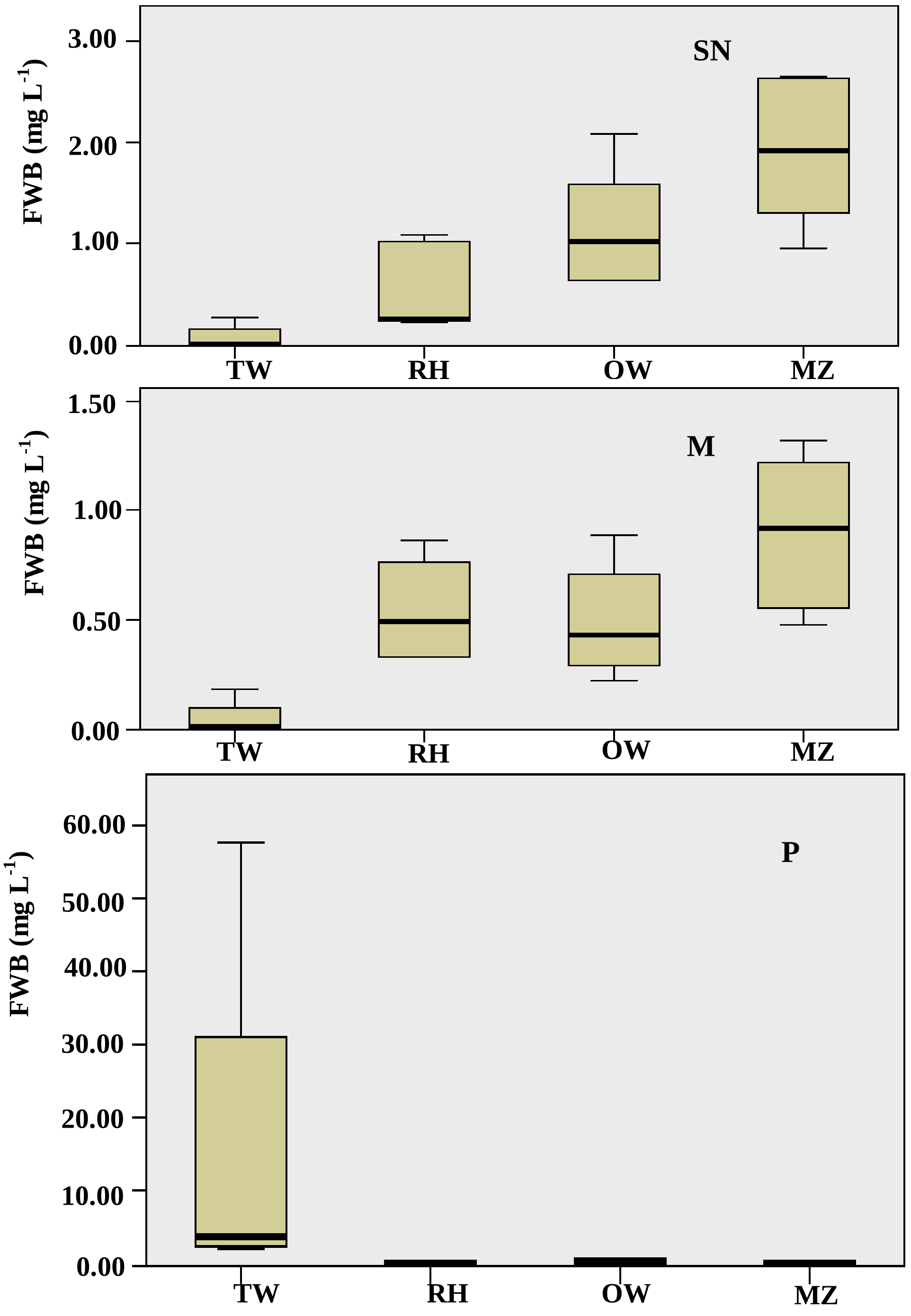
Table 6. Trait-separated functional groups of phytoplankton (RFGs) in Lake Hawassa, Ethiopia based on Reynolds *et al*. (2002) and Padisák *et al*. (2009).

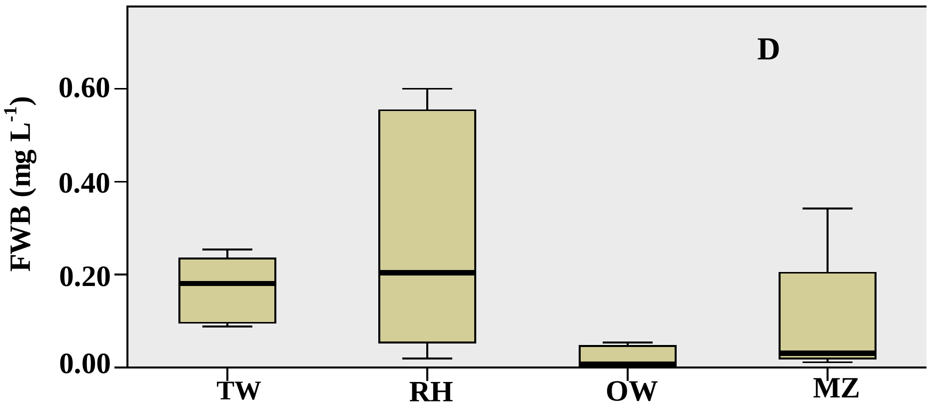
Codon	Habitat	Typical representatives	Tolerance	Sensitivity
D	Shallow enriched turbid water	*Nitzschia dissipata*	Flushing	Nutrient depletion
N	Mesotrophic epilimnia	*Cosmarium depressum Staurastrum tetracerum, S.muticum, S.avicula, Staurodesmus crassus*	Nutrient deficiency	Stratification, pH rise
P	Eutrophic epilimnion	*Aulacoseira granulata*	Mild light, C deficiency	Stratification, Si depletion
SN	Warm mixed layers	*Cylindrospermopsis catemaco, C.raciborskii, C.curvispora*	Light, N_2 deficiency	Flushing
F	Clear epilimnia	*O.lacustris, Ankistrodesmus* and *Botryococcus* species	Low nutrients high turbidity	CO_2 deficiency
L_O	deep and shallow, oligo to eutrophic lakes	*Merismopedia* species *M.tennuissima, Chroococcus minutus, C.minor, C.turgidus, Peridinium* species	Segregated nutrients	Prolonged or deep mixing
J	Shallow enriched lakes	*Tetraëdron minimum, Coelastrum* and *Scenedesmus* species		Settling into low light
M	Eutrophic to hypereutrophic, small to medium-sized water bodies.	*Microcystis* species, *M.flosaquae, M.aeruginosa, M.panniformis, M.wesenberg*	High Temperature/light intensity	Flushing, low total light
K	Short nutrient rich water column	*Cyanodictyon, Aphanothece* and *Aphanocapsa* species	---	Deep mixing
T_D	Mesotrophic standing waters, or slow-flowing rivers with emergent macrophyte	*Cyclotella meneghiniana Fragilaria nana, Ceratoneis arcus, Pinnularia* species	Mixing	Stratification
MP	Inorganically turbid	*F. construens, Cymbella,*	Mixing	---

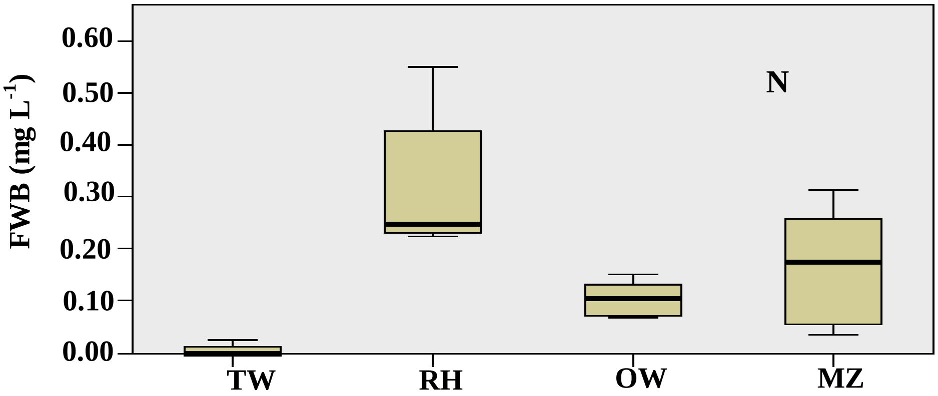
	shallow lakes	*Epithemia, Navicula, Surirella, Achnanthes* and *Gomphonema* species		
G	Nutrient-rich conditions in stagnating water column	*Pandorina morum, Volvox carteri*	High light	Nutrient deficiency
H1	Eutrophic, both stratified and shallow lakes with low nitrogen content	*Aphanizomenon aphanizomenoides*		
W1	Ponds, even temporary, rich in organic matter from husbandry or sewages	*Euglena acus, Phacus longicauda, P. pleuronectes*	High biological oxygen demand	Grazing
W2	Eso-eutrophic ponds, even temporary, shallow lakes.	*Trachelomonas aspera*		
X1	Shallow mixed layers in enriched condition	*Monoraphidium griffitthii*	Stratification	Nutrient deficiency, filter feeding
Y	Usually, small, enriched lakes	*Cryptomonas ovata*	Low light	Phagotrophs

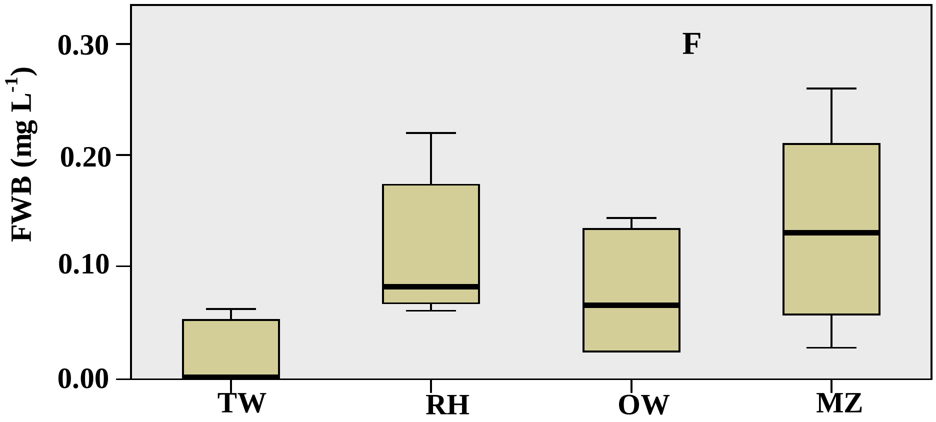
9.3.1. Spatial and monthly variations in fresh weight biomass of RFGs

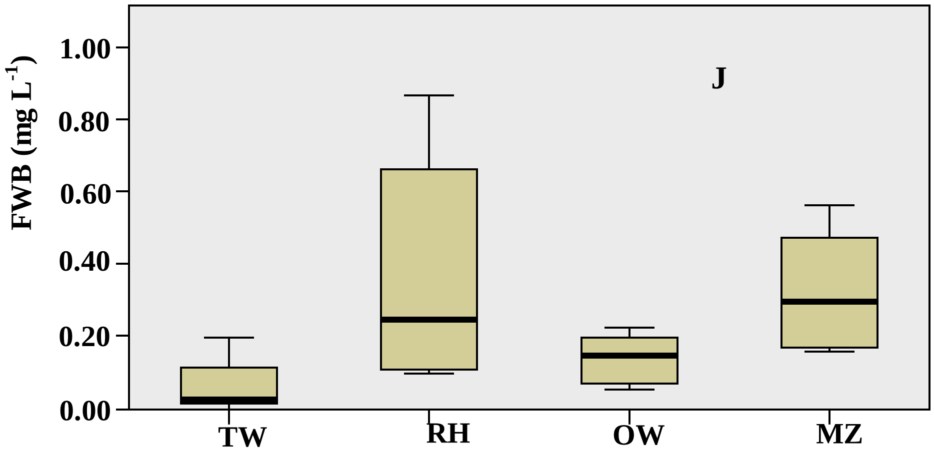
There were variations in the biomass of RFGs among the four sampling sites (**Fig. 5**). **SN**, **M**, **P**, **J**, and **L**$_O$ were the most dominant FGs in their contribution to the total biomass at all sampling sites (**Fig. 5**). RFG **M** (which was represented by colonial blue-green algal species) was predominant next to **SN** at RH, OW and MZ. Adaptation of the RFG **M** to alkaline condition could have favored its abundant occurrence (Bellinger and Sigee, 2010). **SN** showed significantly increasing trend from TW through RH and OW towards the MZ ($p = 0.002$). The highest biomass of **SN** was recorded at MZ.


SN
FWB (mg L -1)
3.00
2.00
1.00
0.00
TW
RH
OW
MZ
M
FWB (mg L -1)
1.50
1.00
0.50
0.00
TW
RH
OW
MZ
P
FWB (mg L -1)
60.00
50.00
40.00
30.00
20.00
10.00
0.00
TW
RH
OW
MZ


D
FWB (mg L^{-1})
0.60
0.40
0.20
0.00
TW
RH
OW
MZ


N
FWB (mg L^{-1})
0.60
0.50
0.40
0.30
0.20
0.10
0.00
TW
RH
OW
MZ


F
FWB (mg L^{-1})
0.30
0.20
0.10
0.00
TW
RH
OW
MZ


J
FWB (mg L^{-1})
1.00
0.80
0.60
0.40
0.20
0.00
TW
RH
OW
MZ

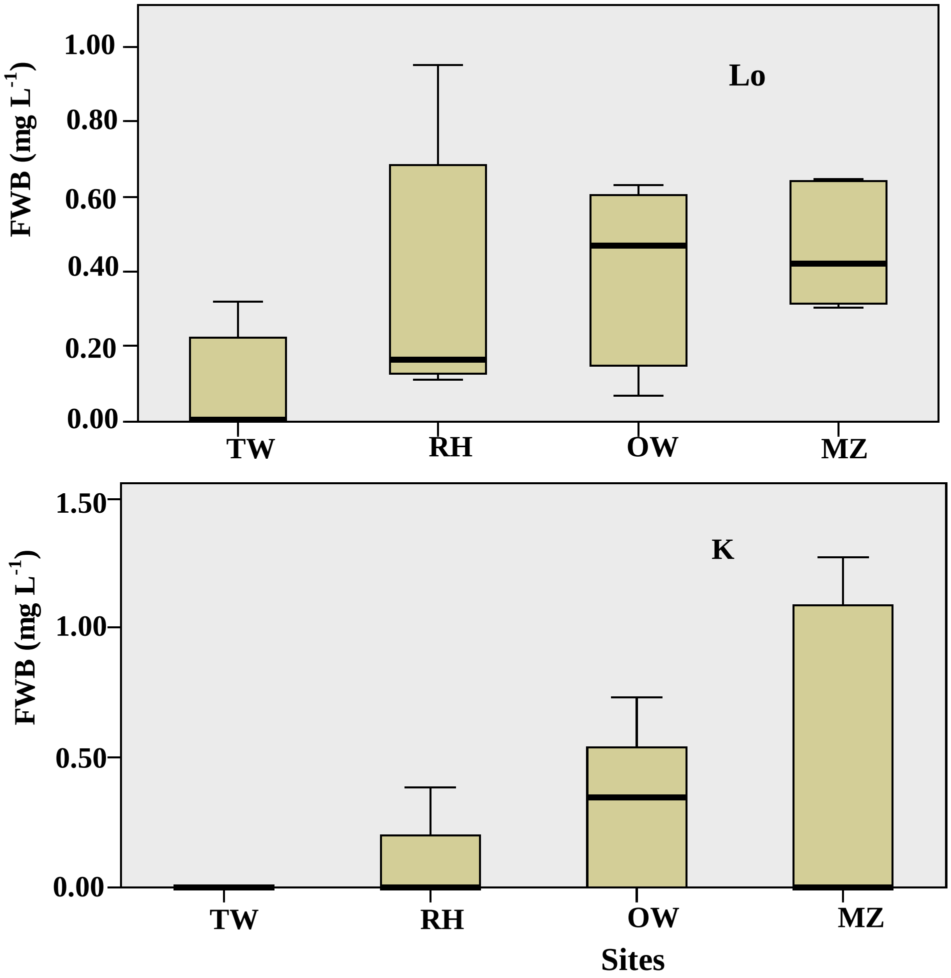


Figure 5. Spatial variations in fresh weight biomass (FWB) of RFGs at the four sampling sites (TW = Tikur Wuha inlet, RH = Referral Hospital influent area, OW = Open Water part and MZ = Macrophyte Zone). The solid line inside the boxes corresponds to the median value.

Relatively higher biomass of **SN** was also recorded for OW than for RH though the difference was not significant (p = 0.1). The dominance of **SN** at MZ can be related to its adaptation to low total irradiance as it can be evidenced from the filamentous and coiled structure of its members (*Cylindrospermopsis curvispora, C. raciborskii* and *C. catemaco*), which increases light harvesting potential (Zapomělová *et al.*, 2008) and prevents grazing (Stoyneva *et al.*, 2007) thereby allowing them to be dominant at MZ where there was the highest number of herbivorous zooplankton *Thermocyclops* species. These results are consistent with the findings of O'Farrell *et al.* (2007) who analyzed the importance of underwater light climate in shaping phytoplankton assemblages and observed prevalence of small, unicellular, non-flagellated organisms, thin filaments or small tubular colonies in light-limited environments.

