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ZOOPLANKTON COMMUNITY GRAZING IN LAKE KURIFTU

BY

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ABSTRACT

Studies on zooplankton community grazing rates were done in Lake Kuriftu from July 2005 to April 2006 using food removal method with chlorophyll 'a' as algal food indicator. The study considered the main factors that affect zooplankton community grazing rates such as density and size of both grazers and phytoplankton. Mean grazing rate at the natural density of zooplankton was 59.3% per day during the study period. Grazing rate values ranged from 18.3 % to 135.6% per day at both sites and all months. Increasing zooplankton density at two to four times ambient density was found to decrease grazing rates. Grazing rates were higher for larger zooplankton (>250μm) than smaller ones (<250μm). Pico and nanoplankton (up to 20μm) especially those of size <10μm were found to be more easily removed than microplankton (up to 63μm). Increasing the natural food density decreased grazing rates while diluting the algal food concentration increased rates, even at ¼ dilution factor. The Cyclopoid ***Thermocyclops consimilis*** dominated the zooplankton community during the study time followed by the rotifer ***Brachionus sp.*** The results suggested that increasing the density of zooplankton in Lake Kuriftu will reduce grazing rates; and on the other hand the natural food concentration should be diluted to increase zooplankton impacts through grazing. Top-down control with large-sized zooplankton can bring the reduction of chlorophyll 'a' concentration in the lake only on smaller and non-cyanobacterial phytoplankton (<10μm). The control of larger phytoplankton and nuisance cyanobacteria may be of limited use using the existing zooplankton community. Controlling external nutrient inputs into the lake should be given priority in controlling the algal productivity of the lake, since bottom-up route is

significantly important in controlling larger and filamentous cyanobacteria. However top-down approaches should not be ignored since large-sized zooplankton grazers have contribution in removing smaller-sized phytoplankton.

1. Introduction

Tropical lakes are often highly productive and like any other water body they provide water for consumption, power generation, irrigation, recreation etc and other uses. Although they are limited and sensitive resources, they are probably among the most abused natural resources (Zinabu Gebremariam, 2002). Human activity is contributing much for accelerating the eutrophication process in the lakes throughout the world (WHO, 2003).

Many eutrophic lakes suffer from bloom of toxic algae. Toxic freshwater cyanobacteria are very common worldwide and have been responsible for animal and human intoxication (Vasconcelos, 1999). Colony forming and toxic cyanobacteria create problems in surface waters of shallow lakes for recreation and other purposes (Dionsio ***et al***., 2005). So it is important to understand what regulates the abundance of phytoplankton. The regulation of aquatic systems is a recent issue in aquatic biology and has some practical applications (Ventella ***et al***., 2002).

According to Benndorff (1988), reducing external load of substances like nutrients, organic matter, etc, and controlling the internal ecological processes are means of managing the water quality resources. Studies on many temperate and some tropical lakes have shown that zooplankton grazing as a means of water quality regulation of aquatic systems plays a great role by controlling the abundance of phytoplanktons (e.g. Shaprio, 1995).

Biomanipulation, series of manipulation of the biota of lakes and their habitats to facilitate biological interactions, can result in the reduction of excessive algal biomass,

in particular of Cyanobacteria. The success of biomanipulation depends primarily on the efficacy of zooplankton grazing, which in turns depends on species composition, body size and biomass of zooplankton (e.g. Shapiro, 1995).

Eutrophic lakes produce much more plant material than can be used by herbivores, which accumulates in the lakes until decomposed by bacteria. This case is responsible for progressive decline in dissolved oxygen in deeper strata and, in extreme cases, to anoxia, and accumulation of nutrients released from sediments of these deep layers (De Bernardi and Giussany, 1995). These variations in the chemical environment initiate modifications in the biological communities. The consequence of eutrophication can be the reason, in both deep and shallow lakes, for alterations in trophic structure and function (Jepenssen ***et al***., 1997)

Integrated biomanipulation showed good prospects for managing eutrophic aquatic environment with a view to the ultimate recovery of their quality (De Bernardi and Giussany, 1995). Biomanipulation should be seen as a supporting operation, which can facilitate and accelerate the recovery process by the intervention in those mechanisms that are responsible for the power processes which arise within the ecosystem. The possibility of recovering eutrophic environments when the nutrient load derives from non-point sources (undefined sources e.g. farms) that are not easy to control; and its relatively low implementation costs, are among the most important advantages for applying these techniques.

Improving the quality of water bodies by implementing these management techniques requires detailed knowledge of the principal trophic relationships between the species

present; assessment of the environmental role of the key species making up the trophic network and other related environmental processes.

Even in the light of some problems, e.g. the difficulty in stabilizing of strong populations of piscivorous fish and ***Daphnia***, there is undoubtly success in biomanipulation researches, and in biomanipulation as a lake strategy (Kasprzak, 1995). Particularly, experiments in small lakes have been found more likely to be come successful (McQueen, 1990).

Although the productivity of lakes is primarily dependent on nutrient levels (bottom up factors), secondary effects like zooplankton grazing also should be considered as biological regulation control (Hubble and Harper, 2000). Removal by grazers is one way of reducing the negative effect of cyanobacterial blooms (Reeders and Bij de Vaate, 1990). A few decades ago it was strongly argued that food web structure and interactions in the pelagic of the lakes was exclusively determined by “bottom-up” forces through nutrient availability; however it is now evidential that food webs may be controlled by “top-down” factors, too.

Zooplankton interact with phytoplankton at several levels. Haney (1987) has shown these levels of interactions, particularly with cyanobacteria. The first order interaction is through direct grazing and fertilization of cyanobacteria through nutrient release, which was also shown by Carney and Elser (1990). Second order effects are indirect effects and include the influence of selective grazing on competition between species of cyanobacteria and cyanobacteria and non-cyanobacteria species.

When grazing by zooplankton is intense, the phytoplankton biomass and productivity can be reduced and clear water phase can be produced (Lampert ***et al***., 1986). The two major components of mesozooplakton, Cladocera and Copepoda contribute significantly to grazing pressure on phytoplankton. Strong top-down effects on phytoplankton have been reported for cladoceran-dominated zooplankton in some lakes (Sommer ***et al***., 1986) and for copepod-dominated zooplankton in the sea (Bautista ***et al***., 1992). However, the relative significance of predatory control can vary along a nutrient gradient (Jeppesen, 1998).

Grazing and feeding by zooplankton can be affected by several factors. Several studies have indicated that grazing rate measured in different communities vary with zooplankton biomass, food concentration and zooplankton taxonomic composition (Cyr and Pace, 1992), as well as body size of the grazers (Peters, 1984). One factor is the abundance of food. Feeding would increase linearly with food concentration had it not been for other limiting factors. There are mechanical and physiological upper limits to feeding rate due to mechanical processing of food during capture and ingestion, the volumetric constraints of the digestive tract, and the time required for digestion (Bamstedt ***et al***., 2000).

It is well reported that communities of large-sized zooplankton, e.g. ***Daphnia*** can graze more intensively on phytoplankton than communities of smaller zooplankton species (e.g. rotifers and ***Bosmina***) (e.g. Sterner, 1989). The increase in the individual crustacean size and zooplankton mass resulted in higher grazing activities in some biomanipulated lakes, often exceeding phytoplankton growth rate (Gulati, 1990).

Size and quality of the food item are other factors that affect feeding. Colonial cyanobacteria are not generally grazed as rapidly as smaller phytoplankton. Cyanobacteria generally have deleterious effect on grazing zooplankton. Filamentous cyanobacteria such as ***Anabaena*** and ***Oscillatoria*** can inhibit filtering by cladocerans (Haney, 1987). Therefore it is important to consider such factors when studying grazing by zooplankton. The contribution of zooplankton grazing to water clarity must be studied and hence the measure of grazing rate should be known before corrective measures are anticipated.

In the case of Ethiopia, some studies have been done regarding the threats and strategies for conservation of Ethiopian lakes. These studies were mainly focused on Ethiopian rift valley lakes (e.g. Zinabu Gebremariam 1994, 2002). There are also other limnological studies done on Ethiopian rift valley lakes especially on phytoplankton composition, biomass and primary productivity (eg. Demeke Kiflie, 1985; Girma Tilahun, 1988), and ecology of zooplankton. Taylor ***et al.***, (2002), stated that Lake Awassa is the best-known lake with respect to its zooplankton abundance, biomass, composition and production due to the work of Seyoum Mengistou (e.g. Seyoum Mengistou, 1989, Seyoum Mengistou and Fernando, 1991a and 1991b). Kassahun Wodajo and Amha Belay (1984) studied the species composition and seasonal abundance of zooplankton in Lake Abijata and Langano. Semeneh Belay (1988) also studied zooplankton composition and seasonal dynamics in Lake Ziway.

However the internal interactions between aquatic organisms of many Ethiopian lakes have rarely been studied, so that the importance of their interaction and its application are largely unknown. Since phytoplankton and zooplankton are at the base of aquatic

ecosystems, understanding their properties and the relationships between them will allow us to detect and avoid potential crash in the ecosystem (Conway, 2005).

The study done by Habte Jebessa (1994) can be considered as an example among these few works. He tried to estimate the grazing rate of zooplankton in Lake Awasa, Hora, Hayk and Legedadi reservoir. He found that grazing rates by zooplankton community are higher in oligotrophic and mesotrophic lakes but not in eutrophic lakes. Otherwise little information is available on the other Ethiopian lakes regarding the interaction of zooplankton and phytoplankton.

The crater lakes of Ethiopia have been the subject of a number of recent limnological studies. However, little is known about the ecology of zooplankton (Green, 1986), unlike the rift valley lakes. Green (1986) studied the ecology of zooplankton in these lakes. However, the above and most other works did not include Lake Kuriftu, which is one of the crater lakes of the country found in Debrezeit town.

Brook Lemma ***et al***. (2001) studied the interaction among cladocerans and their response to fish predation in Lake Kuriftu using enclosure experiments. It was suggested that that the size factor has apparently played an important role in fish predation and cladocerans relation based on the observations of this study. In addition, the size efficiency hypothesis seemed to be at work in these experiments. Otherwise, studies on the interaction between zooplankton and phytoplankton of the lake have not been undertaken so far. As stated in the next section of this paper, the aim of this work is to assess zooplankton community grazing rate on phytoplankton by manipulating the density of both the grazers and the food; and by fractionating the size of both the grazers and the food.

Since the lake is partly exposed to human interference, there is a need to give it attention. According to Zinabu Gebremariam (2002), the close proximity of urbanization and human settlement to Ethiopian lakes is among the greatest potential causes of changes in water quality. The growing population and the agricultural practices around the lake have serious impacts on Lake Kuriftu. It is possible for the wastes from these sources to find their way to the lake and cause eutrophication.

2. Objectives of the study

General objective

To investigate the impact of zooplankton community grazing on algal biomass in Lake Kuriftu, and to observe the interaction between zooplankton and phytoplankton in the lake.

Specific objectives

1. To estimate daily percentage grazing rate of zooplankton community in Lake Kuriftu;
2. To determine the effect of zooplankton density changes on the grazing rates on phytoplankton;
3. To determine which size group of phytoplankton are removed more by zooplankton community;
4. To determine which size group of zooplankton are efficient grazers in Lake Kuriftu;

5. To determine the effect of phytoplankton density change on zooplankton grazing rates; and

6. To assess which route (top-down or bottom-up) is more effective control for the algal productivity of Lake Kuriftu.

3. Description of the study area

Lake Kuriftu is one of the crater lakes located 47 km southeast of Addis Ababa in Debrezeit town, within the main Ethiopia rift. The lake is located at $8^0$47' North and $39^0$00' East, and found at an altitude of 1860m. It is an artificial lake and originally was a crater depression filled by diverting the tributary (Belbela) river of Mojo river for irrigation practice in the area (Seifu Kebede ***et al***., 2001). Conserving the water and introducing fish to the lake in order to provide supplementary protein to the surrounding population were other reasons for diverting the river (Brook Lemma ***et al***., 2001).

The lake gained a large part of its water from the river and small proportion from precipitation. Groundwater inflow plays a minimum role in the water balance of this lake. The lake has an approximate maximum depth of 8m (Seifu Kebede, 1999).

The chemical composition of the lake (Zinabu Gebremariam ***et al***., 2002) and some physical parameters of Lake Kuriftu (Brook Lemma ***et al.***, 2001) are reported in Table 1.

Zooplankton species composition of Lake Kuriftu was reported in Brook Lemma ***et al***. (2001) (Table 2). The fish and phytoplankton species found in the lake are not well reported, however ***Oreochromis niloticus***, ***Cyprinius carpio*** and ***Barbus*** species are known to occur in the lake. Currently, the temporal dynamics, biomass and primary production of phytoplankton are being studied in relation to some physico- chemical factors of the lake.

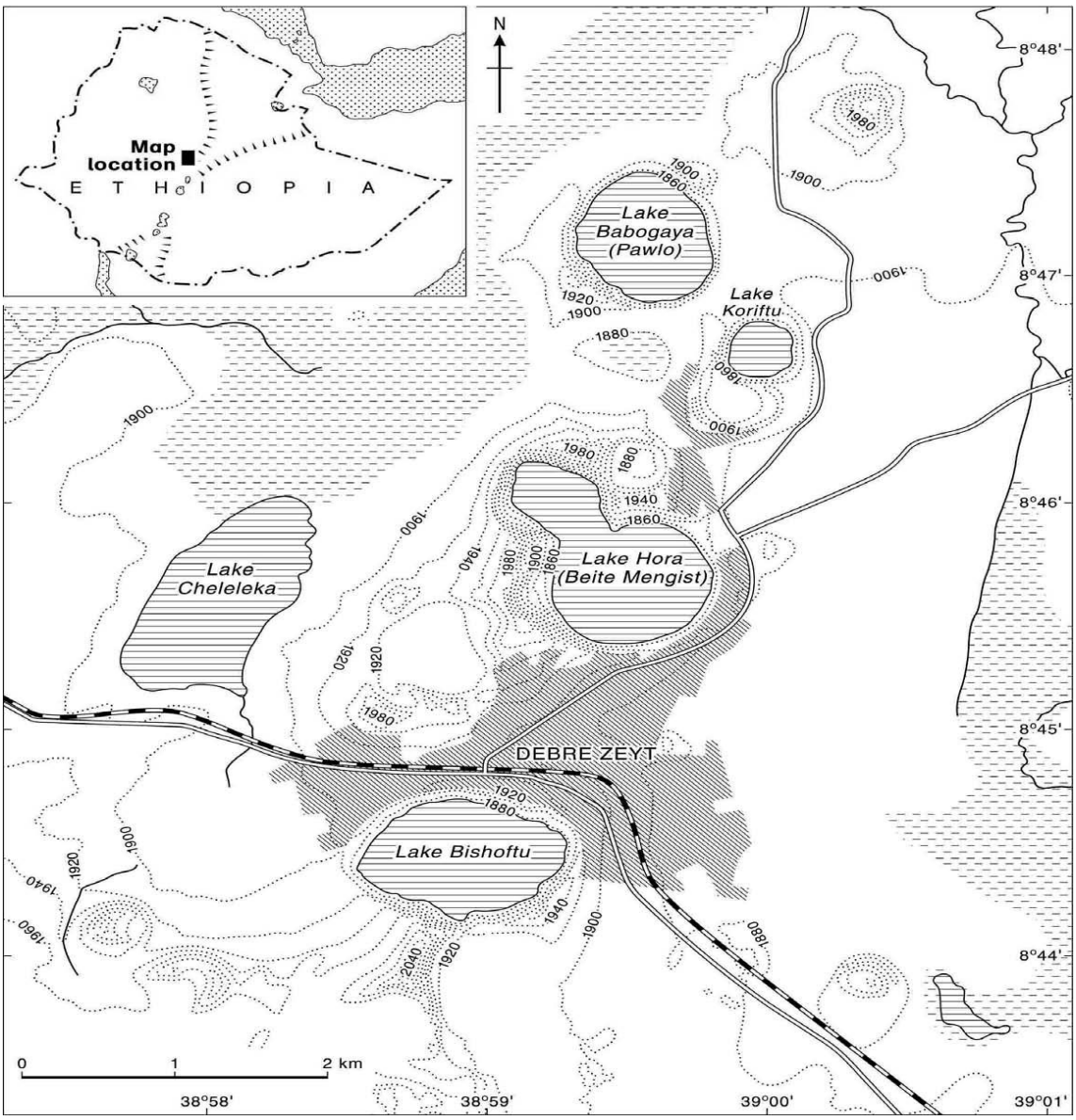

Fig.1 Map of Debrezeit and crater lakes surrounding Lake Kuriftu

(After Lamb, 2001)

Table 1. Physico-chemical features of the Lake Kuriftu

Area (Km^2)	0.4
Max. depth (m)	6
Mean depth (m)	2
pH	7.9-8.4
Volume (m^3)	$3.0x10^6$
Secchi depth (m)	0.15-0.20
Conductivity (μScm^{-1})	3.190
Salinity (g/l)	0.260
Cations (meq/l)	3.187
Anions (meq/l)	3.461
Na^{1+} (meq/l)	1.000
Ka^{1+} (meq/l)	0.154
Ca^{2+} (meq/l)	1.250
Mg^{2+}(meq/l)	0.783
Alkalinity (meq/l)	2.890
Cl^{1-} (meq/l)	0.571
SO_4^{2-} (meq/l)	0.000

(After Brook Lemma ***et al***., 2001 and Zinabu Gebremariam ***et al***., 2002)

Table 2. Zooplankton species identified in the lake

Groups	***species***
Cladocera	***Daphnia barbata*** ***Moina micrura*** ***Diaphanosoma sp.*** ***Ceriodaphnia sp.***
Rotifera	***Brachionus falcatus*** ***B. calciflorus*** ***Synchaeta vorax*** ***S. petinata*** ***Asplanchna sp.*** ***Lecane sp.*** ***Polyarthra minor*** ***Filinia sp.*** ***Hexarthra sp.*** ***Conochilus dossaurius*** ***Euchlanis sp.***
Cyclopoida	***Thermocyclops sp.***

(After Brook Lemma ***et al***., 2001)

4. Materials and methods

4.1. Plankton sampling

Zooplankton and phytoplankton samples were collected from the open water, deepest water column (6m), and the littoral zone of the lake (2m) from July 2005 to April 2006. Zooplankton samples were collected using a haul net of mesh size of 67 µm and Schindler patalas sampler of 0.014 m^3 volume, and phytoplankton samples were collected with a Ruttner sampler. This is used because this sampler allows collecting phytoplankton of all sizes. Zooplankton samples were preserved with 5% formalin and phytoplankton with Lugol's iodine solution.

4.2. Zooplankton community grazing rate calculation

Zooplankton community grazing rate was estimated, as percentage per day using food removal method (Bamtstedt ***et al***., 2000 and Gauld, 1951), which provides direct information regarding the interaction between phytoplankton and zooplankton. The method involves incubating zooplankton with phytoplankton ***in situ*** for a certain time and measuring the change in food concentration using biomass of phytoplankton (Chlorophyll 'a') as indicator.

Zooplankton and phytoplankton were incubated in 1-litter bottles ***in situ*** for 4 to 24 hours in controlled and treatment condition with two replications for each bottle. The change in Chlorophyll 'a**'** in zooplankton bottles (with food) was measured and compared with Chlorophyll 'a' concentration in the initial bottle.

After the incubation period, zooplankton were filtered with 80µm sieves for enumeration (see 4.2.1), while for chlorophyll 'a' analysis, 200ml to 500ml sample was filtered on a GF/C or GF/F filter. The pigments were extracted with alkaline (basic)

methanol. The filter is ground with a glass rod so as to facilitate the extraction, because the cell wall of some phytoplankton doesn't release the pigment easily. The extract was then transferred into a centrifuge tube and centrifuged at 3000 rpm at least for 10 minutes.

The pigment extract was decanted in to 10 or 25ml volumetric flask and made up to the mark with methanol. The extract was then transferred to 1cm cuvette after overturning several times. The absorbance of the pigment extract was made and read at 665 and 750nm in a spectrophotometer (SP6-350 model).

Chl 'a' (µg/l) was calculated without acidifying, using the formula of Talling and Driver (1963), which is approximated and doesn't require correction for phaepigment.

$$\text{Chl a (µg/l)} = \frac{13.9x\ (E_{665} - E_{750})\ x\ Ve}{Vf\ x\ PL}$$

Where E_{665} and E_{750} are extinction at 665nm and 750nm respectively

Ve = Volume of extract in ml

Vf = Volume of sample filtered in the lake in litter

Pl= Path length of the cuvette (1cm)

The percentage of grazing rate was calculated after measuring the chlorophyll a, clearance rate and ingestion rate. Clearance rate and ingestion rate was calculated following Marin ***et al***. (1986).

Clearance rate (filtration rate) was calculated using the following formula

$F = V/Nt\ (\ln Ci/Cz)$

Where F is clearance rate in ml/ind/ day, V is volume of the container in 1000 or 2000ml, t is time of incubation per day and N is number of zooplankton grazers in the container, Ci is initial chlorophyll concentration, Cz is final chlorophyll concentration in the bottle that contains grazers (after incubation). The method assumes that change in biomass is only due to grazing, since other causes of death of phytoplankton (e.g. washing out) are unlikely to occur in enclosure experiments.

Cp, which was prepared to observe the net phytoplankton growth or final chlorophyll a concentration in the control bottle (without grazer), was ignored in calculation except for the first study. It is because there was no significant statistical difference between Ci and Cp at $p<0.005$ (Appendix 7), and it indicated that production didn't significantly affect grazing rate in this study. It was probably because often the study was done in late afternoon. For the first study day, Cp (no grazer bottle) was considered, since the biomass in the bottle was appreciably higher. The following formula was used for this case after Vijverberg (2003).

$F= V/Nt * (\ln Ci/Cz - \ln Ci/Cp)$

Ingestion rate as cell/ind/day was calculated by multiplying the food concentration with clearance rate.

$I = F Co$

$\% G = I/Co \times 100$

Where % G is percentage of algal grazed per day

I is ingestion rate cell/ind/day, and

Co is food concentration as cell per ml from the initial bottles (see 4.2.2).

4.2.1 Enumeration and Identification of zooplankton

The remaining volume of sample, after filtering for phytoplankton biomass estimation, was filtered and sub sampled for estimating number of zooplankton per liter. 20-25ml of sub sample was taken for counting using pipette with wide mouth and poured into a grided petridish. Three grids were counted for each sample after allowing the sample to settle and checking the uniform distribution throughout the grids and then extrapolation was made. Counting was done under a stereoscope microscope (magnification of 50 X).

Zooplankton species were identified using Defaye (1988) and Dussart and Fernando (1988).

4.2.2 Phytoplankton cell counting and identification

Phytoplankton samples were counted as stated in Kobayashi ***et al.*** (1998). Each phytoplankton sample was allowed to settle in a 50ml graduate cylinder for more than 24 hours. Excess water was removed by syringe to leave 5ml of the sample water in the graduated cylinder from the concentrated sample. From the concentrated sample, 1 ml of sub sample was taken with a syringe for counting. Phytoplankton cell counts were made using a Sedgwick rafter under an inverted microscope (Nekkon) at magnification of 100x or 400x. Number of cell per ml was calculated as follows after Hotzel and Croome (1999).

$$Co = \frac{N \times 1{,}000 m^3 \times 1}{A \times D \times FX10}$$

Where N is number of cells, A is area of field (mm^2), D is depth of a field (1mm) and F is number fields counted and 1/10 is concentration factor.

Phytoplankton species were identified using Whitford and Schumacher (1973), Hindak (2000) and Komarek and Cenberg (2001). A compound microscope at 1000x magnification power was used for phytoplankton identification.

4.3 Manipulated Zooplankton grazing rates

4.3.1 Zooplankton density change study

The natural density of zooplankton was manipulated experimentally by concentrating zooplankton density at 1x, 2x and 4x, following Cyr and Pace (1992) and incubating each with natural phytoplankton assemblage separately. The incubation was done in bottles, which are labeled as Cz1x, Cz2x and Cz4x, respectively. 1x concentrated means ambient density or filtering a known volume of natural lake water once. 2x and 4x sample were prepared in the same way from the same depth by filtering the natural lake water volume (ambient density of zooplankton) twice and four times, respectively. The idea is that filtering more volume of water would concentrate the zooplankton density likewise.

4.3.2 Size fractionation study

Zooplankton size was fractionated using sieve gauze with 250μm. After zooplankton were filtered and separated by these sieves, they were transferred into bottles, which contain phytoplankton (food), for incubation. Phytoplankton size was differentiated into three size classes (<l0μm, <20μm and <63μm) using Nitex mesh with pore size of 10, 20 and 63μm, respectively. After that three types of samples were prepared for incubation, <10, <20 and <63μm, and then grazers were added to each bottle (samples) after filtering the same volume of water for each bottle. The <10 μm size group are present in all bottles.

4.3.3 Food density change study

The effect of food density change was studied by altering the natural food density with various factors, 1x, 2x and 4x. Three types of bottles were prepared for each. For the first type of bottle, a known volume of lake water was filtered once and added to the

bottle with grazers, and for the second, the volume of lake water filtered was doubled and added to the bottle with the same volume of water with grazers as for the first. The same work was done for the remaining bottle by quadrupling the amount of filtered water.

For the dilution study, the natural water was diluted with various ratio like ½, ¼, and 1/8. It was done by mixing the diluted (filtered with filter GF/F paper) and unfiltered water at these ratios.

4.4. Statistics and index used in the study

Simple t-test was used to check if the variation in grazing rate between the two sites was statistically significant, and ANOVA was used to check if there is statistical difference between Cp and Ci using SPSS (statistical package for social students). Regression analysis was made to check the effect of grazing on chlorophyll a concentration in the lake using Minitab 1-4 Version.

Carlson's trophic state index, Carlson (1977), was used to assess the productive status of the lake using the following formulae.

Chlorophyll-***a*** TSI (TSIC) = 9.81*[ln (Chlorophyll-***a*** average)] + 30.6

5. RESULT AND DISCUSSION

5.1 Zooplankton and phytoplankton Species composition

The Cyclopoid copepod, ***Thermocyclops cosimilis*** dominates the zooplankton community in Lake Kuriftu (Table 3), followed by rotifers. No ***Calanoid*** was encountered during the study time. ***Brachionus*** species dominate among rotifers, while ***Keratella*** and other species were found rarely. The cladocerans (***Diaphanosoma***, ***Moina*** and ***Ceriodaphnia*** spp.) are found with lower abundance than rotifers and cyclopoids. ***Daphnia barbata***, which was reported by Brook Lemma ***et al***. (2001) was not found in this study. On the other hand ***Mesocyclops*** species were observed in this study, unlike previous studies, although it has low occurrence. The phytoplankton species composition of the lake is mainly represented by colonial algae and filamentous cyanobacterial forms. Some of the species identified are listed in Table 4.

The dominance of cyclopoid copepods is common in most Ethiopian lakes. Cyclopoids were reported to be dominant in Lake Abijata (Kassahun Wodajo and Amha Belay, 1984) and in Lake Awasa (e.g. Seyoum Mengistou, 1989). Tesfaye Wudineh (1998)

also reported that cyclopoids like ***Thermocyclops*** and ***Mesocyclops*** species are found abundantly in Lake Tana. These species are also reported to occur commonly in many tropical African lakes by Serruya and Pollingher (1983) and that is probably due to their wide range of feeding habit.