Similarly, **M** attained the highest biomass at MZ whereas its lowest biomass was documented from TW. The greater biomass of **M** was probably due to their adaptation to the stagnant water column at MZ, as water column mixing can affect them negatively by disrupting their suspension in the water's surface (Kruk and Segura, 2012). Comparably, high level of **M** biomass was noted at RH and OW as a result of probably the higher levels of ammonium-nitrogen at these sites than at the other sites (**Table 3**) as ammonium-N pools are known to enhance the growth of non-nitrogen fixing cyanobacteria (Blomqvist *et al*., 1994). The present findings are in agreement with the works of Stević *et al*. (2013) which demonstrated that high nutrient concentrations and water column stability led to the dominance and high biomass of cyanobacteria. The spatial variations in RFGs can also be linked to the availability of utilizable dissolved CO_2. CO_2 seemed to be limiting to **J** and **F** due to the high pH level especially at MZ where hydroxide and carbonates were the predominant ions (**Appendix 1B**). Bicarbonates and carbonates were the predominant dissolved inorganic carbon species at RH and OW sites, while bicarbonate was predominant at TW (**Appendix 1B**). This may have favored the dominance of **SN** and **M**, which are capable of utilizing HCO_3^- and CO_3^{2-} as alternative carbon sources (Golman *et al*., 1971). At high pH levels, the availability of CO_2 is known to become limiting to phytoplankton growth (Chenl and Durbin, 1994).

The potentially toxigenic cyanobacterial species that have great public health importance belong to RFGs **SN** and **M**. The possession of gas vesicles by both groups may provide them with a special advantage of remaining suspended in upper water columns under relatively stable conditions.

M (large colonial *Microcystis*) and **SN** (filamentous forms such as *Cylindrospermopsis*) are known to be dominant in productive lakes (Reynolds, 1984) and possess the superior potential to succeed under both illuminated and turbid conditions (Gliwicz and Lampert, 1990). Reynolds *et al*. (2002) have, however, indicated that **SN** is typical of the warm mixed layer of a water system. Entrainment in the mixed water column is one of the strategies used by phytoplankton to explore and exploit resources (Padisák *et al*., 2003). Efficiency in nutrient uptake is less relevant in eutrophic lakes like Lake Hawassa, while light availability is a major force shaping phytoplankton assemblages in eutrophic and hypereutrophic environments (Naselli-Flores *et al.*, 2007). The dominance of **SN** at MZ was most probably linked to the low total irradiance rather than nutrient fluctuations. The environmental fluctuations influence any functional strategist not only through their effect on the availability of sufficient materials to be assembled into new algal biomass but also via their impact on the accessibility of the resources (carbon, light and other nutrients) for use by the algal cells (Reynolds, 1984). The coverage by the macrophyte *Echinochloa* could hence affect phytoplankton growth by reducing the accessibility of resources.

Phytoplankton assemblages are shaped by a local condition as it favors groups of species that share similar adaptive features (Webb *et al.*, 2010). For instance, environmental conditions, including sunlight, high nutrient levels, low turbulence and warm weather, can promote the growth of the nuisance species of blue green algae (WHO, 2011). Despite the higher nutrients and temperature levels, the lowest biomass of **SN** and **M** recorded at TW was most probably due to the presence of continuous water inflow at this site.

P has the highest biomass (14 ± 30 mg L^{-1}) at TW followed by those at OW (0.3275 ± 0.552 mg L^{-1}), RH (0.1722 ± 0.096 mg L^{-1}) and MZ (0.164 ± 0.091 mg L^{-1}) (**Fig. 5**). **D** was noticeable at TW next to **P** due to the adaptation of both FGs to lotic ecosystems. **D** and **P** are tolerant of water column mixing and characterize flowing water systems (Stević *et al.*, 2013). The difference in the biomass of **P** between TW and other sites was statistically significant ($P \leq 0.043$). **P** attained the highest biomass at TW due to its adaptation to lotic systems and high frequency of light fluctuations (Reynolds *et al.*, 1994). This corroborates the habitat description given by Reynolds *et al.* (2002) whereby they emphasized the strongly apparent dependence of species from group **P** upon physical mixing, requiring a continuous or semi-continuous mixed layer of 2–3 m in thickness and adapted to proliferate in light-limited habitat (Reynolds, 1999). *A. granulata* as an R-strategist has good adaptability to high water instability (Wang *et al.*, 2011).

There was significantly higher biomass of **J** at MZ and RH than at TW ($p \leq 0.038$). **J** biomass was low at OW compared to those at MZ and RH although it was still higher than that at TW and attained its highest biomass at RH indicating their tolerance to low light condition. Members of **J** inhabit turbid, nutrient-rich environments (Izaguirre *et al*., 2012), similar to the conditions characteristic of the present study lake, indicating their tolerance to the low light environment. **D** and **N** had significantly higher biomass at RH than at the other sites (TW, OW and MZ) (p = 0.01) depicting the low grazing potential of the dominant zooplankton (rotifers) at this site. On the other hand, the two FGs exhibited very low biomass, of **D** at MZ and **N** at OW, which can be due to increased consumption of these FGs by *Thermocyclops* at MZ and by cladocerans and *Thermocyclops* at OW part. Differences in size structures and feeding preferences of the grazer community are known to affect functional assemblages of algae meaningfully (Colina *et al*., 2015). In addition, *Oreochromis niloticus* at adult stage often inhabits the limnetic region and is known to selectively feed on **N** (e.g. *Cosmarium* species) and **F** (e.g. *Oocystis* species) (Workiyie Worie and Abebe Getahun, 2015).

F exhibited low biomass at all sampling sites compared to the other RFGs. CO_2 limitation is likely to ensue due to the high pH level of the water system, which could be the major cause for the low biomass of **F**. However, significantly higher biomass of **F** was recorded at MZ than at TW (p = 0.038). This RFG discriminated MZ from the other sites as the group was found to be prominent due to the large size and mucilaginous nature of the colonies, which deter grazing by zooplankton like *Thermocyclops* species and reduce sinking velocity (Happey-Wood, 1988) making them competent under calm condition.The biomass of **K** was higher at OW and MZ which could be due to its adaptation to relatively calm water environments as suggested by Reynolds *et al*. (2002).

Downwind drifting of phytoplankton can give a particularly spectacular impression of localized abundance in their biomass. This could not be the case for the higher biomass of **SN** and **M** at MZ during all sampling months as the distribution of all FGs in calm months (April to May) was the same as those observed in windy months, which extend from June to August (Weather Spark.com). Instead, it could cause fluctuations that may selectively affect growth rate by alternatively providing and overriding localized microhabitat offering specifically preferred condition (Reynolds, 1984).

Spatial and temporal variations of RFGs are interlinked and driven by environmental variabilities that have a great impact on phytoplankton ecology. At a large scale, the environmental fluctuations can be determined climatically and at a small scale, by short-lasting weather conditions (Reynolds, 1984). Accordingly, the cloud cover during three sampling months (June, July and August) might have given a special advantage for those FGs that are tolerant to light limitation. In the present study, rainfall patterns seemed to have a predominant regulating impact on phytoplankton dynamics as it can cause changes in water level, nutrient concentrations and light levels. Contrary to the declining trend in biomass of **P** (**Fig. 6A**) increasing trend in algal biomass was observed at all sampling sites from April to August (**Fig. 6B**).

The increasing trend observed in biomass of most FGs (**D**, **SN**, **M**, $\mathbf{L_O}$, **F**, **N**, **K**, **W1** and **W2**) from April to August can be related to the concomitant increase in the levels of nutrients (**Appendix 2F**). This seems to indicate the higher risk of algal bloom occurrence in August. This is consistent with the findings of Tadesse Fetahi and Seyoum Mengistou (2014), who have elucidated the coincidence of the rise in phytoplankton biomass with the major rainy season and the associated nutrient enrichment via runoff from the catchment area. The temporality of phytoplankton FGs is a function of changes in mean temperature, irradiance, hydraulic factors and nutrient availability (Reynolds, 1984). **P** exhibited very high biomass in May (**Fig. 6A**), which was probably associated with the highest level of SRP during this month as diatoms, in general, are known to be opportunistic phytoplankton (Kemp and Villareal, 2018). In contrast, the biomass of **J** showed a unique temporal pattern whereby it alternatively increased and then decreased during consecutive months (**Fig. 6B**). The high monthly variability of **J** can be due to the high edibility and hence susceptibility of this FG to grazing (Kruk and Segura, 2012).

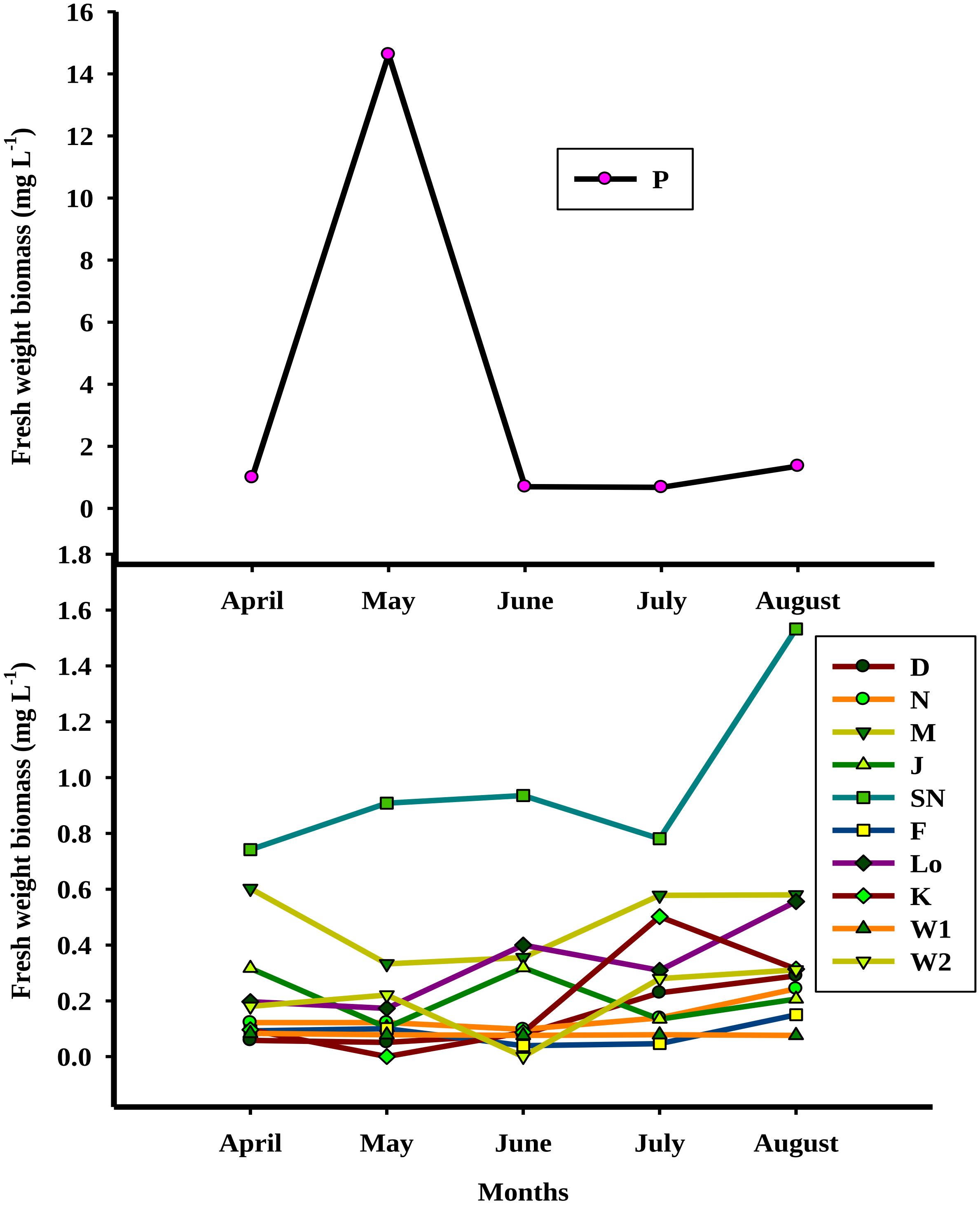


Figure 6. Temporal variations in the fresh weight biomass of RFGs (**A** and **B**).

9.3.2. Spatial distribution and temporal disparities of MBFGs

Group **III,** which included large filamentous phytoplankton possessing aerotopes (**Table 7**), accounted for 14.49% of the total biomass. It was mainly constituted by *Cylindrospermopsis* species. The colonial mucilaginous cyanobacteria and green algae, which come under group **VII,** accounted for 8.145% of total phytoplankton biomass (**Table 7**). This group was dominated by *Merismopedia* species, *Microcystis* species, *Oocystis lacustris* and *Botryococcus braunii*. Group **VI** contributed 69.333% of the total biomass, and included non-flagellated organisms with frustule. Large unicells, colonies and filaments lacking any of the categorical morphological traits (aerotopes, flagella, heterocysts, mucilage and siliceous exoskeletal structures) were all included in Group **IV (Table 7)** and accounted for 4.18% of total algal fresh weight biomass.

Table 7. Morphology-based functional groups of phytoplankton (MBFGs) based on Kruk *et al*. (2010) and Kruk and Segura (2012) in Lake Hawassa, Ethiopia.

MBFGs	Description	Representatives	Fresh weight biomass (mg L^{-1})
I	Small organisms with high S/V ratio	*Chroococcus* species.	1.44
III	Large filaments with aerotopes	*Cylindrospermopsis* species, *Aphanizomenon aphanizomenoides and Komvophoron constrictum*	20.93798
IV	Algae with medium size lacking specialized traits	*Monoraphidium griffithii, Scenedesmus, Pediastrum, Coelastrum and Cosmarium* species	6.0147
V	Unicellular flagellates of medium to large size	*Euglena* species, *Cryptomonas ovata, Trachelomonas aspera and Phacus* species	4.5499
VI	Non flagellated organisms with siliceous exoskeletons	*Aulacoseira granulata, Nitzschia dissipata, Gomphonema, Cymbella* species and *Cyclotella meneghiniana* etc…	99.7899
VII	Large mucillaginous colonies	*Microcystis, Botryococcus and Oocystis* species	11.7225

The representative taxa of this MBFG were *Pediastrum*, *Scenedesmus* and *Staurastrum* species. Group **V** which consists of *Euglena* and *Phacus* species contributed for 3.86% of total biomass of the phytoplankton.

The fresh weight biomass of **III** and **VII** increased consecutively from their levels at TW through those at RH and OW to those at MZ (**Fig. 7**). The possible explanation for this trend may be the difference in levels of environmental parameters among the sites (**Table 3**). The relatively calm condition associated with the buffering effect of *Echinochloa pyramidalis*, might has selectively favored these FGs as they are equipped with efficient suspension mechanisms such as gas vesicle and mucilaginous sheath. Though members of **III** have large size and consequently low growth rate, their high S/V ratio enabled them to be tolerant of light limitation (Naselli-Flores and Barone, 2007). The presence of mucilage, along with lipids and aerotopes in **VII**, provides them a controllable buoyancy mechanism (Kruk *et al.*, 2010). The mucilaginous nature can also help to reduce population loss of the group due to grazing (Reynolds, 2007). The higher biomass of **VII** at MZ where elevated number of the herbivorous zooplankton *Thermocyclops* species prevailed was, therefore, the result of their potential resistance to grazing. Despite having high sensitivity to resource scarcity, their ability to produce toxins and antagonistic chemicals enhances their success (Kruk *el al.*, 2010).

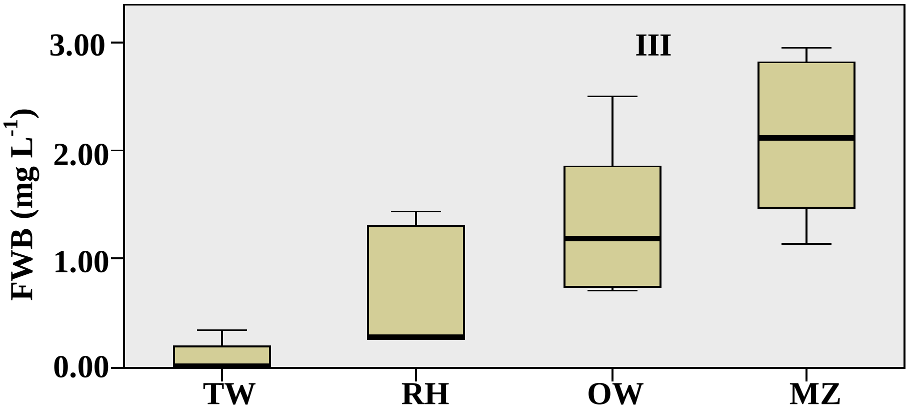
VII can grow extensively under the condition of enhanced resource supply attaining high population biomass and resulting in surface scum (Dow and Swoboda, 2000). Biomasses of **III** and **VII** were significantly higher at MZ than at TW and RH ($P \leq 0.042$). The continuous water flow at TW, which does not favor these groups and the presence of competitors (e.g green algae) at RH may be the causes for the observed differences. O'Farrell *et al.* (2007) reported high physiological plasticity of *Cylindrospermopsis* species in response to alteration in light level. They found a decrease in the number of aerotopes of *Cylindrospermopsis* species 72 h after removing macrophytes from experimental tanks revealing its sensitivity to high light intensity. Therefore, the dominance of **III** at MZ (**Appendix 2G**) is possibly due to its preference to the habitats shaded by *Echinochloa pyramidalis* (**Appendix 3**).