Feeding habits of ***Thermocyclops,*** however, are less defined (Seyoum Mengistou, 1989). ***Thermocyclops*** was reported as being herbivores and raptorial on colonial ***Microcystic*** colonies by Moriarity ***et al***. (1973) in Lake George. On the other hand they have also been observed to prey on cladocerans and chironomids (De Carvalho, 1984). Gophen (1995) also reported that adult cyclopoids are raptorial feeders and prey on other zooplankton (mostly ***Ceriodaphnia***) and detrital particles. The result from the experiment made by Feuchtmayr ***et al***. (2004) indicated that predation by cyclopoid copepods could be reason for the decrease in number of cladoceran in Lake Schöhsee.

One reason for lower abundance of cladocera in Lake Kuriftu could be competition among them. Brook Lemma ***et al***. (2001) pointed out that ***Moina micrura*** and ***Daphnia barbata*** were more efficient grazers in the lake than ***Diaphanosoma*** and ***Ceriodaphnia*** species, and competition as a result of this may lead to suppression of ***Diaphanosoma*** and ***Ceriodaphnia***. In addition high water temperature in tropical lakes than in temperate ones has deleterious effect on reproductive biology of cladoceran and can be reason for low density of these groups of zooplankton (Havens ***et al***., 1996).

Brook Lemma ***et al***. (2001) stated that the presence of ***Daphnia spp.*** in Lake Kuriftu could be assisted by the availability of refuge such as high turbidity, in spite of the

presence of planktivory in the lake. But the increase in secchi depth from 0.2 (Brook Lemma ***et al***., 2001) to 0.5m (Zelalem Dessalegn unpublished thesis, 2006)), indicates lowering of turbidity. This case might have facilitated fish predation and may be reason for the absence of ***Daphnia barbata*** and lower occurrence of other cladocerans during this study. The other most probable reason for lower occurrence of cladocerans could be the common occurrence of blue green algae, particularly larger cyanobacteria, because they affect filtration capacity by interference and also clog feeding apparatus. These phytoplankton are less edible, and sometimes toxic to cladocerans (De Bernardi and Guissani, 1990).

Although ***Ceriodaphnia***, ***Moina*** and ***Diaphanosoma*** are reported in lower percentage composition (Table 5) than ***Thermocyclops*** and rotifers, they most probably have contribution in removing small-sized phytoplankton like diatoms (Fig 5). Gonzalez (2000) reported that these cladocerans mainly prefer diatoms than other food sources.

On the other hand the existence of ***Mesocyclops*** during this study could indicate carnivory or predation by zooplankton as becoming an important food chain in the lake. These species are well known for their carnivorous mode of feeding in many lakes, for example in Lake Awasa and some east African lakes (Seyoum Mengistou, 1989).

Rotifers (particularly ***Brachionus*** spp.) were found abundantly during the study period. This case is common in tropical lakes. For example, Fernando (1980) stated that ***Brachionus*** contributes more than 50% of rotifer species in tropical lakes. Similarly in

Lake Awasa, ***Brachionus*** and ***Keratella*** made up more than half of the rotifer assemblage numerically, between 1983-1987 (Seyoum Mengistou, 1989).

Rotifers can remove phytoplankton, particularly ***Brachionus*** species can resist toxicity of blue greens, but they mainly ingest particulate material (e.g. Gonzalez, 2000). The size fractionation study in the lake (see Appendix 5) also indicated that they probably have lower contribution in removal of phytoplankton.

5.2 Zooplankton grazing rates at ambient (natural) density

The mean zooplankton community-grazing rate obtained during the study period (59.3%) is lower than Lake Hora (75%) and Lake Hayq (72%) but equal to Lake Bishoftu (59.39%) as reported in Habte Jebessa (1994). But some higher values (>100%) were reported in September and December during this study period in Lake Kuriftu.

The above lakes were oligotrophic (Lake Hayk) and mesotrophic (Lake Hora and Bishoftu) during the study period. Grazing rate depends on the trophic status of the lake. In oligotrophic systems abundance of edible algae and zooplankton are lower. And there is a shift in dominance to copepods, which have lower ***per capita*** filtering rates than cladocerans (Carney, 1990). So that grazing rate is expected to be lower in oligotrophic systems than in mesotrophic ones. However, high grazing pressure is reported to higher suppressing effect on phytoplankton in some oligotrophic lakes in some cases (e.g. Gulati ***et al***., 1982; Habte Jebessa, 1994). It is because of the presence of larger zooplankton, which can survive at lower food level in such system and utilize it efficiently.

In mesotrophic lakes, edible and nutritious algae are in higher concentration than in more nutrient poor waters, and the proportion of these algae is greater than eutrophic systems, even though edible algae like diatoms may be common in some cases in olgotrophic lakes due to other factors (e.g. Lake Shalla). In these intermediate systems, there are also sufficient concentrations of cladoceran herbivores, which have high *per capita* filtering rates. So that grazing rate is expected to be higher in such systems than eutrophic and oligotrohic lakes (Carney, 1990).

Carney and Elser (1990) confirmed the weak effect of grazers on large-sized, cyanobacteria – dominated algal assemblage in eutrophic lakes, which supports the view that grazers' impact is weaker in eutrophic and hypertrophic systems. In such nutrient-rich system, colonial and other large algal taxa can dominate and weaken the ability of crustacean zooplankton to graze them efficiently.

The trophic status of the lakes, mentioned above, at that particular study period, may explain the higher grazing rates than the present study in Lake Kuriftu. There are some indications that Lake Kuriftu is in the eutrophic state or in the process of being euthrophic. One indication is the Carlson trophic state index value. The TSIC (trophic state index of chlorophyll) value was 69.1 (with methanol extraction). The Carlson trophic state index indicated that this value lies in the range that shows eutrophic status.

It is not surprising for the lake to be in this trophic state because shallow lakes like Lake Kuriftu (with mean depth 2m and maximum depth 8m (Seifu Kebede, 1998)) usually have a set of conditions that enhance nutrient recycling. Sediments deposited on the lake bottom are able to exchange nutrients easily with upper regions of the lake for algal growth. Activities of microbes and burrowing animals and resuspension of sediments further increase the release of nutrients into the water. In general, there is a tendency for productivity to be correlated negatively with the depth of a lake.

According to De Bernardi and Guisanni (1995), productive lakes are characterized by blue greens, which are not preferred by grazers and can attain more advantage in competition for CO_2 and nutrients at higher $_P$H values than green algae. Rotifers and smaller cladoceran also commonly occur in such lakes. So that the relative dominance of blue green over green algae and common occurrence of small cladoceran and rotifers may indicate the eutrophic condition of Lake Kuriftu. In addition the occurrence of carps, which can tolerate lower oxygen, can indicate the same situation.

The anthropogenic effect and agricultural practices around the lake seems to have a high contribution in making the lake eutrophic. The organic fertilizers that are being used by the farmers have high probability to get into the lake with runoff. The people living around the lake are using it for drinking and cleaning purposes, and the detergents have most probably impact on the productivity of the lake. Odada ***et al***. (2004) stated that soaps and detergents that are being used within the basins, in East Africa are outdated or banned and are contributing to eutrophication since it add phosphate. The cattle around the lake can affect the quality of the lake since they drop dung around the lake (Personal observation).

The rare occurrence of cladocera and common occurrence of large phytoplankton can be reason for not having higher impacts of zooplankton on natural phytoplankton assemblages in Lake Kuriftu. Similar reason was given for shallow tropical Lake Okeechobee (Crisman ***et al***., 1995), which is characterized similarly by lower concentration of cladocera and common occurrence of larger phytoplankton. Since grazing impact is mainly depend on size structure and taxonomic composition of

grazers and phytoplankton (Cyr and Pace, 1992) than other factors, similar reason can most probably apply for both lakes for lower grazing impact.

Higher daily grazing rate (>100%) was observed during September at the littoral site, and in December at both sites (Appendix 1). Even though grazing rates above 100% were reported in some cases in the littoral site, generally grazing rates were higher in the open water than in the littoral except in the first two studies. The difference in grazing rate between the littoral and open water was confirmed to be statistically significant (t-test, $P < 0.05$, Appendix, 6).

It is not uncommon to see sometimes grazing by zooplankton greater than 100% per day especially in eutrophic lake where cyanobacteria are found abundantly (Haney, 1987). In such lakes the difficulties in consuming filamentous and cyanobacteria algae forces zooplankton grazers to feed intensively on small and edible nanoplankton. In the same way, grazing rate above 100% could most probably be brought due to high biomass of the grazers and high relative abundance of small edible algae at those particular study times in Lake Kuriftu (September and December). Particularly in December, higher grazing rate by ambient density of grazers on natural phytoplankton assemblage (Cz 1X) was similar with manipulated grazing on nanoplankton and picoplankton, and it was above 100% (Appendix, 2).

One important question that can be raised here is that in such system, interference of the filtering mechanisms by filamentous forms and seston concentration would affect zooplankton grazing. And that effect in turn protects small grazable nanoplankton. But the ***in situ*** grazing studies by Haney (1973) on the eutrophic Lake Heart, dominated by

Anabaena and Jarvis (1986) on hypereutrophic Hartbeespoort Dam dominated by ***Microcystis*** refute this argument. Zooplankton community grazing rates on these lake and dam on small, highly edible cells, were well in excess of 100% per day and at times as high as 200 and 300% day.$^{-1}$ Thus, despite lowered individual filtering rates in these highly enriched systems, in the time when there is high biomass of grazers, grazing is clearly capable of inflicting serious loss of rates to edible phytoplankton fraction (Haney, 1987).

The result showed that grazing rates, in most of the study period were higher in the open water than in the littoral site. This is probably due to high fish predation pressure in the littoral region. At planktivore stage, ***Oreochromis niloticus*** are mainly restricted to the littoral and profundal zones where they are known to take up substantial amounts of zooplankton as food (e.g. Eyualem Abebe, 1984; Elias Dadebo, 1988).

Table 3. Zooplankton taxa identified in Lake Kuriftu during the study time

Cyclopoida	Rotifera	Cladocera
Thermocyclops consimilis++	***Brachionus bidentata***	*Diaphanosoma excisum*
Mesocyclops aequatorialis[a]	***B. caudatus***	*Moina micrura*
	B. fulcatus++	*Ceriodaphnia sp.*
	B. calcyflorus	
	Filinia sp. [a]	

	Polyarthra sp. [a]	
	Asplanchna sp. [a]	
	Keratella cochlearis[a]	
	K. tropica[a]	

Key

++ Dominant species

[a] Rare occurrence

Like the report of Brook Lemma ***et al***. (2001), wider range of rotifer species are identified in this study (Table 3). But ***Mesocyclops aequatorialis***, and ***Keratella*** species were rarely found during this study period unlike the previous study.

Table 4. Phytoplankton species identified in Lake Kuriftu

Phytoplankton group	Species name
Cyanophyceae (Cyanobacteria)	*Cylindrospermopsis africana* $^{++}$ *C. Curvispora*$^{++}$ *Planktolyngbya sp*$^{+}$ *Microcystis aeuroginesa* *Anabaena circinalis*$^{+}$ *Psuedoanabaena sp*

	Raphidiopsis sp^{+}
Chlorophyceae (Green algae)	*Pediastrum simplex* *P. duplex* *Scenedesmus armatus* *Chlamydomonas reticula* *Phacotus lenticularis*
Bacillariophyceae (Diatoms)	*Thalassiosira sp* *Navicula cryptocephale* *Nitzschia vernicularis* *N. rostellate*
Dinophyceae (Dinoflagellates)	*Peridinium sp*^{n}
Cryptophyceae (Cryptophyta)	*Cryptomonas obvata*
Euglenophyceae (Euglinophyta)	*Phacus longicauda*^{n} *Lepocincilis sp.*

Key ++ most dominant and + dominant, ^{n} rare occurrence

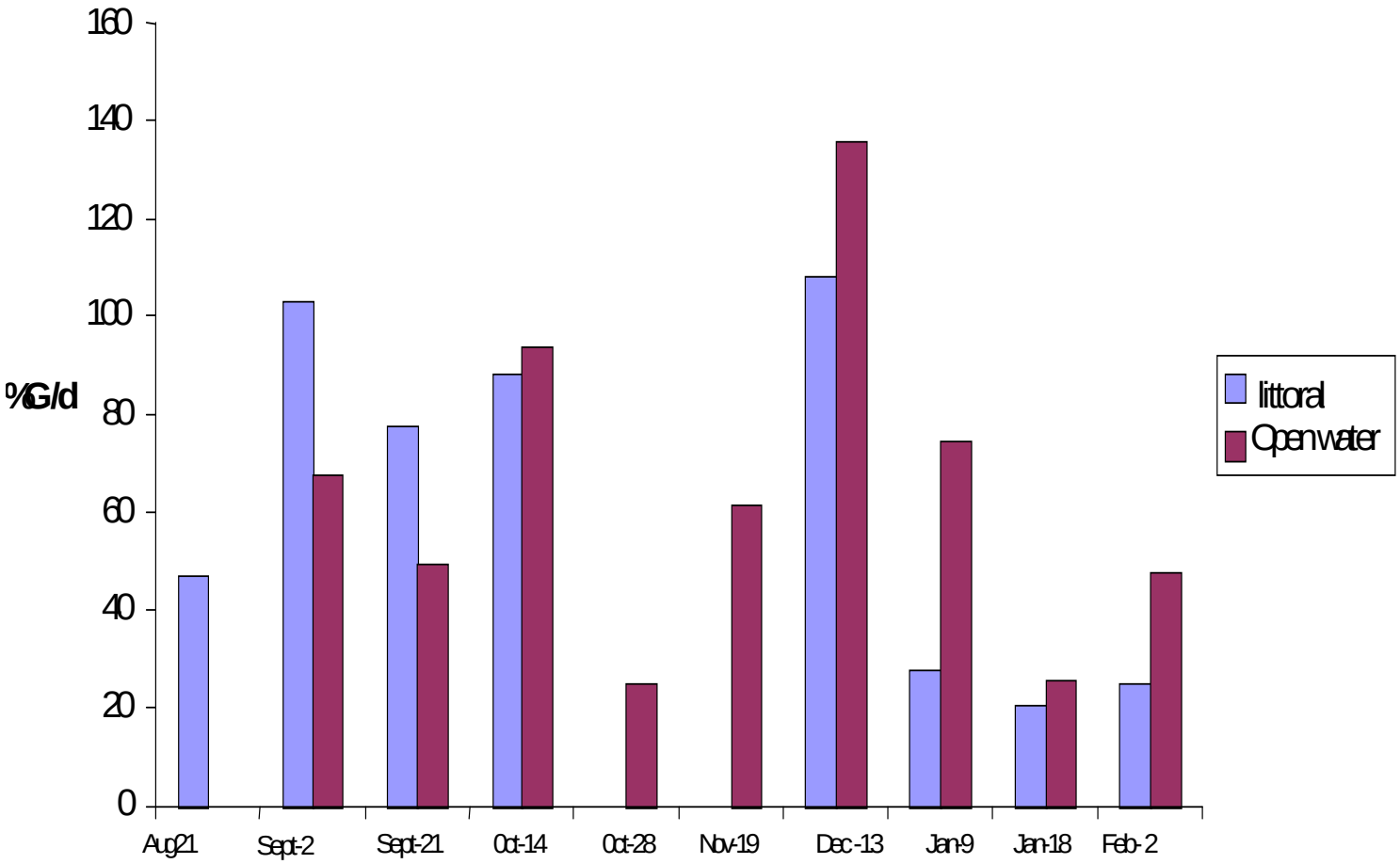

Fig 2. Monthly zooplankton community grazing rate as % d^{-1} in Lake Kuriftu at both sites during the study period (Aug 2005-Feb 2006)

Table 5. Relative proportion of zooplankton abundance in individual count at both sites during the study period

Date	Copepod		cladoceran		Rotifer	
	Open	Littoral	Open	Littoral	Open	Littoral
August 21	-	43.4	-	17.4	-	39.2
September2	63.3	29.2	13	5.8	26.7	65
September21	42	60.2	1	1.1	57	38.7
October 14	30.7	21.3	4.4	12	64.9	66.7
October 28	70.1	-	2.1	-	27.8	-
November19	54.9	-	27.5	-	17.6	-
December13	57.3	36.5	18.6	13.5	24.1	48.9
January 9	66.6	79.2	22.2	18.8	11.2	1.4
January 18	84.3	61.1	8.7	31.8	7	7.1
February 2	82.8	65.6	12.6	19.4	4.4	15
March 1	-	42.4	-	4.2	-	53.4
March 24	-	65.1	-	21.4	-	14.5

5.3 Manipulated zooplankton grazing rates

5.3.1. Effect of zooplankton density changes on grazing rates

The effect of zooplankton density change on grazing rates was studied from August 2005 to March 2006. Except in two cases, (on September 21 and October 28) the highest grazing rates were recorded at ambient density or in Cz1x bottles, which is near to the natural density of the lake but concentrated from depth of 2m(at littoral) and 6m (at open water)(See appendix 1). Grazing trend with increasing zooplankton density is shown in Figures 3 and 4. Grazing rate values ranged from 18.3 to 135.6%. Increasing zooplankton density decreased the grazing rates in all cases, except in two, when an increase in grazing rate was observed when the density was doubled.

The above result agrees with the work of Habte Jebessa (1994) in Lake Bishoftu but is different in other lakes. Increasing zooplankton density decreased the grazing rate only in Lake Bishoftu while it increased in other lakes (Lake Arenguade, Hayq and Hora), at least upto a certain point.

Similarly, the inability of zooplankton community to suppress phytoplankton at higher density was documented with increasing density of grazers in some temperate lakes. For example, one of the surprising results in the experiment of Sommer ***et al***. (2001) was also the inability of even very dense zooplankton populations to depress phytoplankton biomass. Similarly in the mesocosm experiment of Matveev ***et al***., (2000), increasing the abundance of even larger ***Daphnia***, which are known to be efficient grazers couldn't significantly suppress total phytoplankton biovolume and that was probably due to the predominance of colonial forms.

In this study, large volumes of 1000ml and 2000 ml were used, because the larger the container, the more the natural the grazing rate would be (Kobayashi ***et al***., 1998). A

number of workers have found that the grazing rate of copepods is reduced in very small vessels (e.g. Marsh and Orr, 1955), but most of these earlier works assumed that maximum and natural rates were achieved in the largest container used (about 500ml). Keeping the volume of the container constant, while increasing the density of the grazers increases crowding. Peters (1984) was able to observe that experimental conditions such as crowding and duration significantly affect filtering rate. They used multiple regression analysis of secondary data on zooplankton filtering and feeding rates. Crowding reduces the grazing rate of both copepods and cladocerans (Hayward and Gallup, 1976). Crowding can reduce space for grazers, create over competition on available edible algae and can also be responsible for the occurrence of physical and chemical factors.

Lurling ***et al***. (2003) found that a medium which was conditioned by high numbers of cladoceran grazers led to a reduction in grazing rates, and stated strongly that the reduction occurred because of the chemical released by grazers which affect their own mode of feeding.

As stated earlier, in this study, ***Brachionus*** species are found abundantly in Lake Kuriftu. Concentrating these organisms was found to decrease the grazing rate of these rotifers in some studies. For example, Fussmann ***et al***. (2005) observed that encounters of ***Brachionus*** individuals potentially reduce grazing rates through physical interference. Free-swimming ***Brachionus*** individuals that hit an obstacle (or another ***Brachionus*** individual) in a container will retract their anterior corona for a few seconds and stop moving their wheel organ, which is used for both food uptake and locomotion.

Rotifers are more abundant in littoral site than in open water (Table 5). Commonly, smaller zooplankton like rotifers have net positive effect on phytoplankton biomass, particularly on larger phytoplankton (e.g. Lampert ***et al.,*** 1986). One probable reason could be selective removal of smaller phytoplankton by small-sized zooplankton, since these zooplankton graze only smaller phytoplankton selectively unlike larger zooplankton. The second reason could be nutrient release by excretion by these zooplankton. Lehman (1980) reported that rotifers release 3-4x higher phosphorous than other zooplankton. These may be reasons for the mean grazing rate to be below zero at 4x ambient concentration at the littoral site, since concentrating zooplankton necessarily increase the density of rotifers. However the second reason couldn't be significant in this study, since phytoplankton cell couldn't get much light because the incubations were often during late afternoons.

High grazing pressure by higher zooplankton density on edible phytoplankton can favor colonial and other forms cyanobacteria since it removes competitive phytoplankton (Haney, 1987). So, the biomass of phytoplankton may increase at the end of experiments rather than decrease.

The implication of the result of this study for biomanipulation is that increasing the grazers will have no impact on decreasing or clearing phytoplankton in Lake Kuriftu. It seems that the saturation point, for carrying capacity of grazers, in the lake might have already been bypassed, unless concentrating from depth has crowded them in one-litter bottles. Stocking planktivores fish to certain point may reduce the existing natural density of grazers and may increase the impact of zooplankton. But if the appropriate

stocking density is not known, these fishes may severely affect the presence of large and efficient grazers.

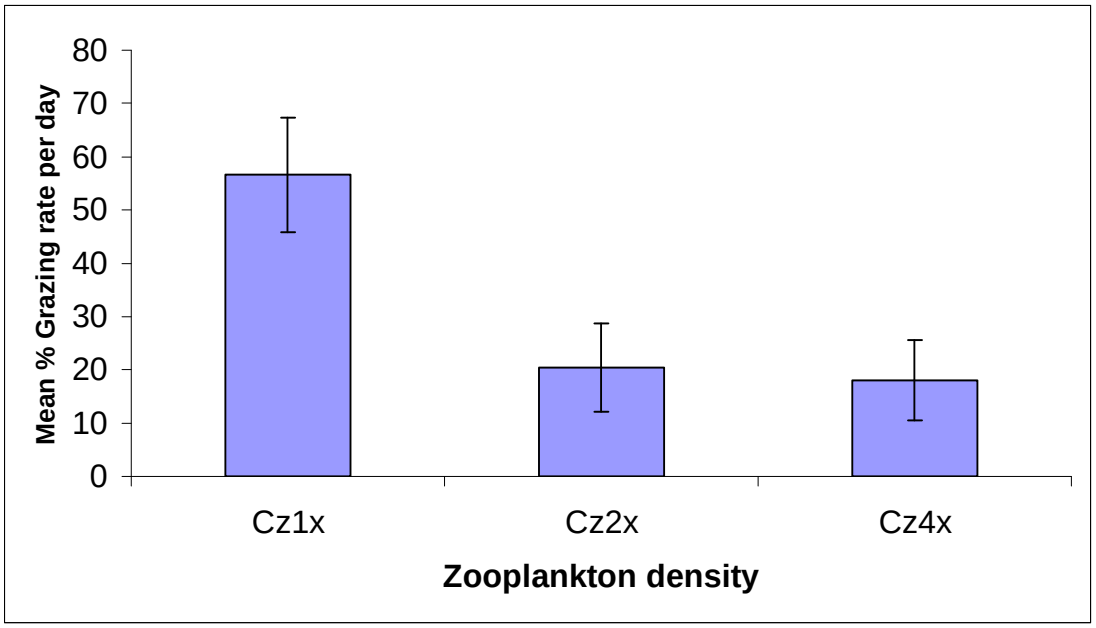

Fig 3. Effect of zooplankton density change on grazing rates in the open water (mean of 33 incubations, bars show standard error).

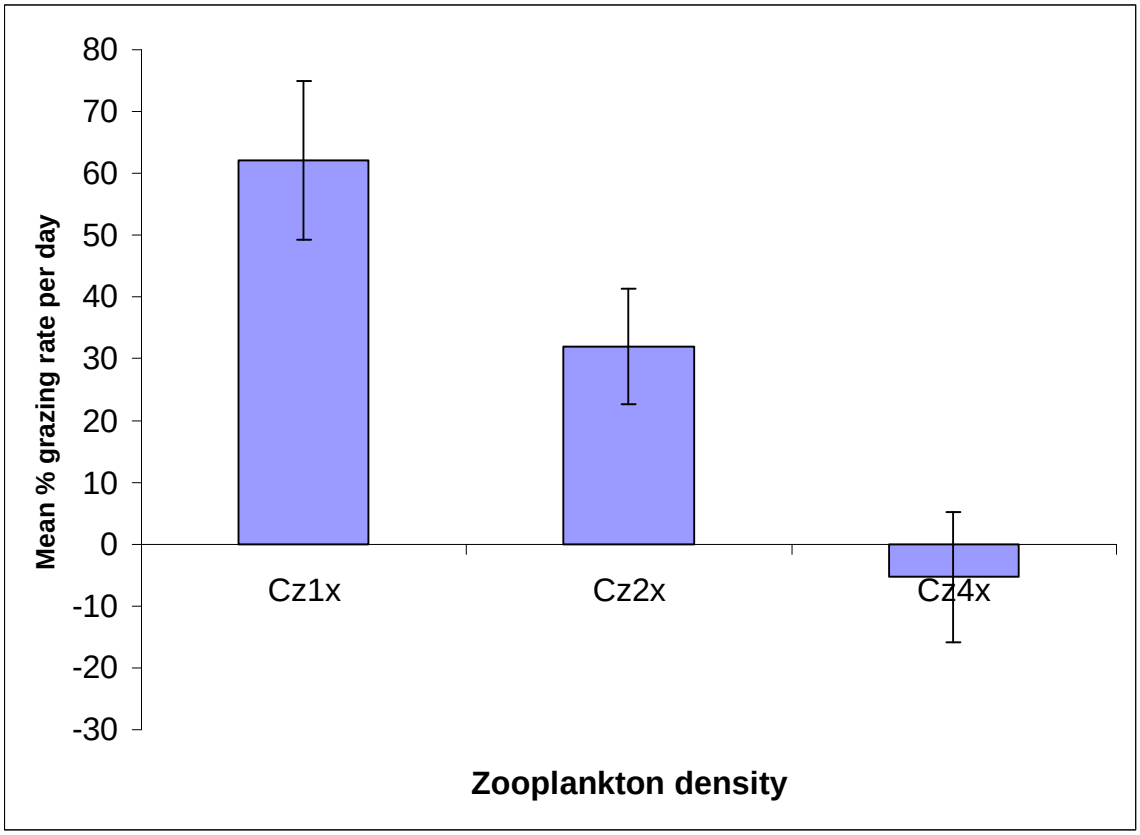

Fig 4. Effect of zooplankton density change on grazing rates in the littoral site (mean of 24 incubations, bar shows standard error)

5.3.2. Zooplankton grazing on size fractionated phytoplankton

Mean higher grazing rate (125.5%) was obtained for the phytoplankton group less than 10µm size (Fig 5). Grazing rates on this size group of phytoplankton was above 100% (appendix 2) in October, November, January and February. The highest grazing rate (288%) was recorded on November 19. The mean grazing rate on phytoplankton size < 20µm (60.8%) was lower than <10 µm sized phytoplankton, but higher than phytoplankton with size of <63µm. Lower mean grazing rates (33.9%) was recorded for larger microplankton (<63µm) as compared to small-sized nanophytoplankton. Even negative grazing rates were obtained on this size group on January 9 and March

1 (Appendix 2). The mean grazing rate trend shows inverse relationship between grazing rate and size of phytoplankton was seen in this study.