The peak biomass of **IV** observed at RH (**Fig. 7**) might be due to the presence of moderate level of turbidity and the effect of wind-induced mixing that maintains them suspended within the euphotic depth since the species in this group are well adapted to thrive in shallow water (Reynolds *et al.*, 2002). Borics *et al.* (2012) emphasized that in well-mixed waters, chlorococcalean green algae (**IV**) were the most characteristic phytoplankton. The dominance of spined *Scenedesmus* species that can deter predation, at RH and MZ can be the reason for the high biomass of this MBFG at these sites. *Scenedesmus* species are known to undergo spine formation in response to infochemicals released by daphnids (Donk, 1997). However, species from Group **IV** are within the most edible size ranges (Lehman, 1988) and are considered to be high quality food (Sterner and Elser, 2002), and are thus susceptible to high losses due to zooplankton grazing. On the other hand, the low biomass of **IV** at OW is likely to result from the grazing effect of cladocerans, whose abundance was relatively high at OW and are known to have feeding preference for **IV** (Kruk and Segura, 2012).

A declining trend in biomass of **VI** from TW site to the other sites (**Fig. 7**) was observed, which was obviously due to reduction in mixing events. Lack of flagella-dependent motility and possession of siliceous exoskeleton make diatoms have high sinking rates (Kruk *et al.*, 2010). MBFG with appropriate adaptations will be dominant when aquatic habitats get constrained by particular combinations of environmental variables (Padisák and Salmaso, 2007). The significantly greater biomass of **VI** ($P = 0.023$) at TW can be the result of the elevated nutrient levels and the increased mobility at this site, which is unsuitable for most of the other FGs. The presence of resistant siliceous wall potentially improves the survival of diatoms in lotic waters (Reynolds, 2006) as it can provide protection against certain type of grazers and infections (Hamm *et al.*, 2003). Generally, very low fresh weight biomasses were observed at TW for all MBFGs except **VI** (**Appendix 2G**).

V was conspicuous at OW and RH with its biomass being relatively higher at RH (**Fig. 7**) though the difference was not statistically significant ($P = 0.368$). Their motility due to the possession of flagella enables them to acquire nutrients effectively and attain high population biomass, especially when the nutrient supply is insufficient. The fresh weight biomass of **V** was significantly greater at RH than at TW and MZ ($P \leq 0.02$). The influent from Referral Hospital of Hawassa University was rich in organic constituents favoring the dominance of **V,** which is typical of organic rich environments (Greeson, 1982). The routinely released effluent of the hospital, which is sometimes released without any treatment into the lake via the RH site had high biological oxygen demand (37.25 mg L^{-1}), and chemical oxygen demand (187 mg L^{-1}) after treatment with a stabilization pond and very high levels of biological oxygen demand (632 mg L^{-1}), and chemical oxygen demand (1388.75 mg L^{-1}) before treatment (Hunachew Beyene and Getachew Redaie, 2011). Dominance of *Lepocinclis* species (**V**) in Lake Chamo due to the input of organic materials from nearby animal farms via Sile River was reported by Girma Tilahun (2006). Organic enrichment from farm animals or plant decay is known to result in blooms of euglenophytes. Compared to the other FGs; **V** had low biomass due to their large size and generally low population growth rate (Kruk *et al*., 2010).

In general, morphological variability of algae is frequently associated with environmental variability. The large and filamentous phytoplankton taxa with linear shape like the centric diatom *Aulacoseria granulata*, and pennate diatom *Nitzschia* species were prominent under conditions of very low stability, while the small spiral shaped filamentous taxa (e.g. *Cylindrospermopsis catemaco*) and the flat mucilaginous colonies were dominant in relatively stable environments. This finding supports the fact that size and form selections are perhaps the strongest driving forces shaping phytoplankton assemblages under variable environmental conditions (Morabito *et al*., 2007).



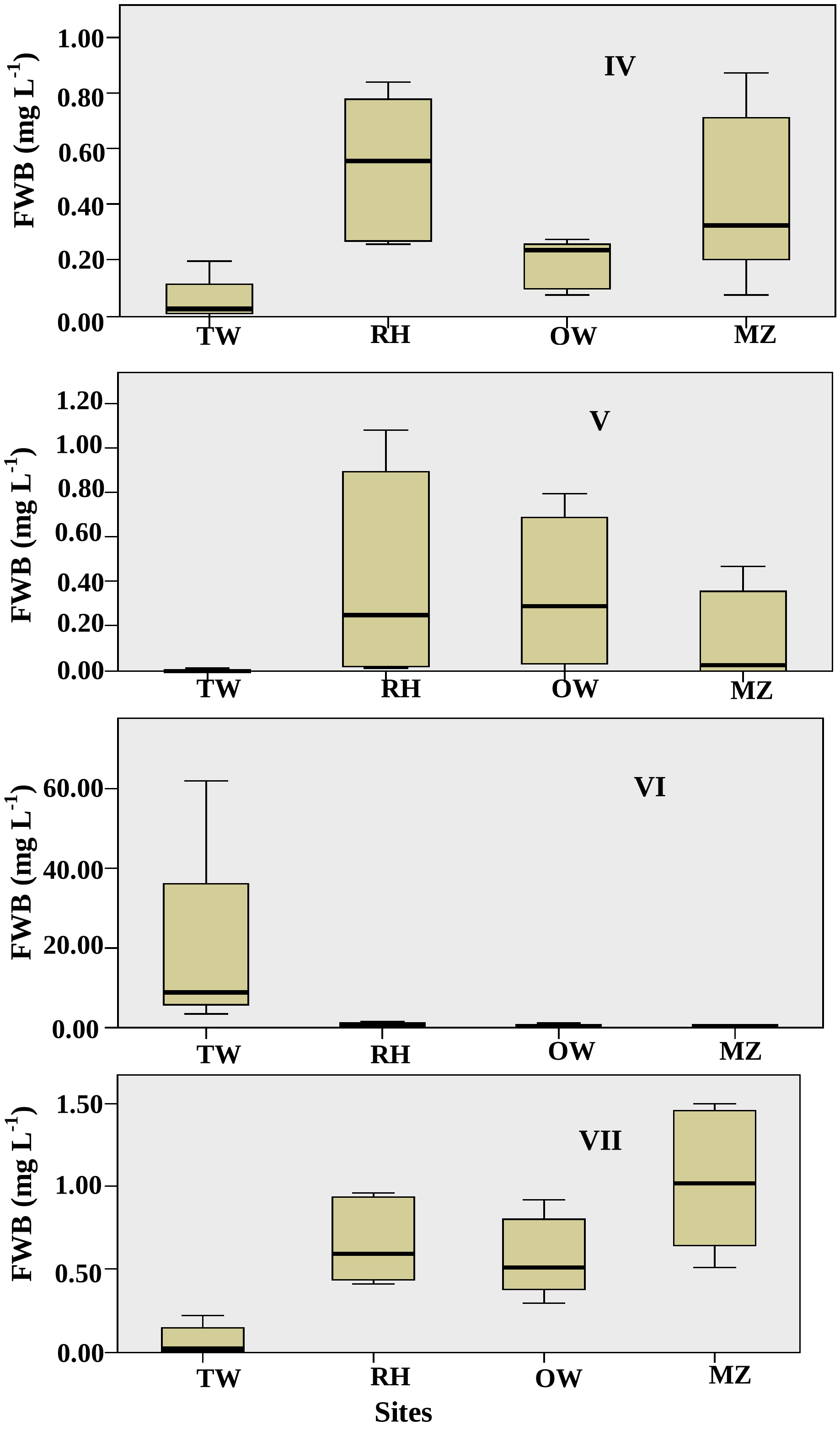


Figure 7. Spatial variations in fresh weight biomass (FWB) of MBFGs in Lake Hawassa.

Except **VI**, all MBFGs had similar level of fresh weight biomass during all sampling months (**Fig. 8**), with a slight increase in August. The determining factor for this trend seems to be the nutrient dynamics. The maximum fresh weight biomass of **VI** was recorded in May which was probably caused by the resuspension of planktonic cells from the sediment during mixing event as there was superficial stratification in April and low extent of mixing below the euphotic depth (**Appendix 2B**). The nutrient pulse in May as a result of the mixing event might also favor **VI** to attain elevated biomass.

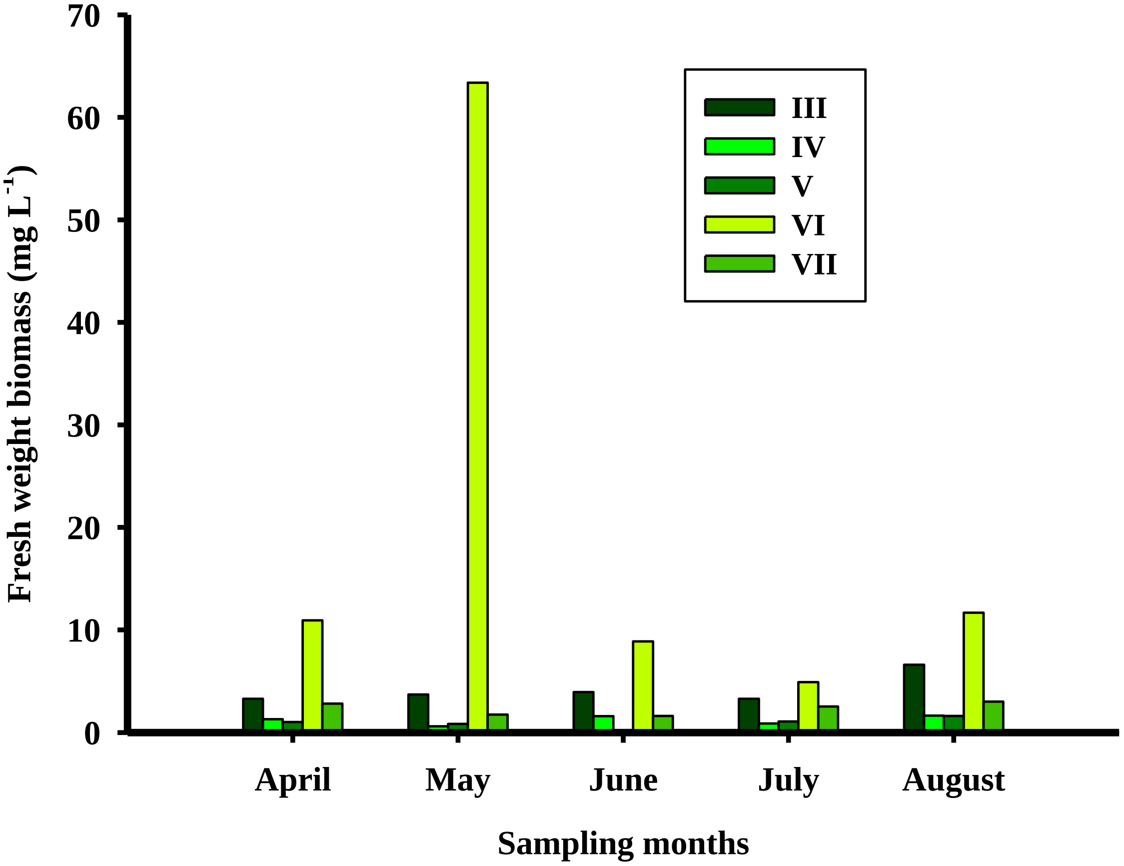


Figure 8. Monthly variations in the fresh weight biomass (mg L^{-1}) of MBFGs in Lake Hawassa.

9.3.3. Relationship of the RFGs and MBFGs with environmental conditions

The first two axes of the RDA ordination collectively explained 90.3% of the variances in the RFGs due to physico-chemical parameters and zooplankton abundance (axis 1: 77%, P = 0.002 and axis 2: 13.3%, P = 0.002) (**Fig. 9A**). Axis 1 which showed the strongest relationship between species and environmental variables was strongly and negatively correlated with DO, EC, Z_{SD} but, weakly and negatively related to total cyclopoids and it was positively and strongly correlated with turbidity and TP (**Table 8)**. Total cyclopoids were strongly and negatively correlated with axis 2 while total rotifers were strongly and positively correlated with axis 2. Alternative food sources such as bacterioplankton in Lake Hawassa, particularly at MZ, which release phytoplankton from grazing may have resulted in the positive interaction of zooplankton with the existing algal assemblages.

96.7% of the variations in MBFGs due to environmental parameters were explained by the first two ordination axes (p = 0.002). Axis 1 explained most of the variances (84%), while axis 2 explained only 12.7% of the gradient of environmental parameters in which the MBFGs could occur (**Fig. 9B**).

The RFGs (**SN**, **K**, **Lo**, **M**, **F**, **N** and **J**) and the MBFGs (**III**, **V**, **VII** and **IV**) were correlated with EC, pH, DO and Z_{SD} (P = 0.002) revealing that these parameters have the main driving impact on the phytoplankton FGs in Lake Hawassa. On the other hand, **P** and **D** of the RFGs and **VI** of the MBFGs were well explained by TP, TSS and turbidity (P = 0.004) indicating that the levels of these parameters have regulating effect on the dynamics of diatoms in the lake.

The observed associations were well matched with the principal environmental changes. The high nutrient concentrations seem to have favored the dominance of S-strategist, K-selected FGs (**SN, III**), R-strategist, r-selected (**D**), and R-strategists, K-selected (**IV, J, P, V, VI**). The Secchi depth was often low, indicating high water turbidity, the development of which ‘filters’ in favor of light deficiency-tolerant species of **VI, P, J and IV** groups. The low transparency became a limiting factor as a consequence of light attenuation through high turbidity. The dominance of algal species with morphological types such as needle-shaped (e.g *Nitzschia* species), long chain-forming and cylindrical taxa (e.g *Aulacoseira granulata*) and filamentous green algae (e.g *Scenedesmus* species), which are all good at light-harvesting ability corroborates the existence of light-deficient condition (Naselli-Flores and Barone, 2007). Their elongated shape is an adaptation to increase light harvesting potential by maximizing exposition of chloroplast to light while maintaining the shortest diameter.

The ratio of mixing depth (Z_{mix} determined from temperature depth profile) to euphotic depth (Z_{eu}/Z_{mix}) may be a limiting factor for phytoplankton production (Talling, 1971). Wood *et al.* (1979) suggested a critical value of 4 to 5, beyond which light limitation is expected to prevail. The Zeu in the current study ranged from 0.15 to 2.22 and Zmix ranged from 1.7 to 18.4 m giving a ratio of >4 confirming the existence of light limitation. Light attenuation by phytoplankton, which is called self-shading can also significantly affect the underwater light climate (Elizabeth Kebede and Amha Belay, 1994).

Nitrogen is potentially the limiting factor as indicated by the low TDIN: SRP ratio i.e. 3.48:1 on mg L^{-1} basis (Assuming very level of nitrite) in Lake Hawassa. Algae are generally known to use N and P in fairly constant proportions, in an atomic ratio of 16 to 1 and mass ratio of 7.5 to 1 (Lee and Jones-Lee, 1998). Since the algae, drawing N and P out of the water at a ratio of approximately 7.5:1, would likely run out of nitrogen before phosphorus during the rainy season in Lake Hawassa as the ratio of concentrations was substantially lower than 7.5 to 1. Nitrogen limitation had also been reported from lakes Chamo and Ziway (Girma Tilahun, 2006) and Debre Zeit Crater lakes (Bishotu and Arenguade) (Afeworki Ghebrai, 1989). Nitrogen-limitation of phytoplankton happens to be very common in tropical lakes (Lewis *et al.*, 1996).

The limiting nutrient can change over an annual cycle depending on the rates of nutrient supply, mineralization, algal growth, and nutrient concentrations (Lee and Jones-Lee, 1998). This means a factor, which limits peak algal biomass during one period of the year, may not limit peak biomass during another period of the year. The limiting nutrient during the season not covered by the present study period is remains to be determined by future study. The dominance of diazotrophic FGs (**SN** and **III**) can be predictable from conditions of nitrogen-limitation as low N:P ratio known to favor the numerousness of nitrogen-fixers (Jensen *et al.*, 1994).

The actual concentrations of available nitrogen (172.8-294.6 µg L^{-1}) and phosphorus (34.28-151.1 µg L^{-1}) were, however, well above the limiting levels, i.e 15 µg L^{-1} for nitrogen and 2 in µg L^{-1} for phosphorus (Lee and Jones-Lee, 1998).

The RDA clustered the sampling sites based on the defining environmental variables. Axis 1 distinguished MZ and OW from TW and RH while Axis 2 separated RH from TW. MZ and OW were characterized by **SN**, **M**, **F** and **N** (RFGs) and **III** and **VII** (MBFGs) whose prominent occurrence was associated with high Z_{SD}, total cyclopoids, DO, and EC. On the other hand, TW was characterized by high level of TSS, turbidity and TP , which favor the dominance of **P** (RFGs) and **VI** (MBFGs) indicating the tolerance of these FGs to light-limitation. **D** and **J** (FGs), **IV** and **V** (MBFGs) also characterized RH, which also had moderately high turbidity.

In general, RDA showed a clear separation of the four sampling sites based on the level of human impact on these sites. Because of their location in areas where human activities are most frequent, the more impacted sites (TW and RH) became turbid systems. The continuous current flow at TW and wind-induced mixing at RH may have acted as factors sustaining the turbid condition.