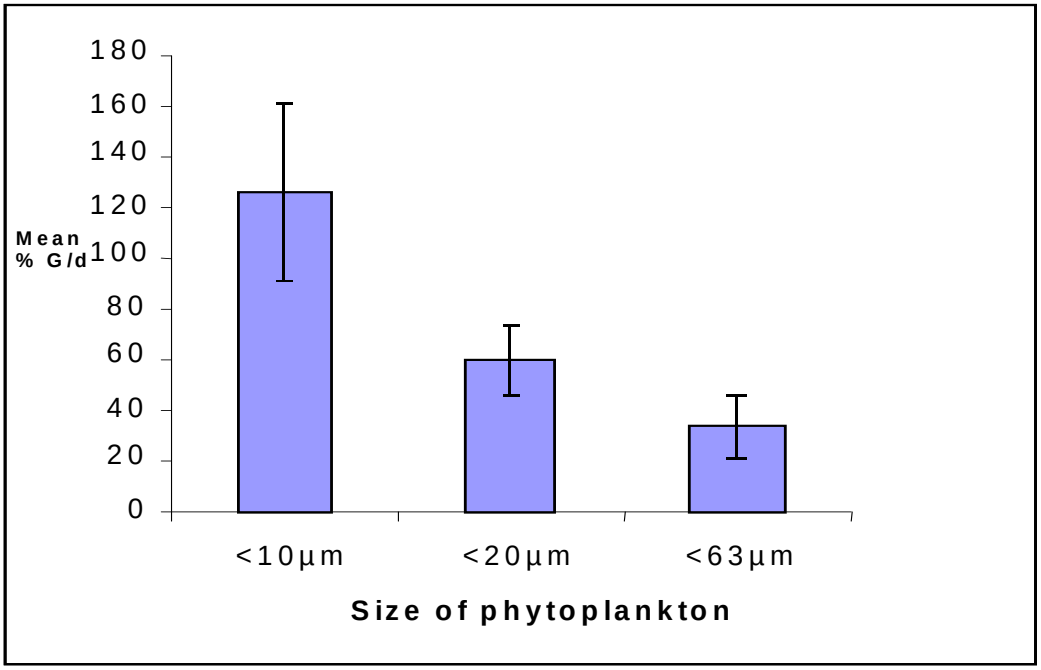

Fig 5. Result for phytoplankton size fractionation study (mean of 18 incubations, and bars show standard error).

The zooplankton community in Lake Kuriftu grazed more efficiently on smaller nanophytoplankton, especially those sizes below 10µm during the study period than the larger phytoplankton (<20 and <63µm). In other words, grazing was very intense on smaller algae (<10µm) (Fig. 5). The “size-efficiency” hypothesis, outlined by Brooks and Dodson (1965) supports this result well. According to their hypothesis, all zooplankton (both larger and smaller) compete for smaller-sized food (1-15µm), because of their ease of edibility, even though larger zooplankton are better competent than smaller ones, particularly when smaller phytoplankton are scarce. Since smaller cells are preferred by both larger and small-sized zooplankton, grazing

on this phytoplankton class (<10µm) is commonly intensive. This could be the reason for the removal of smaller phytoplankton more severely than larger phytoplankton in this study. Brook Lemma ***et al.*** (2001) suggested that size efficiency hypothesis seemed to work in Lake Kuriftu and other studied lakes after their enclosure experiment on fish predation on cladocerans and interaction among them in Lake Kuriftu and other three temperate lakes.

Higher grazing rate (>100%) on smaller phytoplankton (<10µm) coincided with higher relative abundance of larger zooplankton (copepods) in this study. The relative abundance of copepods was 70.1, 84.3 and 82.8% on October 28, January 18 and February 2, respectively (Table 5). On the other hand, the relative abundance of smaller zooplankton (both smaller cladocerans and rotifers) together was 29.9, 15.7 and 17.2 on the same dates. The size efficiency hypothesis and the relative abundance of zooplankton together could indicate that higher grazing rate on smaller-sized phytoplankton in the lake is brought because of grazing by larger zooplankton.

The preference of smaller phytoplankton by zooplankton is not only related to size of grazers but also taxonomic composition. Cyr and Curtis (1999) reported that grazing rate on smaller (<35µm) phytoplankton was intensive by both copepoda and cladocera. According to Peters (1984) freshwater copepods prefer smaller-sized food, and smaller cladocerans also prefer the same sized food (Gliwicz, 1977). Both copepods and cladocera in Lake Kuriftu seem to prefer smaller-sized food and that is probably why higher grazing rate on these phytoplankton size class is observed.

Gliwicz (1977) and (1980) suggested that zooplankton-grazing rate is commonly assumed to decrease with increasing algal size based on observation on gut content

analysis of zooplankton. Although his experiment was done using beads, the result explains size selective feeding by zooplankton.

The removal of smaller phytoplankton (nanoplankton) by grazers than larger ones, is common in productive lakes, because the difficulty in consuming larger phytoplankton forces grazers to feed intensively on small groups of organisms and grazing rate could exceed 100% (Haney, 1987). Grazing rate of 170% was recorded by Lampert ***et al***. (1986) in moderately eutrophic Lake Schöhsee during spring season, which coincides with clear-water phase. According to them, the decline in biomass was neither related to nutrient depletion nor to climatic events, but it was due to grazing on edible nanoplankton.

Burns (1968) stated that planktonic algae up to 35µm are most edible for herbivores. Similarly Cyr and Curtis (1999) stated that algae smaller than 30-35µm sizes are considered edible but algae above this threshold are considered inedible. However feeding strategies of zooplankton are complex and variable among groups and depend not only on size but also on other factors. Size is an important attribute of grazing resistance. There is a lower and upper boundary of edible particle sizes for zooplankton. The upper boundary for small cladocerans and rotifer is about 20µm and for larger cladocerans and copepods it is about 50µm (Sommer and Lampert, 1997). This indicates that even large cladocera and copepod cannot remove larger phytoplankton easily (>50 µm).

Sometimes the presence of smaller zooplankton could favor the presence of phytoplankton, especially the larger ones (Havens, 1993) rather than affecting them,

probably due to nutrient regeneration. This probably supports the negative grazing rate on this size group in January and March. Particularly the time of incubation was longer (18hrs) and partly was in the daytime in March so that nutrient regeneration is expected to be higher.

Quite the reverse result was obtained from the work of Helen and Tiina (2005), in two shallow eutrophic lakes of Estonia. According to their findings, the grazing rates by cladocerans and rotifers were relatively low and had low impact on ingestible phytoplankton (<30µm). Their result suggested that the majority of consumption of the bacterial and phytoplankton primary production was most likely channeled through the microbial loop in those lakes.

Larger phytoplankton must avoid negative net growth rate, and they compensate this by minimizing mortality (Sommer and Lampert, 1997). They must have adaptation to create inconvenience for their grazers to avoid negative growth rate. It is known that most r-selected organisms are smaller and have high edibility unlike K-strategists, which are bigger, and with lower edibility. Having larger size is important for phytoplankton in some aspects, because larger phytoplankton (Microphytoplankton), 20-200µm, have high sinking rates and potential to escape from grazers. On the other hand pico and nanoplankton have low sinking rate and less potential to escape from predators (Margalef, 1978). Grazing rate is most probably related inversely with the size of phytoplankton.

In addition grazers do not prefer larger cells, especially filamentous cyanobacteria, because they affect the filtration capacity by interfering and are less edible (De Bernardi and Guissani, 1990).

The smaller-sized (<10µm), ***Thalassiosira*** species and other unidentified diatoms seem to be preferred by zooplankton grazers as food in Lake Kuriftu. Further, ***Chlamydomonas reticulata, Phacotus lenticularis, Cryptomonas obvata and Scenedesmus spp***, seem to be preferred by grazers because of their smaller size (<20µm). There are many field observations supporting diatoms as an excellent nutritional source for growth of herbivores zooplankton, and most diatoms < 20µm should be threatened by grazing from zooplankton (Willen, 1991). Diatom losses due to grazing are considered more efficient in eutrophic lakes dominated by small centrics than in oligotrophic waters dominated by large diatoms (Sommer ***et al***., 1986).

5.3.3. Zooplankton size gradient grazing study

Zooplankton size <250µm consists of mainly microzooplankton (20-200 µm) such as rotifers, while above this size, mesozooplankton and other larger zooplankton are found. Grazing rates were higher in bottles that contain larger grazers in all the study cases (see Appendix 4 and fig.6). Grazing rate by large-sized zooplankton reached 108% in January. Results obtained in December and March, in the bottles that contain only smaller zooplankton (<250µm), showed that the biomass of phytoplankton was higher than the initial biomass.

The same result was obtained in all lakes that Habte Jebessa (1994) studied and in some temperate lakes (Kobayashi ***et al***., 1998). Matveev ***et al***. (2000) also found that

large grazers to suppress algal biomass more effectively than small grazers, so variation in zooplankton size would lead to variation in grazing impact. Having high biomass and large body size seem to be prerequisite for effective control of phytoplankton by zooplankton grazing (Kobayashi ***et al***., 1998). The reason for that may be the ability of larger zooplankton to consume a wider range of algae types compared to smaller zooplankton (Cooke ***et al***., 1986). Larger-sized zooplankton increase the range of energy rich resources available to them (Hecky, 1984). Paffenhofer and Knoweles (1988) also reported that both feeding and grazing rates increase with animal body sizes. In addition, size efficiency hypothesis suggests that large zooplankton have the ability to utilize large as well as small phytoplankton cells unlike smaller zooplankton, which can utilize only smaller-sized cells (Bogdan and Gilbert, 1984). This ability helps larger zooplankton to have dominance over smaller zooplankton and out compete them often. This could be reason for higher grazing rates in large-sized zooplankton bottles than smaller-sized zooplankton bottles.

As indicated earlier, larger zooplankton were also found to be efficient grazers than smaller sized, but as shown in this study, mean grazing rate for large-sized zooplankton was not as such very high (54.12%). Large grazers are suggested to be effective in suppressing nanoplankton abundance when blooms are in their ‘maturation’ stage, but not when large dense colonies and filamentous already dominate the phytoplankton (Carpenter, 1989). According to the result of this study, even though larger zooplankton have relatively higher impact on smaller phytoplankton size structure (<10 µm), the over all impact of zooplankton community on phytoplankton community structure seems to be low. This result agrees with the

mesocosm experiment of Uitto and Hallfors (1997) on an eutrophic system. Both meso and microzooplankton were not able to control the primary productivity appreciably because enrichment of the system by surplus of inorganic nutrient.

Small cladocerans and copepods clear less water per unit time than do larger individuals, so that they graze less (Knoechel and Holtby, 1986). In addition they can utilize only smaller phytoplankton and cannot compete effectively with large sized zooplankton for smaller edible algae according to size-efficiency hypothesis (Brooks and Dodson, 1965).

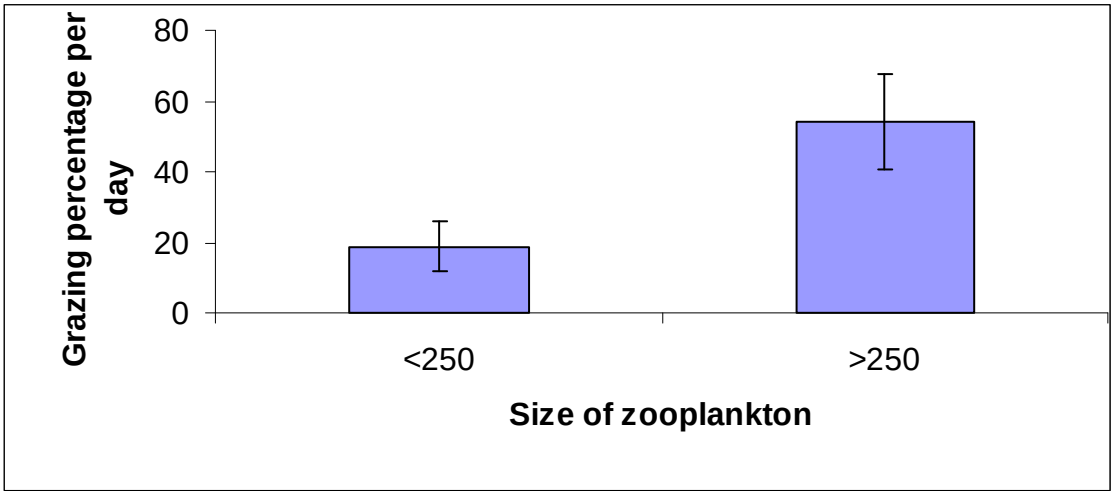

Fig 6. Result for zooplankton size fractionation study (mean of 5 incubations, bars show standard error)

5.3.4. Food density gradient studies

Concentrating the food didn't increase grazing rate in studies done on November 19, 2005 and March 24, 2006 (See appendix 3). On the other hand diluting the natural

food concentration increased the grazing rate with maximum grazing at ¼ of natural concentration.

In all the dilution study made in December 2005 in both the open water and littoral site, the rate of removal of phytoplankton increased at the dilution proportion of ½, and ¼, but not when diluted further. The result was the same on both study sites of the lake.

Some researchers obtained similar results. Folt ***et al***. (1993) found in their experiment that phytoplankton abundance was negatively correlated with zooplankton grazing rates. Thompson ***et al***. (1982) also found in their ***in situ*** experiment that adding 1000 ***Oscillatoria*** filaments per ml reduced filtering rate of adult ***Daphnia*** (1.4-1.6mm) by about 1/30.

Rigler (1971) has formulated three kinds of model to relate feeding rate to food concentration, as follows;

1. Rectilinear model, which implies a constant grazing below the incipient limiting food concentration,
2. The curvilinear model, which implies a decelerating grazing rate as food concentration increases and;
3. The Ivlev model, which permits a reduction in grazing rate at very low food concentration.

The result obtained in Lake Kuriftu showed similar trend with Rigler's curvilinear model. Concentrating the food decreased the grazing rate, and diluting the natural food density of the lake up to ¼ dilution factor increased grazing rate. According to the

results obtained, there might be more than enough amount of food available for grazers. The lake seems to consist densely populated inedible algae and more food than required for grazers (above physiological mechanical limit) in the lake. Both cases discourage grazers to graze intensively.

Concentrating the food in the lake most likely increases the density of colonial forms and filamentous cyanobacteria because these algae are dominant in the lake. Cyanobacteria, like ***Anabaena*** species, are found to inhibit filtering by zooplankton, reducing growth and reproduction (Haney, 1987). These algae are frequently rejected as food (e.g. Porter and Orcurtt, 1980). In addition to that, high densities of such filamentous algae were attributed to interfere with the normal filtering process of zooplankton by clogging their feeding apparatus in the experiment of Boon ***et al***. (1994). So if these species are found in large number within a fixed volume, they negatively affect the grazing rate of zooplankton grazers.

Gliwicz (1980) stated that phytoplankton which are resistant to grazing benefits by being protected and also interfere with the ingestion of edible phytoplankton by filter feeding zooplankton. And according to Sommer and Lampert (1997), if highly inedible algal species, especially filamentous cyanobacteria and large single-cells are drawn into the filtering chamber and then into the food groove of a cladoceran, they must be removed by cleaning movements of the post abdominal claw. This also removes edible algal species. The more frequent such interfering algae, the more they must be removed and the more the filtering process is interrupted (Sommer and Lampert, 1997). Obviously, concentrating the food in the lake facilitate this interruption, and could be responsible for decrease in grazing rate as the food concentration rises.

Bamstedt ***et al***. (2000) suggested that there is probably motivational factor operating to reduce the grazers' interest in feeding in higher food concentration, in addition to upper physiological and mechanical limits. In such cases net phytoplankton growth will exceed well the rate of removal by grazers. Such case could be responsible for negative grazing rates reported in concentrating studies of 2x and 4x (Fig. 7). Particularly on March 24 this condition might be favored due to the longer time of incubation (18hrs) and regeneration of nitrogen and phosphorous by zooplankton faeces favors algal growth.

On the other hand dilution can reduce the density of filamentous algae in the lake and in turn frequency of interruption, so that it could make the removal of edible algae relatively easier. That could be the reason for increased grazing rate, when the natural lake water is diluted by ½ and ¼ factors. The decrease in grazing rate when the dilution factor is increased to 1/8 could be due to decrease in food concentration. The result of this study indicated that the ambient food concentration in the lake is either over saturated or consists of dense inedible algae. Actually as identified phytoplankton species in the lake (Table 4) indicated, inedible forms are very common in the lake. And that might discourage grazers to have significant impact on natural assemblage of algae.

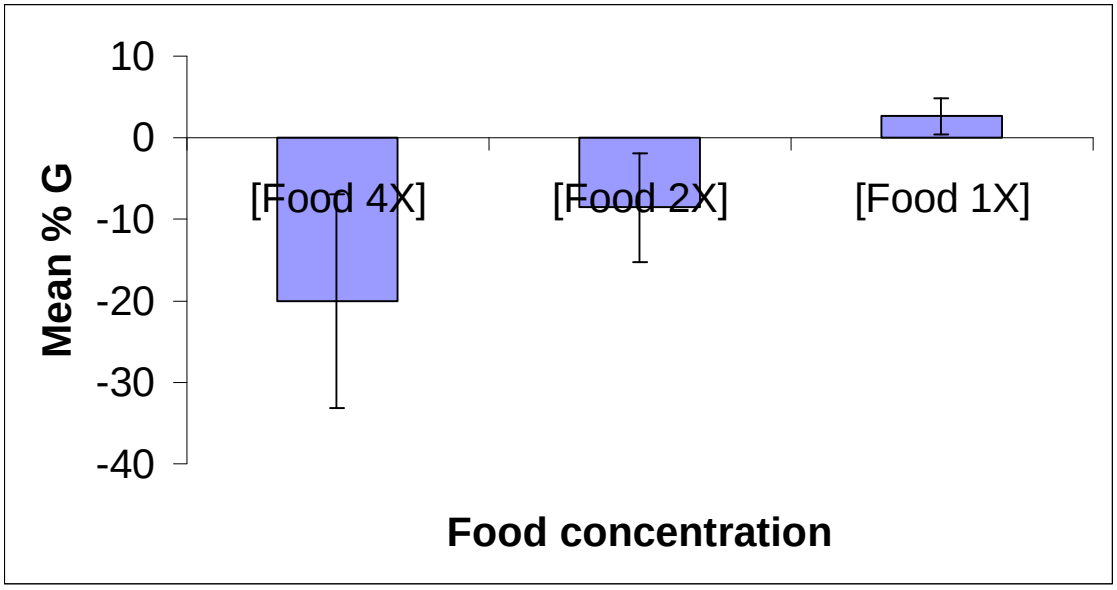

Fig 7. Effect of food concentration on grazing rates in Lake Kuriftu (mean of 6 incubations, bars show standard error)

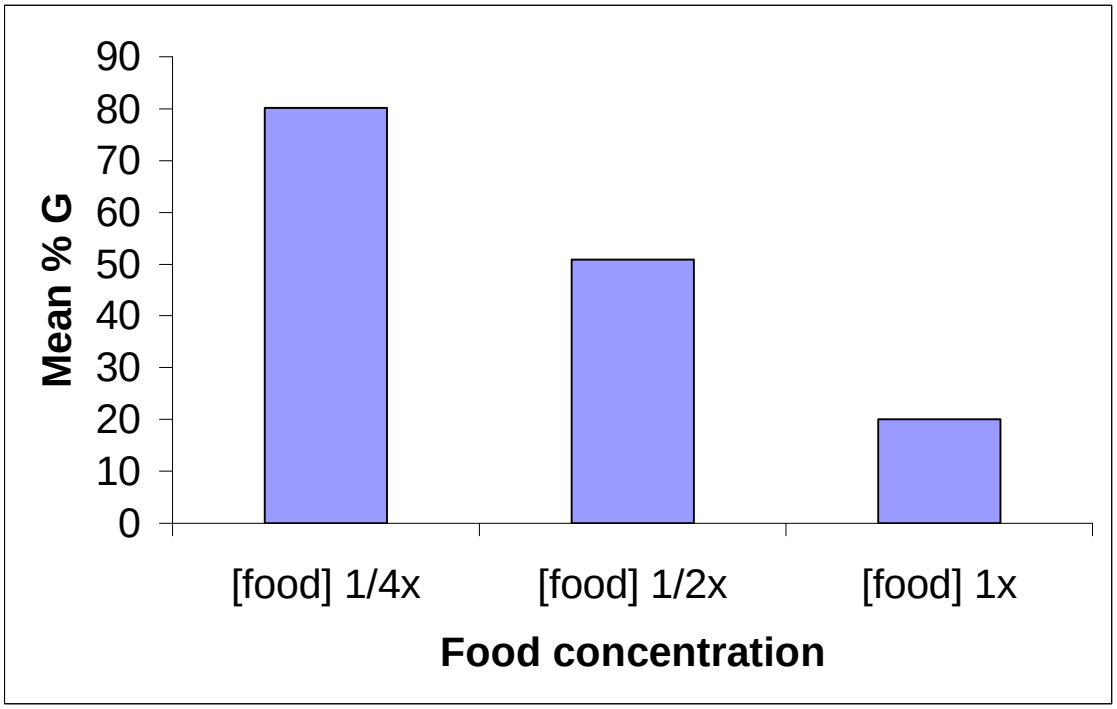

Fig 8. Effect of dilution on grazing rates up to ¼ factors (not replicated)

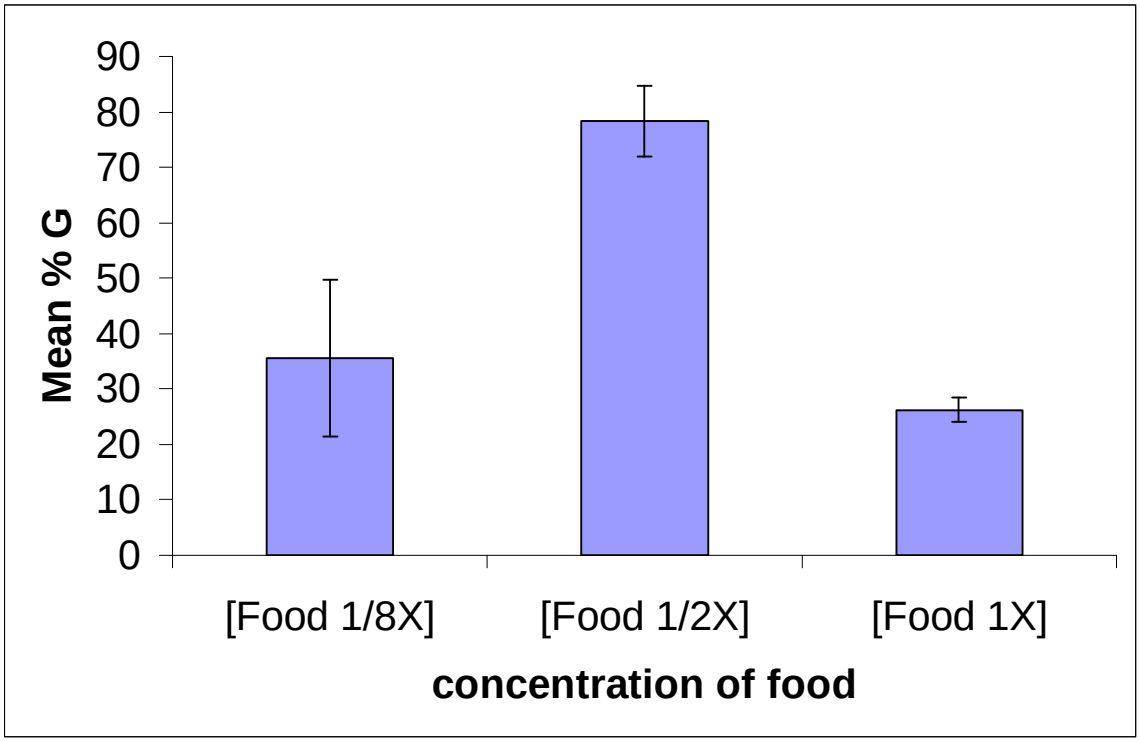

Fig 9. Effect of dilution on grazing rates at the littoral site (mean of 6 incubations, the bars shows standard error).

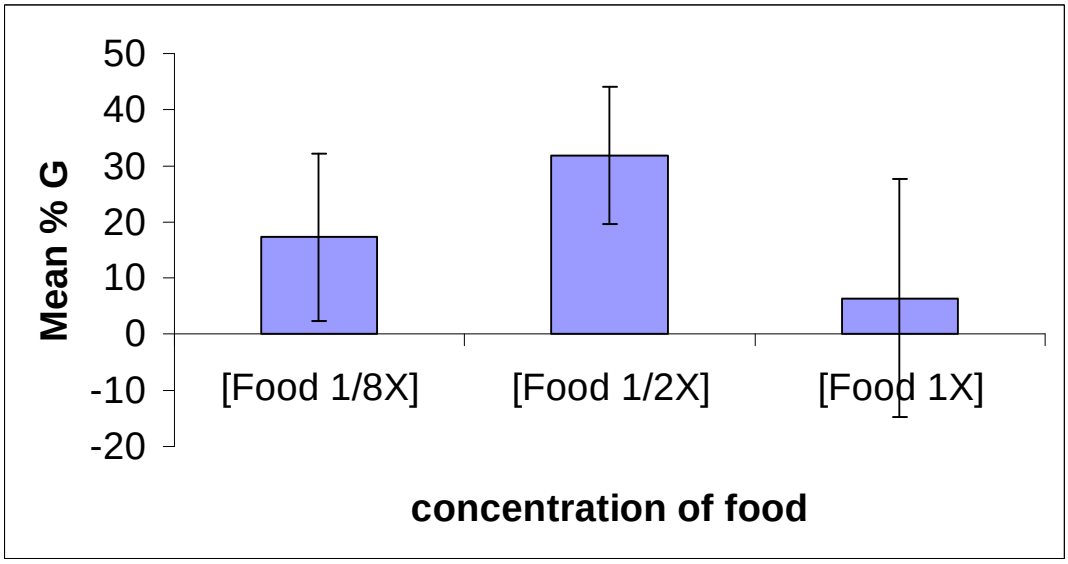

Fig 10. Effect of dilution on grazing rates at open water site (mean of 9 incubations, bars show standard error)

6. Conclusions and Recommendation

The mean percentage-grazing rate of Lake Kuriftu during this study period was lower than most Ethiopian lakes in which grazing rate studies were carried out, although some higher rates were recorded in a few months. The trophic status of the lake could be the reason for the lower grazing rate when it is compared with others. There are some indications that Lake Kuriftu is getting eutrophic or may be it has already become eutrophic. Carlson trophic state index and the species composition of both zooplankton and phytoplankton of the lake indicate eutrophic status. Anthropogenic activities and farming around the lake could contribute largely for the existing eutrophic status of the lake.