RDA indicated that the variances that can be explained by environmental conditions are very high for both the RFGs and MBFGs and the FGs from both approaches were explained comparably by the two canonical axes (**Fig. 9**). Therefore, it is possible to conclude that RFGs and MBFGs are well predictable from the variations in environmental variables. Both approaches of phytoplankton classification have comparable discriminatory power as related to environmental variables. These results are in agreement with the findings of Kruk and Segura (2012) who demonstrated the existence of strong connection among morphologies and ecological preferences of phytoplankton groups. Morphological characteristics are correlated well with functional properties, such as growth rate and sinking rate, and also with the population size and biomass attained in the field (Kruk *et al*., 2010). For instance, groups with larger volume (V) and lower surface area (S) coincided with lower maximum population growth rate and lower numerical abundance. The low biomass of group **V** can be related to this fact.

The RFGs **SN** and **M** and the MBFGs **VII** and **III** were found to have increasing potential with an increase in total rotifers and total cyclopoids. The increase in the abundance of zooplankton can favor the dominance of phytoplankton RFGs constituted by filamentous and colonial forms of algae via their grazing pressure on their competitors (e.g bacterioplankton). This is because bacteria may act at least temporarily as sinks rather than as sources of nutrients (Ducklow *et al*., 1986) thereby reducing the availability of the important resources for use by phytoplankton. But, the correlations of rotifers and total cyclopoids with the phytoplankton FGs were not significant

(P = 0.354) which may suggest the low importance of these zooplankton in structuring algal assemblages in the lake.

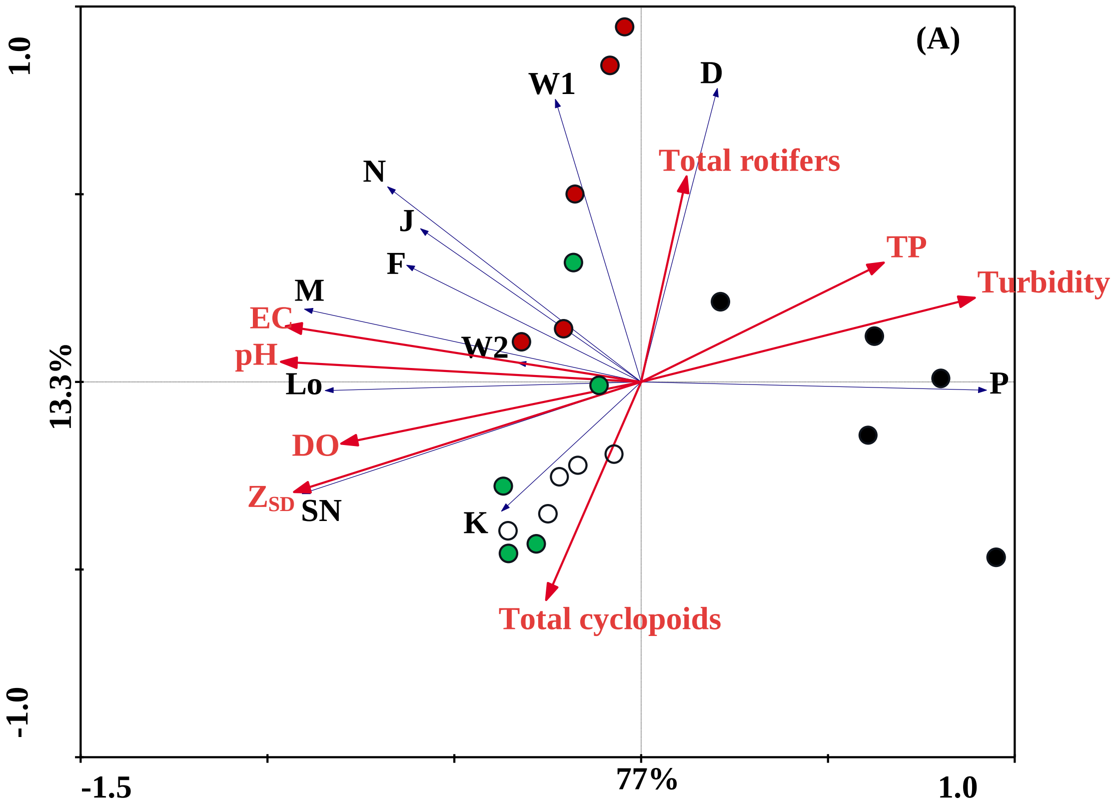
Reduction in grazing pressure by herbivorous fish, particularly *O. niloticus* may be the other factor for the elevated biomass of **VII** as the study was conducted during the rainy season, which is the peak spawning season of Nile tilapia.

Botryococcus and *Microcystis* (**Appendix 4**) were reported as the important food items of Nile tilapia in Lake Hawassa, during the dry season (Getachew Teferra and Fernando, 1989). During the wet season, however, *O. niloticus* is known to move to the macrophyte coverage site for the purpose of reproduction, and feeds mainly on macrophytes (Agumassie Tesfahun and Mathewos Temesgen, 2018). In addition, during the months of intense breeding, the male tilapia engaged in building and guarding breeding nests at bottom habitats, while the female tilapia is busy with mouthbrooding activity in its breeding nests, with both sexes consequently spending much of their time in breeding activities than feeding (Zenebe Tadesse, 1997).

The variations in nutrient levels and zooplankton abundance in relation to rainfall patterns seem to be the most important factors affecting the functional dynamics of phytoplankton from both spatial and temporal perspectives in tropical lakes. Rainfall increases plankton production because of the resulting increased nutrients load by runoff (Elizabeth Kebede *et al*., 1994). However, the dominance of the less efficient grazer taxa and the absence of larger herbivorous zooplankton species such as *Daphnia* and the smaller number of *Diaphanosoma* species in the lake relieve the phytoplankton assemblages from grazing. In addition, the predominant functional assemblages (**SN**, **P**, **M**, **L_O**, **III**, **IV**, **VI** and **VII**) in the lake, which are constituted by colonial and filamentous forms are known to be resistant to grazing revealing the importance of a bottom up control (nutrients, light and hydrologic factors) than the top down effect of zooplankton (Tadesse Fetahi and Seyoum Mengistou, 2014) in shaping the FGs. Kruk *et al*. (2016) also reported that zooplankton grazing has minor importance in determining the phytoplankton assemblages in tropical ecosystems in contrast to that in colder regions.

Table 8. The correlations of physico-chemical parameters, total rotifers and total cyclopoids with the three ordination axes constructed based on RFGs and MBFGs.

	RFGs			**MBFGs**		
Parameters	Axis1	Axis 2	Axis 3	Axis 1	Axis 2	Axis 3
DO	-0.7742	-0.1228	0.1283	-0.7554	0.0288	-0.123
EC	-0.9166	0.136	0.121	-0.877	0.2429	0.0236
Turbidity	0.8615	0.1846	-0.0423	0.8701	0.0208	0.0977
Z_{SD}	-0.8965	-0.2503	-0.0219	-0.9168	-0.1145	-0.0197
TP	0.6254	0.2866	0.2794	0.6353	0.3483	-0.1057
pH	-0.9301	0.0437	0.1453	-0.9013	0.2134	0.0546
Total rotifers	0.1219	0.5348	-0.3414	0.1963	0.095	0.499
Total cyclopoids	-0.2505	-0.5593	0.3308	-0.3223	-0.116	-0.5963
Sum of canonica eigen values	0.792			0.835		



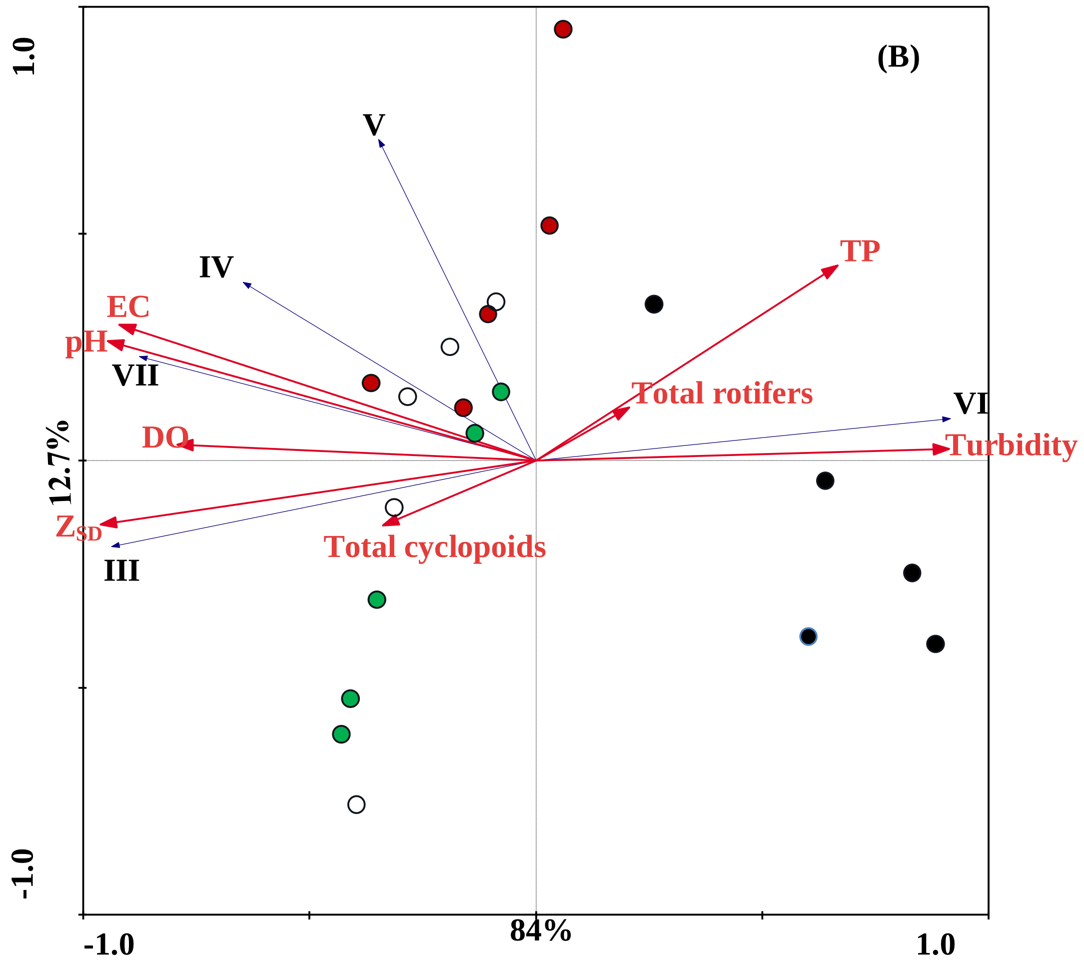


Figure 9. RDA triplot of the RFGs (**A**) and MBFGs (**B**) of phytoplankton (the response variables/ species data) in relation to the major environmental variables (explanatory variables/independent variables) at the four sampling sites: MZ = Closed green circle, OW= Open circle, RH = Closed red circle and TW = Closed black circle.

Both RFGs and MBFGs approaches are helpful in modeling and making inference about the functioning of different ecosystems containing different taxonomic compositions as they are useful for predicting and managing nuisance algal blooms and represent verifiable quantitative methods of describing community structure and changes (Kruk and Segura, 2012). The approaches were found to be efficient tools to explore the effects of environmental variables, including hydrological, physico-chemical, and food web interactions on phytoplankton community structure from both spatial and temporal perspectives. This finding is consistent with the results of many previous studies including those of Mesfin Gebrehiwot *et al.* (2017), Kruk *et al.* (2010, 2011, 2012, 2016), Reynolds *et al.* (2002), Padisák *et al.* (2009) and many others.

9.4. Water quality assessment based on TSI, functional diversity and levels of physico-chemical parameters

The trophic status of Lake Hawassa was hypereutrophic (69.04) based on Chlorophyll-a and TP levels with no significant variation among sites (P = 0.08). The lake was also classified as hypereutrophic based on the composition (Reynolds, 1984) of the dominant RFGs. The TSI values based on both Chlorophyll-a and TP were very high and comparable revealing that the lake was highly productive both chemically (in terms of nutrients) and biologically (in terms of algal biomass).

Significant difference in functional diversity was observed among the four sampling sites ($P<0.05$), with the diversity values of MBFGs ranging from 0.0703 at TW to 1.594 at RH. The OW site (1.404) and MZ site (1.24) had comparable diversity values. The diversity of RFGs varied from 0.2 to 2.1. Similar to MBFGs, the lowest diversity level was recorded at TW whose phytoplankton assemblage was completely dominated by **P** (*A. granulata*) whereas the highest value was recorded for RH, which was associated with the prominent occurrence of the RFG **J** and MBFG **IV**. Slightly higher value was documented for OW site (1.77) than for MZ site (1.681). There was a consistently increasing trend in the biomass of the RFGs measured as fresh weight biomass, from RH (3.276 mg L^{-1}) through OW (3.48 mg L^{-1}) and MZ (4.95 mg L^{-1}) to TW (14.8 (mg L^{-1}), while the levels of functional diversity followed the reverse trend. These results are in agreement with the findings of Vörös *et al.* (2013) who reported the presence of an inverse relationship between functional diversity and biomass. Total phytoplankton biomass, as a measure of trophic state, has already been shown to significantly influence phytoplankton diversity (Jacobsen and Simonsen, 1993). But, high phytoplankton biomass can also be related to the occurrence of the different functional strategists in large numbers at the same time.

Considering the composition of MBFGs, **V** which comprises *Euglena* species was the conspicuous functional group and had higher biomass at RH than at other sites ($p \leq 0.02$)

revealing the presence of organic pollution. Euglenoids are generally found in environments where there is abundant decaying organic material (Bellinger and Sigee, 2010) and are indicative of such waters rich in organic pollutants as those found below domestic sewage outfalls (Greeson, 1982). The release of organic-rich influents from the Referral Hospital of Hawassa University is the major contributor to the organic enrichment of the water at this site (Hunachew Beyene and Getachew Redaie, 2011). Based on functional diversity index, RH can be regarded as the least impacted site, while the water at TW was the most degraded. The high functional diversity at RH does not, however, seem to indicate less impact; it could rather be the result of constraints that are less species-selective. The remaining sites (MZ and OW) seemed to have an intermediate level of disturbance.

Cool water is generally more palatable than warm water as high water temperature enhances the growth of microorganisms and may increase problems related to taste, odor, color and corrosion (WHO, 2011). The water temperature at OW was relatively lower than the remaining sites (**Table 3**). On the other hand, the highest water temperature, which is slightly greater than the standard temperature (25 ^{o}C), was recorded at TW (**Table 3**). But, the temperature level at all sampling sites generally seemed to be tolerable by most aquatic organisms as the optimum temperature range for normal growth of plankton and fish is 22-31 ^{o}C (Korai *et al*., 2008).

For drinking purpose, the turbidity of water systems is recommended to be no more than 1 NTU (WHO, 2011; Health Canada, 2017). For recreational purpose, the turbidity level should not be more than 50 NTU. Extremely high turbidity can increase the potential health hazard in relation to infection transmitted by microorganisms and injuries resulting from impaired visibility in turbid waters. In addition, particles that cause turbidity can harbor pathogens and other toxicants (WHO, 2011). The turbidity level was high at all sampling sites and greatly exceeded the permissible limit. But, there was a significant difference in the level of water quality deterioration among sites. Based on turbidity, TW was the most deteriorated compared to the remaining sites ($P \leq 0.037$), followed by RH, while OW and MZ had relatively low turbidity.

The palatability of water with a total dissolved solids (TDS) level of less than about 600 mg L^{-1} (WHO, 2011) is generally considered to be good; drinking-water becomes significantly and increasingly unpalatable at TDS level greater than about 1000 mg L^{-1} (WHO, 2011). The average level of TDS (410.7- 504.2 mg L^{-1}) was lower than the upper limit of palatability.

The pH of the water, which ranged from 7.6 to 9.13, was within the normal range (6.5-9) for freshwater systems (Schmirz, 1996) and recreational purpose (5-9) (CCME, 1999) at all sampling sites.

The mean level of nitrate at all sampling sites (**Table 3**) were much lower than the maximum permissible limit for aquatic life (11000 µg L^{-1}; EPA, 2001) and for drinking purpose (10000 µg L^{-1}; Health Canada, 2017). The nitrate concentration measured at all sampling sites (**Table 3**) was tolerable by fish and other aquatic organisms and satisfies surface water quality standards (< 5 mg L^{-1}) (Chattopadhyay and Banerjee, 2007). According to WHO (2011), the level of ammonia at alkaline pH for odor and taste threshold is 1500 and 35000 µg L^{-1}, respectively. But, it does not have any health based relevance at this level. The level of ammonia in Lake Hawassa ranged from 141 to 275µg L^{-1}, which was well below the threshold level for drinking water. But, according to EPA (2001) when the level of ammonia in water is above 100 µg L^{-1}, it could indicate the presence of sewage pollution and the consequent possible presence of pathogenic micro-organisms. The levels of ammonia were also higher than the upper limit recommended by Levit (2010; 0.02 mg L^{-1}) and EPA (2001; 0.02 mg L^{-1}) for normal growth of fish. DO ranged from 5.33 to 6.6 mg L^{-1} at the three sampling sites and exceeded the minimum recommended level (5 mg L^{-1}) (USEPA, 2008), which is good for fishes and plankton. But, at TW where there were high water flow and turbidity, the DO level was much lower than this optimum indicating intense anthropogenic impact.

The observed concentration of SRP (**Table 3**) surpassed the upper permissible limit by Chapman (1996; 5–20 µg L^{-1}), Olajire and Imeokparia (2001; 10^{-3}µg L^{-1}), and Yajurvedi (2008; 0.01–0.03 µg L^{-1}) to be used for drinking purpose. In general, based on both the major biological and physico-chemical parameters, TW can be regarded as the most pretentious site followed by RH, both having very low quality water to be used for drinking and recreational purposes as well as for supporting aquatic life. However, the remaining two sites (OW and MZ) seem to have a relatively low level of deterioration though the levels of their physico-chemical and biological parameters were not good enough to warrant all intended uses.

9.5. Species composition of zooplankton and spatio-temporal variability in their abundance

22 species of zooplankton have been identified from water samples of all sampling months (**Table 9**). Rotifers were the most important both in species richness and in abundance (**Appendix 2H**). Rotifers were responsible for 56.5% of total zooplankton abundance with *Brachionus calciflorus* and *B. caudatus* accounting for the large proportion of total zooplankton abundance (**Appendix 2H)**. *Brachionus* species accounted for nearly half of total rotifer density in Lake Hawassa reaching a total abundance of 13601 ind m^{-3}, which is comparable with the abundance value that was reported previously (15000 ind m^{-3}) by Seyoum Mengistou (1989). The dominance of *Brachionus* species were also reported from Debre Zeit Crater lakes (Bishotu and Arenguade) (Afeworki Ghebrai, 1989), the rift valley Lake Tinishu Abaya (Yirga Enawgaw and Brook Lemma, 2018**)** and Lake Kuriftu (Girum Tamire, 2006).

Table 9. List of zooplankton species identified in samples from Lake Hawassa, Ethiopia.

Copepoda	Rotifera continued
Mesocyclops aequatorialis Kiefer	*B. f. spinosus*
Microcyclops varicans (Sars)	*B.caudatus* Barrois and Daday
Thermocyclops consimilis Kiefer	*B. diversicornis* Daday
T. species	*B. quadridentatus* Hermann
Cladocera	*Filinia terminalis* Plate
Diaphanosoma brachyurum (Liévin)	*F. pejleri* Hutchinson
Diaphanosoma excisum Sars	*Hexarthra oxuris* Zernov
Moina micrura Kurz	*Keratella tropica* Apstein
Rotifera	*Lecane lunaris* Ehrenberg
Asplanchna species	*Lecane luna* Müller
Brachionus angularis *Gosse*	*Platyias quadricornis* (Ehrenberg)
B. calciflorus f.amphiceros	*Trichocerca ruttneri* Donner

According to Taylor and Zinabu Gebre-Mariam (1989), rotifers are prey for cyclopoid copepods in Lake Hawassa. So, the low abundance of cyclopoid copepods in recent time might have favored the dominance of rotifers due to a reduction in competition and predation pressure of the copepods (Tadesse Fetahi, 2010). The tolerance of rotifers as smaller zooplankton to the high biomass of blue green algae (Bouvy *et al.*, 2000) may have also positively influenced their dominance over the large sized-crustacean in Lake Hawassa where cyanobacteria were the dominant phytoplankton. Furthermore, life strategies of rotifers including their less dependence on phytoplankton, opportunistic feeding behavior and rapid reproduction rate would allow them to succeed in eutrophic lakes as Lake Hawassa (Yeshiemebet Major, 2016). Tamiru Gebre (2006) also reported the dominance of rotifers when the density of cyanobacteria was highest revealing the presence of positive interaction between them. Rotifers dominance over crustaceans in the present study is in agreement with previous reports for the same lake by Tadesse Fetahi (2010) and Tadesse Fetahi *et al*. (2014). The dominance of rotifers was not unexpected, as rotifers have been reported as the numerically most important zooplankton group from a number of other lakes in Ethiopia (e.g. Adamneh Dagne *et al*., 2008; Yeshiemebet Major, 2016).

The crustacean zooplankton community of Lake Hawassa was dominated by a few species, a finding which is consistent with the results of previous studies made by Seyoum Mengistou and Fernando (1991), Tadesse Fetahi (2010), and Tadesse Fetahi and Seyoum Mengistou (2014). Adamneh Dagne *et al*. (2008), and Yirga Enawgaw and Brook Lemma (2018) have also reported a low number of copepod species from other rift valley lakes such as Lake Ziway and Lake Tinishu Abaya, respectively. However, copepods were the second zooplankton group in terms of species richness and abundance.

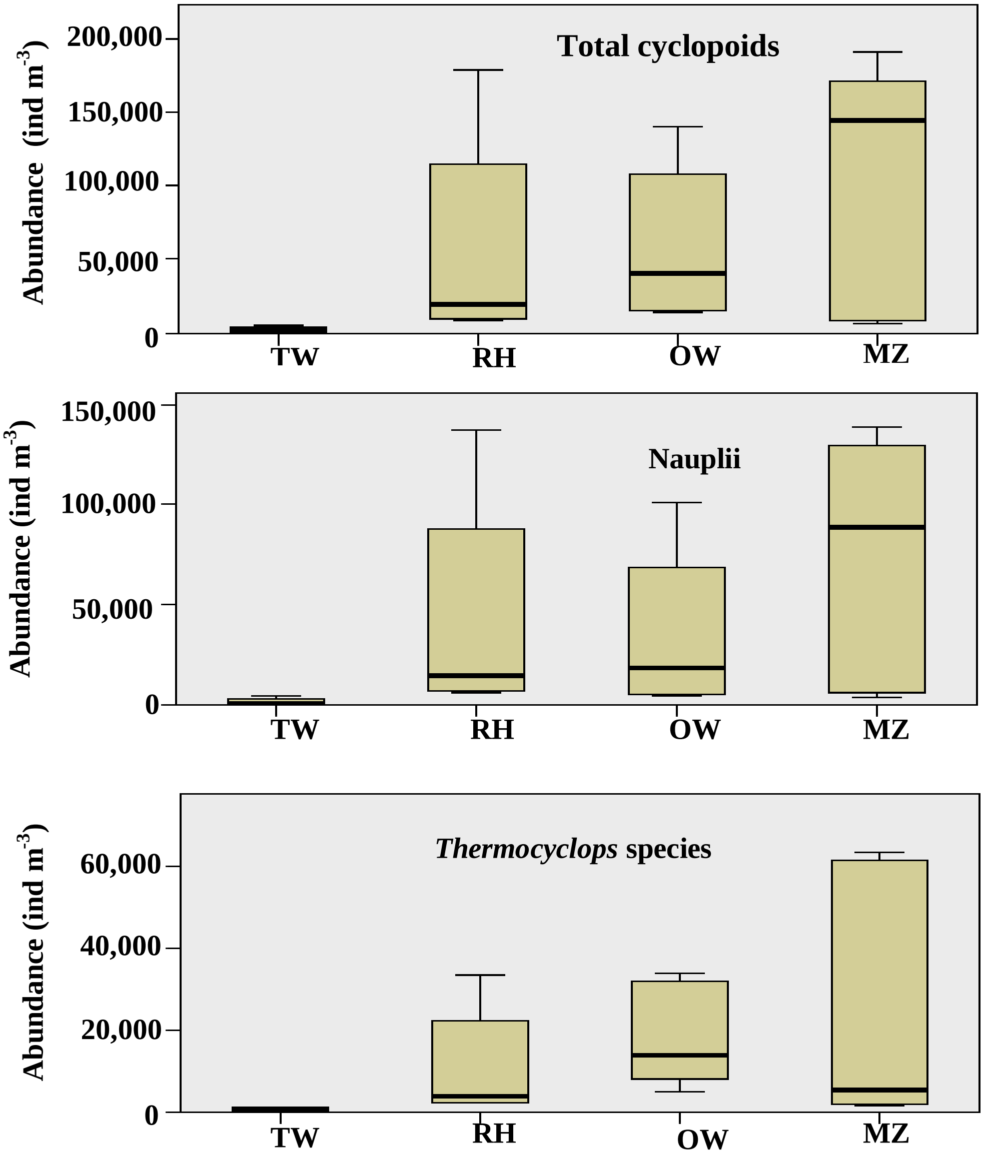
The cyclopoid copepods *Thermocyclops consimilis* and *Mesocyclops aequatorialis* were the most common species (**Appendix 2H**) that made a considerable contribution to the total abundance of zooplankton. The density of cyclopoid copepods observed in this study (53143 ± 15008 ind m^{-3}) was comparable with that reported previously (58000 ± 9200 ind m^{-3}) by Tadesse Fetahi (2010). Cyclopoid copepods in total accounted for 42.57% of the total zooplankton abundance, which was constituted largely by *Thermocyclops consimilis* (11.33%). *Thermocyclops* species is generally regarded to be omnivorous with a preference for phytoplankton and eutrophic waters (Duchovnay *et al*., 1992). In addition, *Thermocyclops* is known to feed on bacteria, cladocerans and chironomids (De-Carvalho, 1984). In this study, the high number of *Thermocyclops* coincided with the high concentration of Chlorophyll-a and algal biomass as biovolume revealing its affinity for herbivorous food. The increase in phytoplankton biomass with the increase in abundance of *Thermocyclops* could be related to the omnivorous feeding habit of the species that would reduce its grazing impact on phytoplankton biomass especially when alternative food sources are available adequately. In addition, the positive role of *Thermocyclops* in supporting phytoplankton growth via its role in nutrients regeneration may have outweighing importance in Lake Hawassa. Consequently, the zooplankton may not be able to buffer the increase in phytoplankton density completely as a result of nutrient enrichment (Vanni, 1987). In comparison, Seyoum Mengistou (1989) and Tadesse and Seyoum (2014) reported the high density of the inefficient grazer zooplankton from the same lake (Lake Hawassa). The dominance of *Thermocyclops* was also reported from: Lake Kuriftu (Girum Tamire, 2006), the two highland Ethiopian lakes such as Lake Hayq (Tadesse Fetahi, 2010) and Lake Wonchi (Fasil Degefu *et al*., 2014). *Thermocyclops* species is known to occur commonly in many tropical African lakes (Serruya and Pollingher, 1983) and that is probably due to their wide range of feeding habits (Girum Tamire, 2006). Nauplii of cyclopoid copepods accounted for the largest part (29.55%) of total cyclopoids abundance.

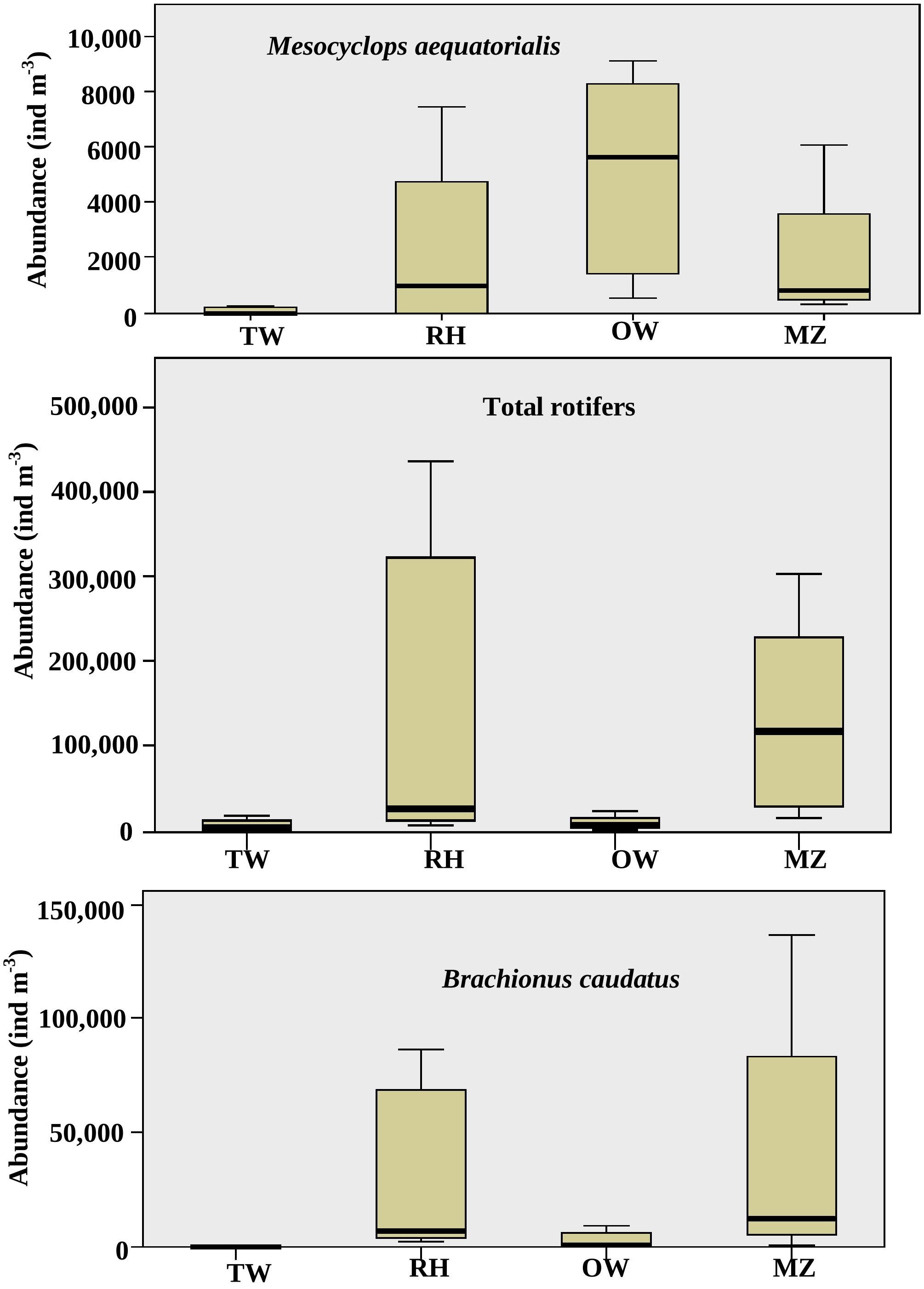
In contrast to the previous report by Seyoum Mengistou and Fernando (1991), the abundance of copepods was found to be low. This can be due to increased grazing pressure by zooplanktivorous fish like *Clarias gariepinus,* which preferably feed on zooplankton in their adult stage (Yosef Tekle-Giorgis *et al*., 2016).

But, cladocerans were the rarest zooplankton taxa in their abundance contributing only 0.93% of the total zooplankton abundance. The present mean abundance of cladocerans (1170 ind m^{-3}) in Lake Hawassa is extremely low compared to those reported previously in the studies made by Seyoum Mengistou and Fernando (1991, 15000-25000 ind m^{-3}) and Tadesse Fetahi (2010, 2600 ind m^{-3}) in the same lake. Low abundance of cladocerans has also been reported from Lake Ziway by Adamneh Dagne *et al*. (2008).

The dominance of colonial and filamentous cyanobacteria together with the high turbidity in Lake Hawassa is likely to be the major factor for the low abundance of cladocerans in the lake. It is well known that blue-green algae have a negative influence on filter feeders by affecting ingestion rates and energy balance of large and small cladocerans (Porter and McDonough, 1984). Suspended clay particles and toxic substances released by cyanobacteria can reduce filtration rates of *Daphnia* by 50% or more (Gliwicz and Lampert, 1990). Kassahun Wodajo and Amha Belay (1984) have also reported that low abundance of cladocerans in Lake Abijata could be due to the high biomass of cyanophytes. To sum up, the species composition of zooplankton was typical of nutrient-rich systems (since it is dominated by rotifers, which are the smaller sized zooplankton groups) as eutrophic environments are known to support higher biomass of smaller individuals than more oligotrophic ones (Esteves and Sendacz, 1988).

There was spatial disparity in abundance of the zooplankton among sites (**Fig. 10**).




Mesocyclops aequatorialis
Abundance (ind m-3)
10,000
8000
6000
4000
2000
0
TW
RH
OW
MZ
Total rotifers
Abundance (ind m-3)
500,000
400,000
300,000
200,000
100,000
0
TW
RH
OW
MZ
Brachionus caudatus
Abundance (ind m-3)
150,000
100,000
50,000
0
TW
RH
OW
MZ

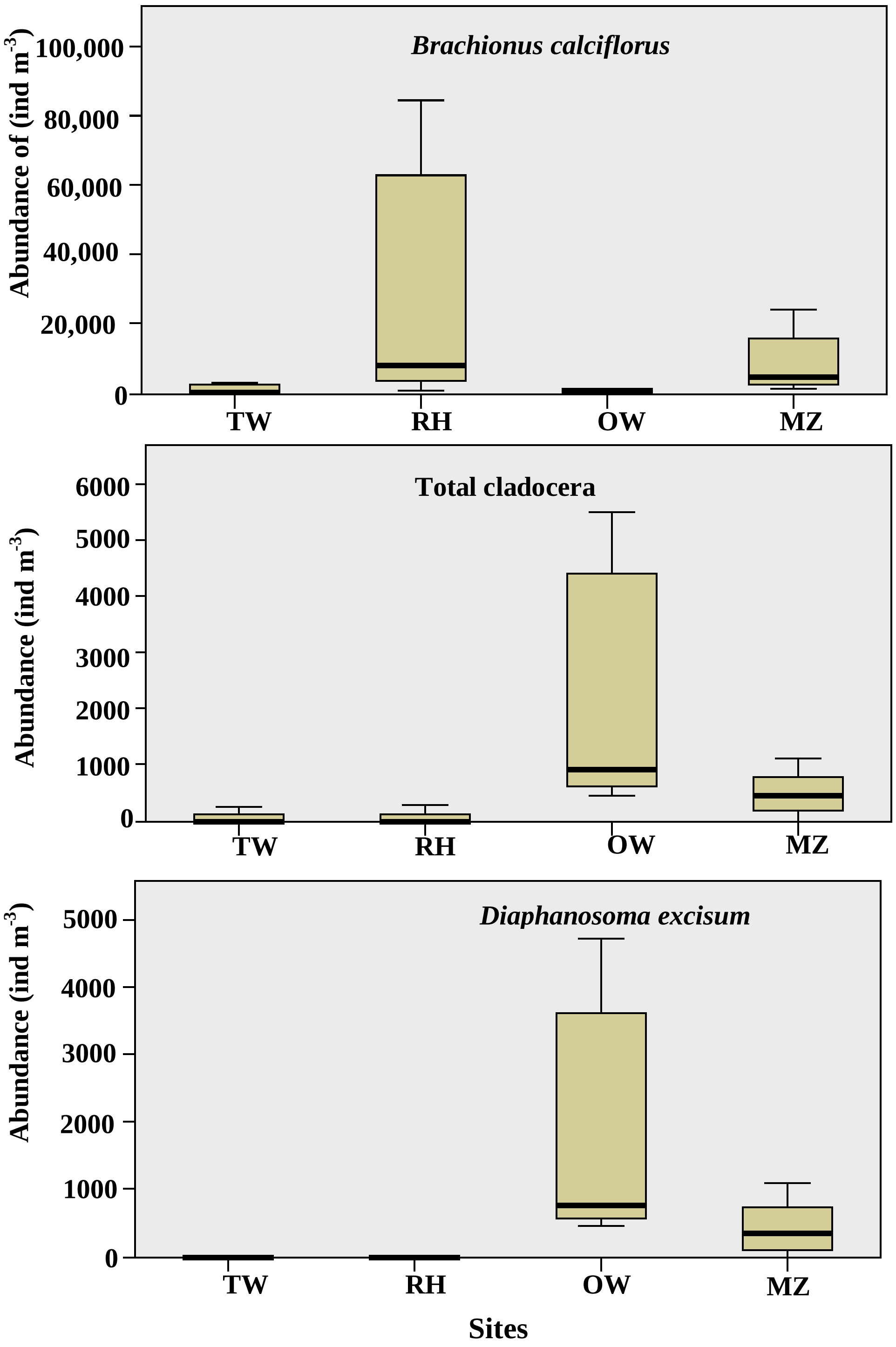


Figure 10. Spatial variation in the abundance of taxonomic groups and major species of zooplankton in Lake Hawassa (ind = individual).