Higher grazing rates were measured in the open water than in littoral sites except in a few cases. This could be due to high fish predation on large zooplankton grazers in the littoral site, since immature ***Tilapia*** can feed on zooplankton and are concentrated in the littoral zone.

Manipulated studies showed that increasing zooplankton density decreases grazing rates. Many other studies showed that crowding and duration of incubation has significant effect on grazing rate of grazers. Larger (>250µm) or mesozooplankton were found to be efficient grazers than microzooplankton (<250µm), whereas smaller phytoplankton, particularly (<10 µm) were found to be more easily removed than larger phytoplankton (<20 and <63). These findings also agree with the results of most researches and theoretical explanations. Larger grazers are known to feed on a wide variety of food and have high filtration rate than smaller ones. Edibility of phytoplankton decreased as the size increased, although some factors which affect

edibility, like quality of the food and toxicity were not included in this study. Concentrating the food decreased grazing rate whereas diluting the food increased grazing rate. The above result indicated that there might already exist enough amount of food or the saturation point has been reached. In addition it indicated that grazing would have more contribution, if the lake could be diluted or zooplankton density is reduced by stocking planktivorous fish into the lake since the ambient natural density seems to be weak to control algae. But one has to try some densities like ½ or ¼ of the ambient density, which are not considered in this study, before reaching at this conclusion.

The lake is exposed to nutrient input at two sites. On one end, it is exposed to intervention by local people, where they wash their clothes and bath using detergents and soaps and drink their cattle. Farms, which use organic fertilizers, are near to the opposite side of the lake. Controlling both sources most likely will reduce the productivity of the lake and would change the species composition of phytoplankton and zooplankton in the lake. If it is possible, planting or protecting macrophyte will also have great contribution for the clarity of water and have negative impact on the colonial and filamentous ***cyanobacteria***, by competing for nutrient and light, and producing allelopatic compounds. Macrophyte (Grasses) around lakes are important since they used as nutrient sinks and protect erosion or in other words thy stabilize shores.

The above recommendations are forwarded first, because it is after the change of the species composition of the lake that it can regulate itself. Since there is a strong correlation between phosphorus and chlorophyll-a (bottom-up control) in most other

studies (although cyanobacteria can withstand great variation in their P content), it is suggested that eutrophication could be avoided by controlling phosphorous input to the lake.

Grazing rate has lower effect on regulating the biomass of phytoplankton or chlorophyll 'a' concentration as indicated by R^2 (1.7% for littoral and 10.7% for open water) for both sites (Appendix 8). It seems 'bottom-up' route is important in regulating phytoplankton biomass, and probably the nutrient input and loading is favoring the density of these inedible algae. The results obtained in this study suggest to focus on 'bottom-up' control first, because the species composition of the lake must be changed in order to see 'top-down' impact. And that can be accomplished by controlling nutrient input to the lake. It can be done either by applying some engineering techniques or by using precipitating agents. Other means like controlling the internal loading are not easy. However top-down approaches also should be considered since larger grazers intensively feed on smaller-sized phytoplankton.

Top-down control can bring the reduction of chlorophyll a concentrations in waters, particularly when smaller and non-cyanobacterial phytoplankton are found abundantly. But concerning the control of nuisance ***cyanobacteria***, such as ***Microcystis*** and ***Anabaena***, using the existing zooplankton community may still be of limited use. Most other researches, both in temperate and tropical lakes have shown that impact on phytoplankton depends largely on species composition of both zooplankton and phytoplankton. Sometimes, even in the presence of larger ***Daphnia***, the impact can be less because of the predominance of inedible algae. It appears that bottom-up forces are more important in controlling nuisance cyanobacteria than top-down.

Better clear view for biomanipulation would have been obtained if the feeding biology and other important information on fishes of the lake were known. Studies addressing this gap should be carried out. As stated earlier in this paper food removal method was used for this study, which can give direct information regarding zooplankton and phytoplankton, because it is suitable for the objectives of this study. But, for anyone who is interested in working on grazing, it is recommended to use more than two approaches in order to observe contrasting aspects of feeding of zooplankton.

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APPENDICIES

Abbreviations used in the appendices

Chl “a” – Chlorophyll a concentration in µg/l

N - Number of zooplankton grazers per litter

Co – Number of phytoplankton cell (Cell/ml)

F – Filtration rate (Clearance rate) in ml/ind/day

I – Ingestion rate in cell/ind/day

%G – percentage of grazing rate per day

t – time of incubation

Cz1x – Ambient density of zooplankton

Cz2x – Twice ambient zooplankton density

Cz4x – four times ambient zooplankton density

Appendix 1. Zooplankton density gradient grazing rate

Date	Sample	station	Chl "a"	N	Co	F	I	%G	t
21/08/05	Cp	littoral	139						
	Ci	littoral	21.3						
	Cz1X	littoral	56.52	4,075		0.47		47	20hrs
	Cz2X	littoral	61.62	4,675		0.37		37	
	Cz4x	littoral	75.98	4,900		0.24		24	
2/9/2005	Cp	littoral	27.8						
	Ci	littoral	24.1						
	Cz1x	littoral	6.5	5050	143750	1.03	148062.5	103	6hrs
	Cz2x	littoral	13.9	7575	215625	0.289	62315.6	28.9	
	Cz4x	littoral	47.26	8100	431250	-0.333	-143606.2	-33.3	
	Cp	Open water	52.82						
	Ci	Open water	27.82						
	Cz1x	Open water	17.03	2500	58500	0.676	39546	67.6	7hrs
	Cz2x	Open water	25.02	4000	117000	0.089	10143	8.9	
	Cz4x	Open water	30.58	6100	234000	-0.05	-11700	-5	
21/09/05	Cp	littoral	15.29						
	Ci	littoral	17.375						
	Cz1x	littoral	11.12	3450	71750	0.774	55534.5	77.4	4hrs
	Cz2x	littoral	15.985	5100	143500	0.098	14063	9.8	
	Cz4x	littoral	31.327	7200	287000	-0.393	-1127912	-39.3	
	Cp	Open water	29.537						
	Ci	Open water	32.665						
	Cz1x	Open water	29.19	1081	94500	0.493	46588.5	49.3	5hrs
	Cz2x	Open water	23.63	1728	189000	0.89	168210	89	
	Cz4x	Open water	22.24	2888	378000	0.825	311850	82.5	
14/10/05	Cp	littoral	36.14						
	Ci	littoral	78.5						
	Cz1x	littoral	45.175	2500	219500	0.883	193818.5	88.3	6hrs

	Cz2x	littoral	54.9	2620	98750	0.545	53818.75	54.5	
	Cz4x	littoral	107	2840	452666.7	-0.437	-197815.34	-43.7	
	Cp	Openwater	63.2						
	Ci	Openwater	79.2						
	Cz1x	Openwater	55.6	1300	102750	0.936	96174	93.6	7hrs
	Cz2x	Openwater	59.77	2500	309333	0.338	120021.2	33.8	
	Cz4x	Openwater	58.4	4,900	159500	0.214	34133	21.4	
28/10/05	Cp	Openwater	3.48						
	Ci	Openwater	68.8						
	Cz1x	Openwater	33.7	3432	54000	0.25	13500	25	20hrs
	Cz2x	Openwater	12.51	4536	52000	0.37	19240	37	
	Cz4x	Openwater	9.73	6186	124000	0.38	47120	38	
19/11/05	Ci	Openwater	44.5						
	Cz1x	Openwater	30.58	3060	441100	0.613	270394	61.3	6hrs
	Cz2x	Openwater	36.7	8520	248200	0.11	27302	11	
	Cz4x	Openwater	40.03	10590	150800	0.039	345881.2	3.9	
13/12/05	Ci	littoral	132.05						
	Cz1x	littoral	70.72	1,920	1435200	1.08	1550016	108	8hrs
	Cz2x	littoral	57.45	2,940	1436200	0.845	1213589	84.5	
	Cz4x	littoral	76.45	4575	987600	0.358	353560.8	35.8	
	Ci	Openwater	13.9						
	Cz1x	Openwater	2.32	1500	1562000	1.356	211807.2	135.6	7hrs
	Cz2x	Openwater	13.2	3960	804400	0.042	33784.8	4.2	
	Cz4x	Openwater	15.568	4540	1474200	-0.088	-129729.6	-8.8	
9/1/2006	Ci	littoral	38.92						
	Cz1x	littoral	19.46	3350	560750	0.275	154206.25	27.5	8hrs
	Cz2x	littoral	16.68	4200	1174400	0.201	236054.4	20.1	
	Cz4x	littoral	32.665	5300	282600	0.098	27694.8	9.8	
	Ci	Openwater	25.72						
	Cz1x	Openwater	15.98	3850	616000	0.745	458920	74.5	7hrs

	Cz2x	Openwater	30.84	5450	411800	-0.2	370620	-20	
	Cz4x	Openwater	16.68	12700	1232500	0.2	246500	20	
18/1/2006	Ci	littoral	41.7						
	Cz1x	littoral	15.985	5650	1149600	0.203	233368.8	20.3	6hrs
	Cz2x	littoral	34.055	8300	1839800	0.117	215256.6	11.7	
	Cz4x	littoral	45.2	11600	533600	-0.008	-4268.8	-0.8	
	Ci	Openwater	78.765						
	Cz1x	Openwater	48.09	2194	1174000	0.256	30054.4	25.6	7hrs
	Cz2x	Openwater	58.38	3366	587600	0.11	64636	11	
	Cz4x	Openwater	36.14	8900	103800	0.109	11314.2	10.9	
2/2/2006	Ci	littoral	75.06						
	Cz1x	littoral	50.73	5400	651200	0.25	162800	25	
	Cz2x	littoral	61.85	7300	1375400	0.091	125161.4	9.1	
	Cz4x	littoral	67.415	21100	791400	0.047	37195.8	4.7	
	Ci	Openwater	67.415						
	Cz1x	Openwater	39.62	4500	1025800	0.472	484177.6	47.2	
	Cz2x	Openwater	43.09	8700	965750	0.205	197978.75	20.5	
	Cz4x	Openwater	49.346	10457	897200	0.102	91514.4	10.2	
1/3/2006	Ci	Openwater	41.1						
	Cz1x(P1x)	Openwater	31.3	1966	1282400	0.183	234679.2	18.3	18
	Cz1x(P2x)	Openwater	31.9	5083	1548800	0.066	102220.8	6.6	
	Cz2x(P1x)	Openwater	25	7783	1000580	0.17	170098.6	17	
	Cz2x(P2x)	Openwater	54.2	10266	2513200	-0.07	-175924	-7	
24/03/06	Cp	Openwater	26.69						
	Ci	Openwater	29.88						
	Cz1x(P1x)	Openwater	11.82	5115	397600	0.242	96219.2	24.2	18
	Cz2x(P2x)	Openwater	15.98	6780	367000	0.122	44774	12.2	
	Cz4x(P4x)	Openwater	15.98	11450	31783.6	0.0724	31783.6	7.2	

Appendix 2. Grazing rate on different phytoplankton size group

Date	sample	station	Chl "a"	N	F	I	%G
28/10/05	<10	Openwater	6.95	1468	1.88	103400	188
	<20	Openwater	40.87	2205	0.28	61600	28
	<63	Openwater	39.6	1782	0.37	62900	37
19/11/05	<10	Openwater	25.5	960	2.88	1351840	288
	<20	Openwater	31.7	3300	0.509	263954.675	50.9
	<63	Openwater	32.24	2190	0.735	304584	73.5
13/12/05	<10	Openwater	7.645	6,180	0.322	235124.4	32.2
	<20	Openwater	8.34	550	1.045	821161	104.5
	<63	Openwater	8.34	4140	0.408	282580.8	40.8
9/1/2006	<10	Openwater	22.24	2850	0.101	103888.6	10.1
	<20	Openwater	18.76	1500	0.419	87152	41.9
	<63	Openwater	32.66	3750	-0.127	-82391.25	-12.7
18/1/2006	<10	Openwater	18.76	5160	1.675	1108515	167.5
	<20	Openwater	20.85	5950	1.134	821242.8	113.4
	<63	Openwater	49.35	9167	0.307	158227.8	30.7
2/2/2006	<10	Openwater	50.04	1074	0.118	552948	118
	<20	Openwater	59.77	1680	0.028	426720	28
	<63	Openwater	53.515	1008	0.085	57178.65	85
1/3/2006	<10	Openwater	34.1	1058	0.0226	26473.64	22.6
	<20	Openwater	29.2	2250	0.204	168626.4	20.4
	<63	Openwater	49.3	3525	-0.078	99013.2	-7.8
17/3/2006	<10	Openwater	27.8	1232	1.782	14323.5	178.2
	<20	Openwater	23.63	2999	0.992	10005.8	99.2
	<63	Openwater	39.615	1998	0.247	3456.9	24.7

Appendix 3 Grazing rate values for concentrating studies

Date	Sample name	study site	Chl a	N	F	I	%G
19/11/05	[food]1x	Open water	43.4	3060	0.048	19555.2	4.8
	[food]2x	Open water	58.4	9000	-0.152	-133083.6	-15.2
	[food]4x	Open water	94.52	104	-0.331	-4,437,567.75	-33.1
24/03/06	[food]1x	Open water	29.46	3125	0.0042	2833.3	0.42
	[food]2x	Open water	31	2800	-0.019	-28899	-1.9
	[food]4x	Open water	34.05	2450	-0.07	-66395	-7