There was a statistically significant difference in the abundance of total cyclopoids between TW and OW (P = 0.045) and TW and MZ (P = 0.023). *Thermocyclops* (26413 ± 40180 ind m^{-3}) and younger stage zooplankton cyclopoid nauplii (72128 ± 78211 ind m^{-3}) reached their highest abundance at MZ, which may be related to reduced carnivory as the macrophyte can provide refuge for them. In addition, juveniles of *Clarias gariepinus* (piscivorous) may have exerted top down controlling effect on juveniles of *O. niloticus* (planktivorous), which was most pronounced at MZ, thereby relieving the zooplankton from grazing and favor their high density (Yosef Tekle-Giorgis *et al*., 2016). Moreover, the small number of the large-sized carnivorous zooplankton *M. aequatorialis* (1796 ± 2981.8 ind m^{-3}) at MZ could favor the dominance of the medium-sized and herbivorous taxa.

Nauplii (**Appendix 5**) were found to be dominant over the adult cyclopoids at all sites, a finding, which is consistent with the observation of a previous study by Tadesse Fetahi (2010). The adult cyclopoids may have been favorably grazed by the juvenile fish and other zooplanktivorous adult fish resulting in lower number of the mature cyclopoid copepods than the nauplii. Nevertheless, *Thermocyclops* was numerically important next to the nauplii than the *Mesocyclops,* especially at MZ. This can be attributed to the high reproduction rate of *Thermocyclops* compared to that of the *Mesocyclops* species. Seyoum Mengistou (1989) reported that *Thermocyclops* has high rate of reproduction and so can recover fast from grazing losses. On the other hand, the abundance of *Mesocyclops* was higher at OW. Therefore, the lower abundance of *Thermocyclops* and cyclopoid nauplii and rotifers at OW than at RH and MZ may suggest the importance of the carnivorous *Mesocyclops aequatorialis* as grazer of the other zooplankton groups in Lake Hawassa as reported previously by Seyoum Mengistou and Fernando (1991).

Mesocyclops aequatorialis, which was dominant at the OW site showed statistically significant variation only between TW and OW ($p = 0.013$). Though the number of *M. aequatorialis* was relatively higher at the OW site than at the other sites, its abundance was generally low compared to that of the *Thermocyclops* species and nauplii. The low abundance of large-sized zooplankton in many tropical lakes and reservoirs was suggested as an indication of strong fish predation (Fernando, 1994). Planktivorous fish are known to selectively feed on large sized-zooplankton like *M. aequatorialis* (**Appendix 5**). Hence, this can be the reason for the low abundance of *Mesocyclops* at the MZ site. Large sized *C. gariepinus* (>45 cm total length) inhabits the offshore region (Tesfaye Wudneh, 1998) and tends to filter-feed more on zooplankton (Yosef Tekle-Giorgis *et al.*, 2016). The low abundance of zooplankton at the OW site may have so resulted from the intense grazing pressure by the adult fish.

The lowest number of zooplankton at TW may have resulted from the elevated turbidity of the water which causes reduction in the feeding potential of both herbivorous and carnivorous zooplankton. A statistically significant difference in abundance of nauplii was observed between TW and MZ (p = 0.033). The difference in the abundance of *Thermocyclops* was also significant between TW and MZ (p = 0.005), and TW and OW (p = 0.012). Water clarity (Z_{SD}) was significantly and positively correlated with zooplankton abundance especially with the large-sized ones such as *Mesocyclops* (r = 0.638, p = 0.002) and *Thermocyclops* (r = 0.655, p = 0.002) revealing the importance of a high light level for the success of visual predators. Similarly, Hart (1986) has indicated that predation efficiency by visual predators decline as turbidity rises. The low level of DO at TW site could depress their survival success. Comparably, Seyoum Mengistou and Fernando (1991) also reported a low abundance of zooplankton from two stations located at the mouth of the inflowing Tikur Wuha River.

A higher number of rotifers was recorded at RH than at TW (P = 0.023). The numerically important rotifers' species *B. calciflorus* (28066.77 ± 43659 ind m^{-3}) has showed a statistically significant difference in abundance between TW and RH (p = 0.038), and RH and OW (p = 0.02) sites, while the abundance of *B. caudatus* (37748 ± 69734 ind m^{-3}) varied significantly between TW and MZ (p = 0.032), and TW and RH (p = 0.05). The highest rotifers' abundance was recorded from the RH than the other sites (**Fig. 10**). The greater abundance of rotifers at RH than at OW and MZ sites can be attributed to the lower number of carnivorous cyclopoid copepods like *Mesocyclops aequatorialis* that may selectively feed on rotifers. High turbidity of the water at RH could also favor the dominance of rotifers as it would relieve them from visual predators. Rotifera benefited from the high turbidity of the lake as they are less affected than the larger filter feeders under dark conditions (Kirk, 1991). Cyclopoid copepods at OW and MZ, and rotifers at RH were alternately dominant at the three sampling sites indicating the existence of negative interaction between these taxonomic groups. Tamiru Gebre (2006) reported that when the copepods were abundant, rotifers were found in low numbers, which may be due to competition or even predation by the copepods on the small rotifers.

Total cladocerans abundance was very low at the first two sites (TW and RH), while a considerable number of cladocerans, which was dominated by *Diaphanosoma excisum* (**Appendix 5**) was recorded at OW and MZ. Changes in water quality are known to impact zooplankton groups differently because of their specific tolerance to stressful conditions such as eutrophication and pollution (Gorokhova *et al*., 2016). The rare occurrence of cladocerans at the two sampling sites (TW and RH) could indicate their high sensitivity to the stressful condition caused by the high turbidity at these sites (**Table 3**). The higher level of turbidity at TW and RH than at OW and MZ sites could have affected cladocerans negatively by hindering their filtration efficiency.

Zooplankton abundance exhibited monthly variation with higher density occurring during three sampling months (May, July and August) and peaking in August (**Fig. 11**). A considerable increase in zooplankton abundance after July was also reported by Seyoum Mengistou and Fernando (1991) for the same lake. The highest zooplankton abundance concurred with the maximum level of Chl-a. Hence, the high zooplankton abundance during the three sampling months could be related to the availability of sufficient food reflected in the high algal biomass of these months. Though there was considerably high algal biomass in June, zooplankton abundance was low showing the existence of some factors other than algal biomass impacting zooplankton abundance. The elevated pH level in June probably adversely affected the zooplankton as only a small change in pH can have a large effect on the survival of the zooplankton (O'Brien and deNoyelles, 1972). O'Brien and deNoyelles (1972) demonstrated the existence of a narrow threshold of pH, where a change of 0.4 pH units changed the water from almost totally harmless to completely toxic. Considering their small size, the zooplankton may also favorably feed on bacterioplankton (Zinabu Gebre-Mariam, 1988) and their abundance may rely at least to some extent, on the level of the bacterioplankton.

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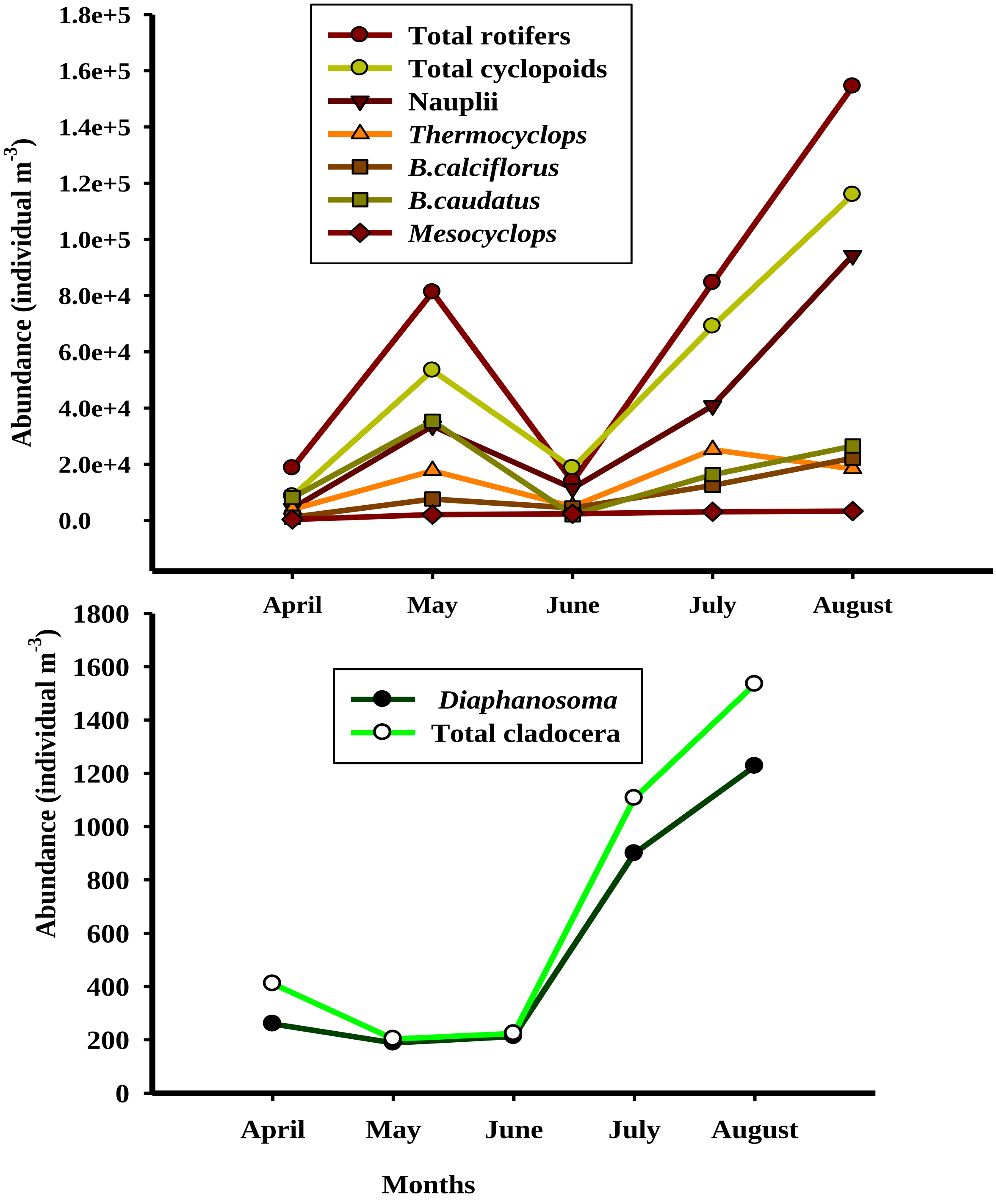

Figure 11. Temporal variations in zooplankton abundance.

9.6. Macrophyte

The dominant macrophyte identified from Lake Hawassa was *Echinochloa pyramidalis* (Lam.) Hitchc. and Chase (antelope grass). It is tall perennial grass with blade shaped leave and very strong fasciculated root system that is able to spread quickly and has potential to reduce biodiversity by replacing native plants in some humid situation e.g. in freshwater wetlands of Mexican tropics (Heuzé *et al*., 2016). In addition, Antelope grass has shared features with African invasive grass including: tolerance to foraging, intense vegetative propagation, high production of above and below ground organic matter and C4 photosynthesis (Lòpez-Rosas *et al*., 2015). *Echinochloa pyramidalis* (**Appendix 3**) is known to be native to tropical Africa and Madagascar (Heuzé *et al*., 2016). This species is an enviromental marker of organic pollution in aquatic ecosystems. Noukeu *et al*. (2019) indicated that *Echinochloa pyramidalis* is resistant to stress caused by over enrichment of nutrients and organic pollutants. Therefore, the dominance of *Echinochloa pyramidalis* at MZ in Lake Hawassa may be the result of elevated nutrients levels in the lake. High density of *Echinochloa* species in nutrient rich condition was also reported from Lake Ziway (Girum Tamire and Seyoum Mengistou, 2013).

10. Conclusions and Recommendations

The levels of nutrients were high at all sampling sites and showed an increasing trend from April to August. However, there were significant differences in the levels of physico-chemical parameters among sampling sites, which were dependent mainly on the levels and types of influents. TW site was found to have the highest concentration of nutrients as Tikur Wuha River continuously brings influents from Hawassa textile factory and agricultural fields. The influents from the Referral Hospital of Hawassa University have enriched the RH site with nutrients and made it turbid. The remaining two sites, OW and MZ, were also enriched with nutrients, but had lower turbidity.

The elevated levels of nutrients in Lake Hawassa has implication for the need for proper management of wastes emanating from point sources (e.g. Hawassa textile factory and Referral Hospital of Hawassa University) using effective treatment system like constructed wetlands etc. In addition, reducing the accumulation of nutrient rich influents from nonpoint sources origin especially from agricultural lands through awareness creation about the appropriate use of fertilizers on the surrounding farmlands is urgent. Increasing the plant cover in the catchment area of the lake should have to be done for ensuring the sustainable use of the water system for various intended uses.

The monthly and spatial dynamics of phytoplankton FGs in Lake Hawassa seem to be the consequence of the combined effects of abiotic factors (extent of mixing, rainfall, influents, nutrients and light levels) and biotic factors (zooplankton abundance, macrophyte coverage). The biomass of phytoplankton functional assemblages tends to increase following the rainy months and the consequent mixing events. Rainfall and destratification favor the growth of algae by enhancing nutrient availability from allochthonous and autochthonous sources, respectively. The spatial variations in both MBFGs and RFGs are primarily driven by the light level and water movement even though the effect of zooplankton grazing and fish predation cannot be overlooked. The predominant RFGs **J**, $\mathbf{L_O}$, **SN**, **M**, and MBFGs **III** and **VII** were found to have comparable biomass at the RH and OW sites. The presence of continuous water current separates TW, which was inhabited predominantly by the turbulence-tolerant RFG **P** and MBFGs **VI**.

The predominant RFGs S**N**, **M**, MBFGs **III** and **VII,** which consisted of potentially toxigenic species, have a strong adherence to macrophyte coverage owing to their preference for low total irradiance and stable water column. The results of the present study support the hypothesis that the biotic (the macrophyte *Echinochloa* species coverage) and human-induced abiotic (the influents) factors have a significant impact on phytoplankton FGs. But, further research is mandatory to better understand the underlying mechanisms governing their interactions. The results of the current study can be used as baseline information for further research in the area. Though all sampling sites were productive both biologically and chemically and hypereutrophic, there was relatively higher level of water quality deterioration at TW and RH sites. The remaining two sites OW and MZ have a relatively low level of eutrophication.

The potentially toxigenic FGs (**SN** and **M**) were dominant in Lake Hawassa. Further studies should, therefore, be conducted to determine: first whether the species present are actually toxigenic or not because it is known that only those species, which possess the gene cluster that is responsible for toxin production can produce toxin. If the species present are actually toxigenic, the concentration and noxiousness of toxins produced by these species should be determined. As the present study is restricted only to the minor and main rainy season, long-term study needs to be conducted to show the water quality changes across time and space, and to generate sufficient information about the seasonality of the phytoplankton FGs.

Rotifers and cyclopoid copepods were the dominant zooplankton taxa. Among the cyclopoid copepods, *Thermocyclops* species was the most important numerically at MZ, while rotifers were predominant at the RH site. On the other hand, the overall zooplankton abundance was low at TW due to the stress associated with very high turbidity and the absence of sufficient time for their proliferation.

The food preference of the dominant cyclopid copepods (*Thermocyclops* and *Mesocyclops* species) and rotifers (*Brachionus* species) was not addressed in this study. Therefore, further study on the feeding habit of the dominant zooplankton taxa including its seasonality is mandatory to have conclusive understanding of the effect of the zooplankton on the phytoplankton FGs.

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12. Appendices

Appendix 1. (**A**) The formula used for calculating Trophic Status Index (TSI) of tropical lakes and (**B**) the contribution of the three major ions to alkalinity of the water in Lake Hawassa calculated based on APHA (1999).

A.

TSI index for tropical environments proposed by Lamparelli (2004) is the method based on the concentrations of TP and Chlorophyll-a. Based on the formulas proposed by Lamparelli (2004) TSI of lakes can be calculated as follows:

Trophic status	Numerical values
Ultra-oligotrophic	$TSI < 47$
Oligotrophic	$47 < TSI < 52$
Mesotrophic	$52 < TSI < 59$
Eutrophic	$59 < TSI < 63$
Super-eutrophic	$63 < TSI < 67$
Hyper-eutrophic	$TSI > 67$

The formulas for TSI of tropical lakes are (Lamparelli 2004):

$TSI\ (Chl\text{-}a) = 10*(6-((0.92-0.34*(\ln [Chl\text{-}a]))/\ln 2))$

$TSI\ (TP) = 10*(6-(1.77-0.42*(\ln [TP])/\ln 2))$

$TSI\ Lamp = (TSI\ (Chl\text{-}a) + TSI\ (TP))/2$

B.

	Ions		
sites	Bicarbonate (meq L^{-1})	Carbonate (meq L^{-1})	Hydroxide (meq L^{-1})
TW	2.4	0	0
RH	1.74	1.92	0
OW	3.12	1.72	0
MZ	0	2.12	0.46

Appendix 2. The levels of *insitu* measured physicochemical parameters (**A**), vertical temperature (**B**) and DO (**C**) profiles, levels of laboratory determined physicochemical parameters (**D**), abundance of the dominant algae (**E**), fresh weight biomass of the dominant phytoplankton FGs (**F** and **G**) and abundance of zooplankton (**H**) at all sites during all study months

A.

		Parameters							
sites	moths	DO (mg L^{-1})	% saturation	Temperaure (°C)	EC (µS cm^{-1})	pH	Turbidity (NTU)	Z_{SD} (m)	Zeu(m)
TW	April	3.9	61.2	28	239.4	7.39	152.5	0.15	0.405
	May	2.44	38.2	25.9	224	7.15	155	0.103	0.2781
	June	5.15	71.9	27.4	526	8.57	32.5	0.35	0.945
	July	2.54	39.86	23.7	332.43	7.3	29.5	0.26	0.702
	August	2.41	35.4	24.7	241.8	7.59	50.4	0.19	0.513
RH	April	3.94	64.033	25.9	815	9.127	10.255	0.85	2.295
	May	7.43	10.9	25.2	786.5	9.12	12.3	0.67	1.809
	June	3.87	55.6	23.8	835.97	8.96	29.45	0.38	1.026
	July	4.85	67.7	22.2	829.18	8.83	31.8	0.44	1.188
	August	6.54	92.5	23	1020.95	9.04	30.15	0.53	1.431
OW	April	7.04	105.3	25.7	793.41	9.22	8.89	0.7167	1.93509
	May	6.687	100.3	25.05	803.5	9.02	9.83	0.725	1.9575
	June	6.5	92.2333	23.7	816.73	9.12	10.1	0.91	2.457
	July	5.5	77	22.35	802.4	9.2	11.2	0.86	2.322
	August	7.12	98.725	22	1040.1047	9.11	14.4	0.9	2.43
MZ	April	5.383	81.85	26.3	770.319	8.63	10.15	0.825	2.2275
	May	6.513	97.73	25.88	767.4	9.097	9.75	0.9	2.43
	June	6.4933	93.87	24.07	812.15	9.1	9.48	0.89	2.403
	July	6.74	93.5	22	793.4	9.21	11.9	0.78	2.106
	August	7.99	111.63	22.5	826.41	9.1	15.2	0.53	1.431

B.

Parameter	Sampling months					
Temp.(^{o}C)	Depth (m)	April	May	June	July	August
	0	27.43	25.73	24.425	22.3	23
	1	25.97	25.6	23.8	22.1	22
	2	25.07	25.3	23.6	22	22
	3	24.65	24.9	23.5	22	22
	4	24.4	24.6	23.5		22
	5	24.3	24.5	23.5		22
	6	24.3				22

	7	24.1	24.3			22
	8	23.7				
	9					
	10	23.6	24.1	23.4	22	22
	11					
	12					
	13					
	14					
	15	21.5	23.3	23.2	21.7	22

C.

Parameter	Sampling months					
DO (mg L^{-1})	Depth (m)	April	May	June	July	August
	0	5.44	6.26	5.59	5.17	6.15
	1	5.83	6.85	6.61	6.06	7.75
	2	4.97	6.71	6.36	5.5	7.25
	3	4.88	5.79	6.02	5.5	6.81
	4	4.76	6.00	6.01	5.5	6.72
	5	4.52	5.72	6.02	5.5	6.67
	6	4.41	5.5	6.01		6.66
	7	3.29	5.3			6.66
	8	1.62	5.23			6.56
	9					6.54
	10	1.48	3.40			6.54
	11					6.53
	12					6.53
	13					6.50
	14					
	15	0.02	0.05	5.18	5.40	6.45

D.

Sites	months	TSS (mg L^{-1})	TDS (mg L^{-1})	PA (meq L^{-1})	TA (mg L^{-1})	Nitrate (µg L^{-1})	Ammonia(µg L^{-1})	SRP(µg L^{-1})	TP(µg L^{-1})	SiO2 (µg L^{-1})	Chl-a (µg L^{-1})
TW	April	101.43	170	0	2.9	22.4286	105.8571	106.8	552.8	75.4258	1.05
	May	166	90	0	4	23.4286	174.4286	410.8	698.8	64.7806	30.07
	June	28	128.5	0	3.2	30.5714	105.8571	6.8	228.8	91.8774	20.05
	July	77	1628	0	1.9	31.5635	37.6429	75.466	347.6	72.9	11.36
	August	85	317	0	0	50.5714	281.7286	155.6	456.8	54.6516	12.03
RH	April	20.5	530	2	2.1	2	195.8571	1.2	288.8	71.5548	2.9
	May	7.5	660	0	6	7.7143	110.5714	16.8	100.8	71.2323	39.7
	June	16	83.5	1.2	1.8	27.6	275.1429	5.8	414.8	94.4581	27.13
	July	96	343	0.9	4	19.1429	527.29	43.244	221.4	45.1677	45
	August	30	637	0.35	2.2	37.7143	270.1429	124.8	255.6	66.5226	55.33
OW	April	4	553	1.1	4	0.4286	135.8571	66.8	198.8	73.0387	5.35
	May	1	680	2	11	7	100.1429	40.8	204.8	78.329	20.16
	June	70.5	99	2	6.8	4.8571	262.6429	6.2	7.8	128.6516	28.07
	July	21	331	0.9	3.2	17.7143	224.8571	23.2	180.8	31.8774	44.33
	August	14	661	2	2.15	76.2857	313	50.4	194.8	69.103	51.86
MZ	April	13	547	1.9	3	4.8571	61.5714	28.8	206.8	73.6839	16
	May	5.5	600	2	3	3.3143	90.4286	57.4	106.8	76.3935	16.37
	June	5.5	93	0.4	2	0.5714	280.8571	6.8	64.8	108.0065	30.74
	July	15	662	1.9	1.9	19	325.8571	35	156.8	45.6194	45
	August	16	619	0.7	1.5	57.7143	213	43.4	132.8	68.7161	51.86

E.

Sites	Taxa	Abundance (individual L^{-1})				
		April	May	June	July	August
TW	*Aulacoseira granulata*	12800000	191000000	9050000	6880000	14160000
RH		0	0	183333	513333	1100000
OW		0	1700000	0	120000	960000
MZ		200000	0	0	586667	330000
TW	*Nitzschia dissipata*	613300	333333	300000	726670	853333
RH		63636	333333	758333	2246667	1900000
OW		26667	25000	18182	172727	273333
MZ		90909	35714	80000	200000	1050000

TW	*Cosmarium depressum*	0	0	16700	0	0
RH		126667	83333	50000	100000	220000
OW		26667	83333	27273	36667	33333
MZ		27273	10000	10000	116667	190000
TW	*Staurastrum muticum*	0	0	0	0	0
RH		5000	50000	58333	110000	93333
OW		310000	100000	36364	63636	53333
MZ		236364	50000	0	0	170000
TW	*S. avicula*	0	0	0	0	0
RH		0	0	16667	0	6667
OW		0	0	0	0	0
MZ		0	0	0	0	0
TW	*S. tetracerum*	0	0	0	0	0
RH		53300	25000	33333	83333	93333
OW		36667	33333	41667	81818	106667
MZ		9091	35714	120000	46667	30000
TW	*Staurodesmus crassus*	0	0	0	0	0
RH		2000	58333	33333	10000	46667
OW		0	0	0	0	0
MZ		63636	0	0	0	0
TW	*Cylindrospermopsis raciborskii*	29088	266667	4133333	720000	213334
RH		8506667	2733333	2866667	2186667	8693333
OW		5973600	733333	7200000	9818182	22186667
MZ		14036364	14800000	10640000	10106667	16000000
TW	*C. catemaco*	18000	48000	18250000	3280000	120000
RH		31320000	5000000	4300000	5360000	24520000
OW		9000000	45100000	56454545	47400000	75800000
MZ		7200000	61885714	60300000	46580000	74460000
TW	*C. curvispora*	0	0	3416667	333333	33333
RH		10836633	1359167	1343333	1240000	7066667

OW		9026667	7191667	8936364	6645455	16960000
MZ		6000000	17171429	8370000	8250000	13930000
TW	*Oocystis lacustris*	760000	10000	675000	0	0
RH		1445455	1250000	891667	1390000	1666667
OW		1263333	1941667	550000	254545	1760000
MZ		2527273	1035714	310000	1353333	1200000
TW	*Ankistrodesmus*	0	0	25000	0	0
RH		72727	0	0	0	0
OW		26667	50000	27273	26667	0
MZ		0	28571	0	10000	10000
TW	*Botryococcus* species	1320000	0	416667	0	0
RH		0	4833333	916667	0	10613333
OW		453333	3441667	0	727273	2666667
MZ		2827273	5112987	800000	1526667	12760000
TW	*Merismopedia tennuissima*	2393300	0	933333	0	0
RH		9873300	5408333	10583333	13400000	15300000
OW		4953333	5300000	7409091	4881818	12920000
MZ		6727273	3100000	4420000	7573333	12170000
TW	*M.* species	0	0	0	0	0
RH		0	0	0	0	11986667
OW		0	0	0	4236667	12826667
MZ		0	0	0	0	10620000
TW	*M. glauca*	0	0	0	0	0
RH		0	0	0	0	2853333
OW		0	0	0	0	2026667
MZ		0	0	0	0	1410000
TW	*Chroococcus minor*	0	0	0	1710000	0
RH		0	0	0	383333	7593333
OW		0	0	2945455	6283333	3886667

MZ		0	0	4240000	4663333	4600000
TW	*C. minutus*	0	50000	3600000	20000	0
RH		50000	525000	826667	700000	3600000
OW		0	2125000	3218182	963333	3160000
MZ		0	2792857	3930000	1216667	3020000
TW	*C. turgidus*	0	0	0	0	0
RH		1463636	325000	225000	5000	26667
OW		310000	141667	18167	0	186667
MZ		1490909	64286	0	0	170000
TW	*Coelastrum* species	11806700	3636	508333	1453333	1133333
RH		5346700	4375000	9325000	20000	14700000
OW		1583333	5716667	4033333	10733333	6666667
MZ		11500000	3192857	4670000	4010000	12020000
TW	*Tetraëdron minimum*	0	0	125000	0	0
RH		363636	483333	275000	410000	600000
OW		226667	441667	109091	290000	260000
MZ		2036364	300000	200000	273333	250000
TW	*T. triangulare*	0	0	41667	0	0
RH		254545	275000	312500	190000	180000
OW		110000	200000	0	145455	153333
MZ		181818	135714	30000	153333	0
TW	*Scenedesmus* species	0	0	0	0	0
RH		5454545	400000	1200000	1080000	566667
OW		0	0	0	109091	266667
MZ		72727	0	0	253333	240000
TW	*S. acuminatus*	0	0	0	0	0
RH		72727	0	100000	333333	140000
OW		0	0	72727	40000	80000

MZ		72727	0	0	16667	0
TW	*S. arcuatus*	0	0	0	0	0
RH		0	66667	33333	0	80000
OW		40000	0	0	0	0
MZ		40000	0	12760000	0	0
TW	*Microcystis* species	90900	181800	9558333	673333	1000000
RH		21546700	11300000	10800000	7236667	22793333
OW		5220000	11966667	10136364	4546667	6140000
MZ		1254545	16064286	2000000	10390000	1400000
TW	*M. flosaquae*	0	0	0	0	0
RH		11783333	200000	2666667	8020000	9333333
OW		2753333	2666667	10745455	13854545	6600000
MZ		1736364	971429	7310000	4453333	6800000
TW	*M. aeruginosa*	0	0	0	0	0
RH		6927300	0	0	0	3713333
OW		3610000	2908333	0	0	9246667
MZ		5981818	2378571	3370000	4000000	23450000
TW	*M. wesenberg*	0	0	0	0	0
RH		5226667	3833333	3000000	7410000	200000
OW		0	0	0	12546667	0
MZ		15800000	2400000	3000000	6910000	4200000
TW	*Cymbella* species	4000	8000	83333	20000	173333
RH		8000	16667	100000	210000	173333
OW		0	0	0	9091	0
MZ		18182	0	40000	26667	20000
TW	*Gomphonema* species	8000	116667	25000	73333	80000
RH		5000	16667	41667	20000	46667
OW		0	0	0	0	0
MZ		0	0	0	0	0
TW	*Gomphonema telegraphicum*	2700	91667	41667	36667	40000

RH		16667	33333	26667	36667	53333
OW		0	0	0	546667	0
MZ		0	0	0	26667	0
TW	*Fragilaria construens*	53300	25000	10000	20000	73333
RH		0	0	0	0	0
OW		0	0	0	0	0
MZ		0	0	0	0	0
TW	*Navicula* species	8000	16667		20000	20000
RH		0	0	0	0	0
OW		0	0	0	0	0
MZ		0	0	0	0	0
TW	*Navicula neoventricosa*	140000	33333	0	0	60000
RH		0	0	0	36667	0
OW		0	0	0	100000	0
MZ		0	0	0	0	0
TW	*Achnanthes* species	26700	16667	0	0	13333
RH		0	0	0	0	46667
OW		0	0	0	0	0
MZ		0	0	0	0	10000
TW	*Achnanthes exilis*	0	0	0	0	0
RH		0	0	0	0	566667
OW		0	0	0	0	0
MZ		0	0	0	0	0
TW	*Cyanodictyon*	900000	2833333	2166667	14000000	1800000
RH		0	2687500	1127273	881818	793333
OW		0	842857	1210000	653333	680000
MZ		0	0	0	0	0
TW	*Aphanothece clathrata*	0	0	0	0	0
RH		2545454	0	0	0	0
OW		0	0	2290909	4820000	2266667
MZ		0	0	0	8453333	5850000
TW	*Aphanothece minutissima*	0	0	0	0	0
RH		0	0	0	0	12073333
OW		0	0	0	0	12900000
MZ		0	0	0	0	13200000

TW	*Aphanocapsa*	0	0	0	0	0
RH		0	0	0	0	2200000
OW		0	0	0	0	7733333
MZ		0	0	0	0	3600000
TW	*euglena acus*	0	8333	0	0	0
RH		180000	186000	192000	186589	188356
OW		0	0	0	0	0
MZ		9091	0	0	0	0
TW	*Phacus* species	0	8333	0	0	0
RH		33330	0	0	13333	6667
OW		0	0	0	13333	0
MZ		18182	0	0	0	0
TW	*Trachelomonas aspera*	0	0	0	0	0
RH		78036	0	0	46667	153333
OW		63333	175000	0	127273	0
MZ		0	0	0	46667	90000
TW	*Cryptomonas ovata*	0	0	0	0	0
RH		0	0	0	0	653333
OW		0	0	0	0	0
MZ		0	0	0	0	30000
TW	*Pediastrum* species	0	16667	0	0	6670
RH		0	8333	25000	0	26667
OW		0	0	0	0	10000
MZ		9091	0	0	0	0

F.

		Fresh weight biomass of RFGs (mg L^{-1})													
Sites	Months	**D**	**N**	**M**	**P**	**J**	**SN**	**F**	**lo**	**MP**	**K**	**TD**	**W1**	**W2**	**Y**
TW	April	0.181402	0	0.001709	3.8528	0.19677	0.000516	0.06216	0.00369	0.114898	0	0.110378	0	0	0
	May	0.098594	0	0.003418	57.491	0.0006	0.003604	0.00054	0.004395	0.145132	0	0.332373	0.019	0	0
	June	0.088734	0.025482	0.179697	2.72405	0.024664	0.295572	0.043964	0.317879	0.050341	0	0.248881	0	0	0
	July	0.214935	0	0.012659	2.07088	0.032202	0.047039	0	0.130008	0.054828	0	0.054268	0	0	0
	Augus	0.2524	0	0.0188	4.26216	0.02756	0.00436	0	0	0.15270	0	0.13347	0	0	0

	t						1			8		8			
RH	April	0.017043	0.240206	0.865366	0	0.559686	1.227349	0.081628	0.410411	0.011441	0.384579	0	0.308478	0.401885	0
	May	0.089271	0.302051	0.327207	0	0.175333	0.267364	0.126943	0.141262	0.026533	0.000677	0.006967	0.295926	0	0
	June	0.203092	0.223441	0.33804	0.068017	0.294492	0.2659	0.059926	0.164634	0.052422	0.000518	0	0.305472	0	0
	July	0.601687	0.248245	0.495299	0.190447	0.160234	0.235795	0.076127	0.112278	0.074368	0.00043	0	0.305703	0.240333	0
	August	0.508845	0.547289	0.654105	0.4081	0.384304	1.041083	0.219701	0.95272	0.292191	0.011268	0.003813	0.304094	0.789667	0.804443
OW	April	0.005299	0.074763	0.219969	0	0.052182	0.669457	0.065007	0.068776	0	0	0	0	0.319897	0
	May	0.004968	0.150462	0.363796	1.0013	0.145216	0.696746	0.144136	0.225639	0	0.000642	0	0	0.883925	0
	June	0.003613	0.067101	0.426555	0	0.087834	1.147522	0.025674	0.470491	0	0.346197	0	0	0	0
	July	0.034324	0.105683	0.887188	0.07068	0.224479	1.09946	0.023994	0.573666	0.264207	0.728031	0	0.00884	0.642855	0
	August	0.054317	0.114472	0.528173	0.56544	0.167036	2.272513	0.121867	0.629585	0.011534	0.352112	0	0	0	0
MZ	April	0.029641	0.172984	1.322866	0.132851	0.456501	1.068975	0.160924	0.305257	0.008209	0	0.0208	0.026518	0	0
	May	0.011645	0.035583	0.636393	0	0.094958	2.66497	0.130184	0.321338	0	0.000201	0	0	0	0
	June	0.026084	0.07681	0.475173	0	0.867703	2.034293	0.02699	0.645113	0.00748	0.000289	0	0	0	0
	July	0.065211	0.201857	0.916743	0.389697	0.120375	1.741836	0.086715	0.420087	0.016667	1.276609	0	0	0.235713	0
	August	0.342357	0.311981	1.11735	0.219205	0.247967	2.811393	0.259429	0.640448	0.05568	0.892439	0	0	0.45459	0.036939

G.

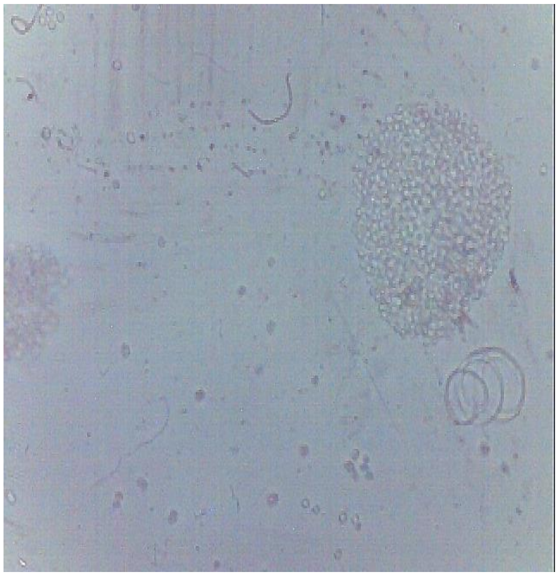
	Fresh weight biomass of MBFGs (mg L^{-1})					
Sites	Months	III	IV	VI	VII	V
TW	April	0.0005	0.1954	10.4487	0.0676	0
	May	0.0036	0.0001	62.0076	0.004	0.019
	June	0.34	0.0339	8.5121	0.2243	0
	July	0.047	0.0241	3.184	0.0127	0
	August	0.0064	0.0188	8.9468	0.0188	0
RH	April	1.4435	0.7116	0.0291	0.9598	0.710363
	May	0.2686	0.2858	0.3503	0.4625	0.295926
	June	0.2758	0.5537	0.3284	0.4143	0.305472
	July	0.2547	0.256	0.8933	0.5921	0.546036
	August	1.1656	0.8365	1.5008	0.8982	1.093761
OW	April	0.711	0.074	0.0053	0.2915	0.319897
	May	0.7585	0.2389	1.0063	0.5142	0.883925
	June	1.2178	0.1253	0.0036	0.4624	0
	July	1.1947	0.2766	0.3693	0.9178	0.651695
	August	2.4905	0.2381	0.6198	0.6871	0
MZ	April	1.1426	0.3222	0.4451	1.4938	0.026518
	May	2.6822	0.0779	0.0116	0.7702	0
	June	2.1108	0.8724	0.0336	0.5088	0
	July	1.7965	0.3264	0.4714	1.0144	0.235713
	August	2.941	0.547	0.6228	1.408	0.45459

H.

		Abundance (individual m$^{-3)}$								
sites	months	Total rotifers	Total cyclopoids	Nauplii	*Thermocyclops*	*Brachionus calciflorus*	*B. caudatus*	*Mesocyclops*	Total cladoceras	*Diaphanosoma excisum*
TW	April	18133	2133	1066	1067	0	0	0	250	0
	May	200	700	700	0	0	0	0	0	0
	June	5687	5145	4333	542	3340	542	271	0	0
	July	249	249	125	0	125	0	125	0	0
	August	4229	1410	705	705	1410	705	0	0	0
RH	April	7039	10056	8044	2011	1006	2011	0	0	0
	May	19413	8213	5973	2240	5973	4480	0	0	0
	June	25473	19595	14696	3919	7838	6858	980	0	0
	July	2104	51446	3808	11358	41424	50778	2004	0	0

		59		3						
	August	435307	178080	137270	33390	84093	86567	7420	273	0
OW	April	6553	15471	4268	10670	142	276	533	923	686
	May	2197	13696	6472	4937	301	301	2288	813	753
	June	8753	40034	18669	13898	1742	166	7467	456	456
	July	9918	74615	36062	29464	913	2116	9088	3320	2490
	August	24038	140332	100628	34069	1685	9031	5634	5476	4713
MZ	April	42716	6806	3990	1995	3521	30159	821	469	352
	May	303033	190911	121213	63637	24243	136365	6061	0	0
	June	15342	9907	7890	1315	4910	438	701	438	395
	July	117597	150070	88992	59973	7462	12160	1106	1106	1106
	August	154296	143997	138556	5150	1360	9619	292	389	194

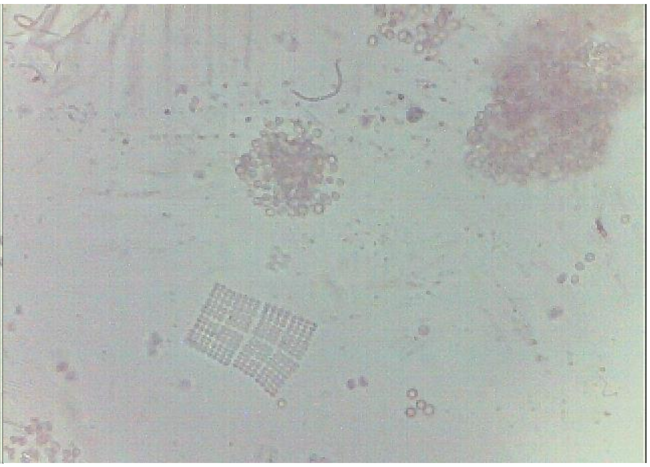
Appendix 3. The dominant macrophyte, *Echinochloa pyramidalis* in Lake Hawassa, Ethiopia (photo taken at MZ).



Cylindrospermopsis curvispora and *Microcystis flosaquae*

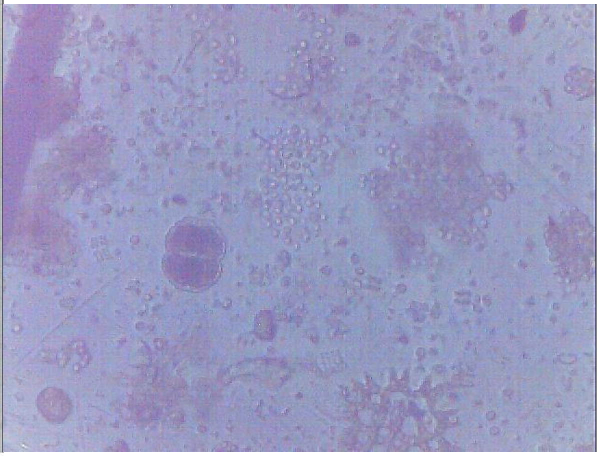
C. raciborskii

C. catemaco

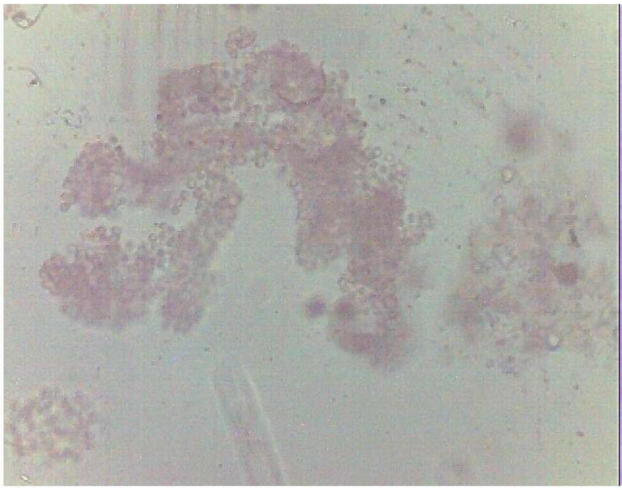


Mesrismopedia tenuissima

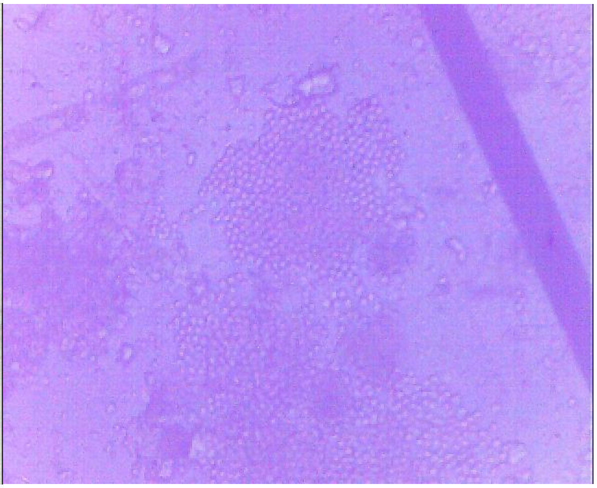
M. flosaquae, Staurastrum and coelastrum sp.,



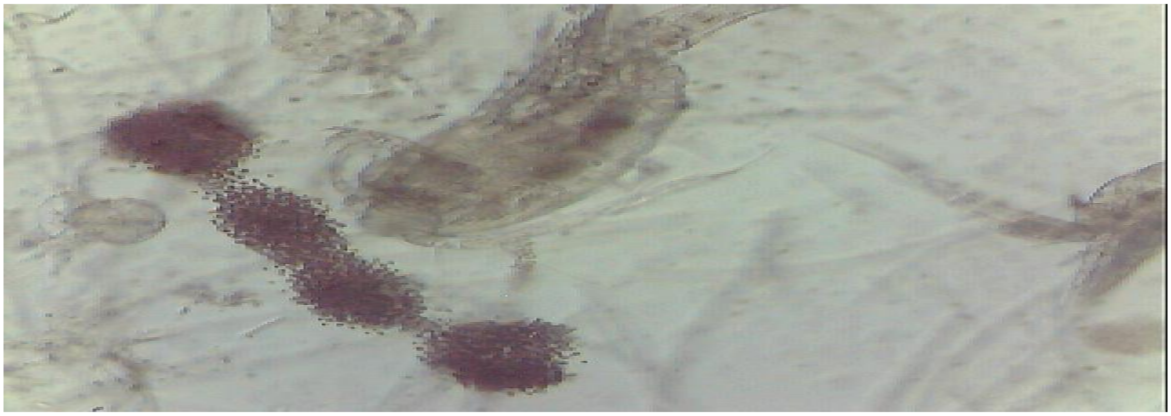
Cosmarium depressum and *pediastrum duplex*



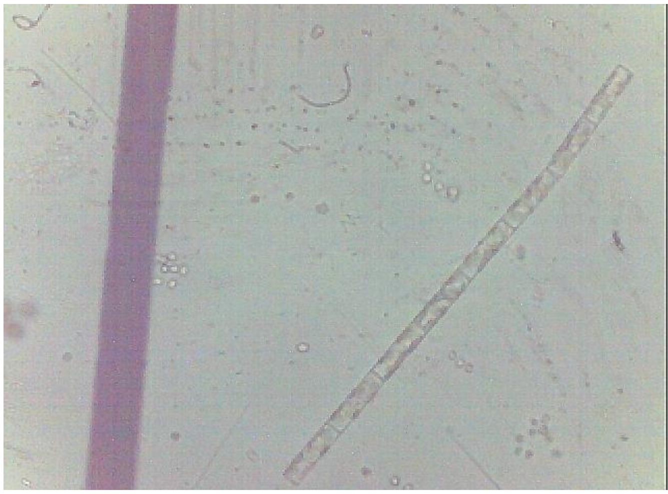
M. aeruginosa



M. panniformis

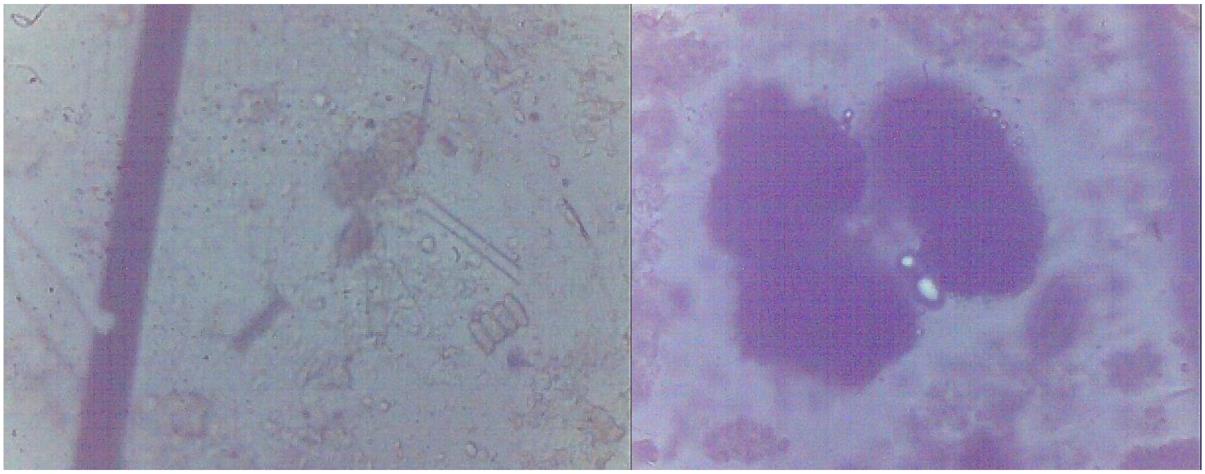


M. botrys



Aulacoseira granulata

Nitzschia dissipata

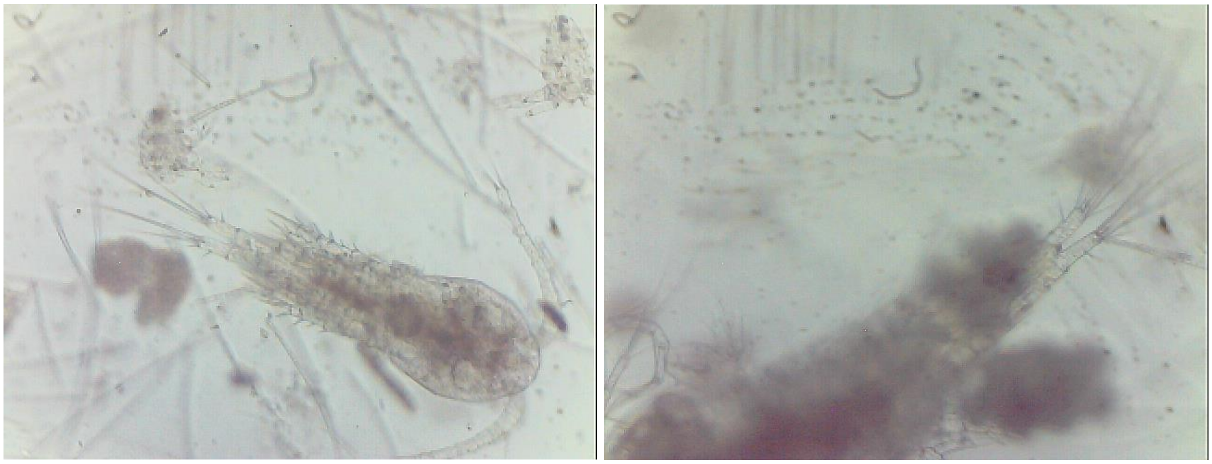


Scenedesmus quadricauda *Botryococcus braunii*

Appendix 4. Pictures of the most frequently observed algal species in Lake Hawassa, Ethiopia.

Diaphanosoma excisum

Diaphanosoma brachyurum



Thermocycyclops consimilis *Mesocyclops equatorialis*

Appendix 5. Pictures of the commonly observed zooplankton species