Appendix 4 Grazing rate values for diluting food concentration studies

Date	Sample name	Study site	Chl a	N	F	I	%G
13/12/05	[food]1x	littoral	62.55	11,140	0.201	234195	20.1
	[food]1/2x	littoral	51.43	5,616	0.508	524560.8	50.8
	[food]1/4x	littoral	34.75	5000	0.802	696456.8	80.2
18/1/06	[food]1x	littoral	34.055	3384	0.284	81848.8	28.4
	[food]1/2x	littoral	25.02	3383	0.719	486619.2	71.9
	[food]1/8x	littoral	27.8	9000	0.214	131267.6	21.4
	[food]1x	Open water	41	4980	0.451	986607.6	45.1
	[food]1/2x	Open water	36.835	5000	0.524	309,893.60	52.4
	[food]1/8x	Open water	41.7	4644	0.472	508249.6	47.2
2/2/2006	[food]1x	littoral	56.99	4575	0.241	179641.4	24.1
	[food]1/2x	littoral	42.39	2695	0.847	937290.2	84.7
	[food]1/8x	littoral	50.04	3257	0.497	574830.2	49.7
	[food]1x	Open water	65.48	3180	0.021	9840.6	2.1
	[food]1/2x	Open water	58.38	4820	0.102	155448	10.2
	[food]1/8x	Open water	64.79	4400	0.031	52904.6	3.1
1/3/2006	[food]1x	Open water	47.9	1000	-0.28	-252000	-28
	[food]1/2x	Open water	26.4	1766	0.33	197802	33
	[food]1/8x	Open water	40.1	1783	0.017	13711.84	1.7

Appendix 5. Zooplankton size gradient grazing rate

Date	Sample name	Study site	Chl a	N	F	I	%G
13/12/05	>250	Open water	10.43	1602	0.26	140192	26
	<250	Open water	15.28	1380	-0.115	-32453	-11.5
9/1/2006	>250	Open water	22.935	1100	0.251	95882	25.1
	<250	Open water	24.325	1100	0.102	40621.5	10.2
18/1/06	>250	Open water	52.125	2300	1.081	-1362768	108.1
	<250	Open water	39.1615	14850	0.283	-251094.8	28.3
2/2/2006	>250	Open water	46.56	4,420	0.335	87569	33.5
	<250	Open water	48.65	4560	0.286	250936.4	28.6
17/3/2006	>450	Open water	36.835	2800	0.301	101460	30.1
	>250	Open water	36.14	1200	0.779	329122	77.9
	<250	Open water	32.08	3680	0.385	122000	38.5

Appendix 6. Statistical test for difference of grazing rate among sites

One-Sample Test

	t	df	Sig. (2-tailed)	Mean Difference	95% Confidence Interval of the Difference	
					Lower	Upper
Littoral	4.389	6	.005	64.2143	28.4157	100.0128
Open water	5.171	6	.002	70.4857	37.1306	103.8408

Appendix 7. Statistical test for the difference between Ci and Cp

ONE WAY ANOVA

	Sum of Squares	df	Mean Square	F	Sig.
Between Groups	668.003	1	668.003	1.281	.277
Within Groups	7302.288	14	521.592		
Total	**7970.291**	**15**			

Analysis of Variance for littoral

Source	DF	SS	MS	F	P
Date	7	9249	1321	*	*
Error	0	0	*		
Total	7	9249			

ANOVA
VAR00002

	Sum of Squares	df	Mean Square	F	Sig.
Between Groups	668.003	1	668.003	1.281	.277
Within Groups	7302.288	14	521.592		
Total	7970.291	15			

One-way Analysis of Variance

Analysis of Variance for littoral

Source	DF	SS	MS	F	P
Date	7	9249	1321	*	*
Error	0	0	*		
Total	7	9249			

At high temperature, cyanobacteria appear to dominate over a wider range of N: P and Si: P ratios than they do at lower temperatures where diatoms are favored (Havens ***et al***., 1996).

Descriptives
VAR00002

	N	Mean	Std. Deviation	Std. Error	95% Confidence Interval for Mean Lower Bound	Upper Bound	Minimum	Maximum
1.00	8	31.8696	19.15513	6.77236	15.8555	47.8837	3.48	63.20
2.00	8	44.7925	26.00510	9.19419	23.0517	66.5333	17.38	79.20
Total	16	38.3311	23.05109	5.76277	26.0480	50.6141	3.48	79.20

ANOVA

VAR00002

	Sum of Squares	df	Mean Square	F	Sig.
Between Groups	668.003	1	668.003	1.281	.277
Within Groups	7302.288	14	521.592		
Total	7970.291	15			

5.4 Statistical result

The statistical analysis was made to check if there is statistical difference in grazing rate between the two sites, and the result showed that there is significant difference between these two sites.

One-way Analysis of Variance

Analysis of Variance for littoral

Source	DF	SS	MS	F	P
Open water	6	8990	1498	*	*
Error	0	0	*		
Total	6	8990			

Appendicies

Abbreviations used in the appendices

Chl “a” – Chlorophyll a concentration in µg/l

N - Number of zooplankton grazers per litter

Co – Number of phytoplankton cell (Cell/ml)

F – Filtration rate (Clearance rate) in ml/ind/day

I – Ingestion rate in cell/ind/day

%G – percentage of grazing rate per day

t – time of incubation

Cz1x – Ambient density of zooplankton

Cz2x – Twice ambient zooplankton density

Cz4x – four times ambient zooplankton density

Appendix 1. Zooplankton density gradient grazing rate

Date	Sample	station	Chl "a"	N	Co	F	I	%G	t
21/08/05	Cp	littoral	139						
	Ci	littoral	21.3						
	Cz1X	littoral	56.52	4,075	-	0.47	-	47	20hrs
	Cz2X	littoral	61.62	4,675	-	0.37	-	37	
	Cz4x	littoral	75.98	4,900	-	0.24	-	24	
2/9/2005	Cp	littoral	27.8						
	Ci	littoral	24.1						
	Cz1x	littoral	6.5	5050	14375	1.03	14806.25	103	6hrs
	Cz2x	littoral	13.9	7575	21562.5	0.289	6231.56	28.9	
	Cz4x	littoral	47.26	8100	43125	-0.333	-14360.62	-33.3	
	Cp	Open water	52.82						
	Ci	Open water	27.82						
	Cz1x	Open water	17.03	2500	5850	0.676	3954.6	67.6	7hrs
	Cz2x	Open water	25.02	4000	11700	0.089	1014.3	8.9	
	Cz4x	Open water	30.58	6100	23400	-0.05	-1170.0	-5	
21/09/05	Cp	littoral	15.29						
	Ci	littoral	17.375						
	Cz1x	littoral	11.12	3450	7175	0.774	5553.45	77.4	4hrs
	Cz2x	littoral	15.985	5100	14350	0.098	1406.3	9.8	
	Cz4x	littoral	31.327	7200	28700	-0.393	-112791.2	-39.3	
	Cp	Open water	29.537						
	Ci	Open water	32.665						
	Cz1x	Open water	29.19	1081	9450	0.493	4658.85	49.3	5hrs
	Cz2x	Open water	23.63	1728	18900	0.89	16821.0	89	
	Cz4x	Open water	22.24	2888	37800	0.825	31185.0	82.5	
14/10/05	Cp	littoral	36.14						
	Ci	littoral	78.5						
	Cz1x	littoral	45.175	2500	21950	0.883	19381.85	88.3	6hrs

	Cz2x	littoral	54.9	2620	9875	0.545	5381.875	54.5	
	Cz4x	littoral	107	2840	45266.7	-0.437	-19781.534	-43.7	
	Cp	Openwater	63.2						
	Ci	Openwater	79.2						
	Cz1x	Openwater	55.6	1300	10275	0.936	9617.4	93.6	7hrs
	Cz2x	Openwater	59.77	2500	30933.3	0.338	12002.12	33.8	
	Cz4x	Openwater	58.4	4,900	15950	0.214	3413.3	21.4	
28/10/05	Cp	Openwater	3.48						
	Ci	Openwater	68.8						
	Cz1x	Openwater	33.7	3432	5400	0.25	1350.0	25	20hrs
	Cz2x	Openwater	12.51	4536	5200	0.37	1924.0	37	
	Cz4x	Openwater	9.73	6186	12400	0.38	4712.0	38	
19/11/05	Ci	Openwater	44.5						
	Cz1x	Openwater	30.58	3060	44110	0.613	27039.4	61.3	6hrs
	Cz2x	Openwater	36.7	8520	24820	0.11	2730.2	11	
	Cz4x	Openwater	40.03	10590	15080	0.039	34588.12	3.9	
13/12/05	Ci	littoral	132.05						
	Cz1x	littoral	70.72	1,920	143520	1.08	155001.6	108	8hrs
	Cz2x	littoral	57.45	2,940	143620	0.845	121358.9	84.5	
	Cz4x	littoral	76.45	4575	98760	0.358	35356.08	35.8	
	Ci	Openwater	13.9						
	Cz1x	Openwater	2.32	1500	156200	1.356	21180.72	135.6	7hrs
	Cz2x	Openwater	13.2	3960	80440	0.042	3378.48	4.2	
	Cz4x	Openwater	15.568	4540	147420	-0.088	-12972.96	-8.8	
9/1/2006	Ci	littoral	38.92						
	Cz1x	littoral	19.46	3350	56075	0.275	15420.625	27.5	8hrs
	Cz2x	littoral	16.68	4200	117440	0.201	23605.44	20.1	
	Cz4x	littoral	32.665	5300	28260	0.098	2769.48	9.8	
	Ci	Openwater	25.72						
	Cz1x	Openwater	15.98	3850	61600	0.745	45892	74.5	7hrs

	Cz2x	Openwater	30.84	5450	41180	-0.2	37062	-20	
	Cz4x	Openwater	16.68	12700	123250	0.2	24650	20	
18/1/2006	Ci	littoral	41.7						
	Cz1x	littoral	15.985	5650	114960	0.203	23336.88	20.3	6hrs
	Cz2x	littoral	34.055	8300	183980	0.117	21525.66	11.7	
	Cz4x	littoral	45.2	11600	53360	-0.008	-426.88	-0.8	
	Ci	Openwater	78.765						
	Cz1x	Openwater	48.09	2194	117400	0.256	3005.44	25.6	7hrs
	Cz2x	Openwater	58.38	3366	58760	0.11	6463.6	11	
	Cz4x	Openwater	36.14	8900	10380	0.109	11314..2	10.9	
2/2/2006	Ci	littoral	75.06						
	Cz1x	littoral	50.73	5400	65120	0.25	16280	25	7hrs
	Cz2x	littoral	61.85	7300	137540	0.091	12516.14	9.1	
	Cz4x	littoral	67.415	21100	79140	0.047	3719.58	4.7	
	Ci	Openwater	67.415						
	Cz1x	Openwater	39.62	4500	102580	0.472	48417.76	47.2	6hrs
	Cz2x	Openwater	43.09	8700	96575	0.205	19797.875	20.5	
	Cz4x	Openwater	49.346	10457	89720	0.102	9151.44	10.2	
1/3/2006	Ci	Openwater	41.1						
	Cz1x(P1x)	Openwater	31.3	1966	128240	0.183	23467.92	18.3	18hrs
	Cz1x(P2x)	Openwater	31.9	5083	154880	0.066	10222.08	6.6	
	Cz2x(P1x)	Openwater	25	7783	100058	0.17	17009.86	17	
	Cz2x(P2x)	Openwater	54.2	10266	251320	-0.07	-17592.4	-7	
24/03/06	Cp	Openwater	26.69						
	Ci	Openwater	29.88						
	Cz1x(P1x)	Openwater	11.82	5115	39760	0.242	9621.92	24.2	18hrs
	Cz2x(P2x)	Openwater	15.98	6780	36700	0.122	4477.4	12.2	
	Cz4x(P4x)	Openwater	15.98	11450	3178.36	0.0724	3178.36	7.2	

Appendix 2. Grazing rate on different phytoplankton size group

Date	sample	station	Chl "a"	N	F	I	%G
28/10/05	<10	Openwater	6.95	1468	1.88	10340	188
	<20	Openwater	40.87	2205	0.28	6160	28
	<63	Openwater	39.6	1782	0.37	6290	37
19/11/05	<10	Openwater	25.5	960	2.88	135184	288
	<20	Openwater	31.7	3300	0.509	26395.5	50.9
	<63	Openwater	32.24	2190	0.735	30458.4	73.5
13/12/05	<10	Openwater	7.645	6,180	0.322	23512.44	32.2
	<20	Openwater	8.34	550	1.045	82116.1	104.5
	<63	Openwater	8.34	4140	0.408	28258.08	40.8
9/1/2006	<10	Openwater	22.24	2850	0.101	10388.86	10.1
	<20	Openwater	18.76	1500	0.419	8715.2	41.9
	<63	Openwater	32.66	3750	-0.127	-8239.125	-12.7
18/1/2006	<10	Openwater	18.76	5160	1.675	110851.5	167.5
	<20	Openwater	20.85	5950	1.134	82124.28	113.4
	<63	Openwater	49.35	9167	0.307	15822.78	30.7
2/2/2006	<10	Openwater	50.04	1074	0.118	55294.8	118
	<20	Openwater	59.77	1680	0.028	42672	28
	<63	Openwater	53.515	1008	0.085	5717.865	85
1/3/2006	<10	Openwater	34.1	1058	0.0226	2647.364	22.6
	<20	Openwater	29.2	2250	0.204	1686.3	20.4
	<63	Openwater	49.3	3525	-0.078	9901.3	-7.8
17/3/2006	<10	Openwater	27.8	1232	1.782	1432.35	178.2
	<20	Openwater	23.63	2999	0.992	1000.58	99.2
	<63	Openwater	39.615	1998	0.247	345.69	24.7

Appendix 3 Grazing rate values for concentrating studies

Date	Sample name	study site	Chl a	N	F	I	%G
19/11/05	[food]1x	Open water	43.4	3060	0.048	1955.52	4.8
	[food]2x	Open water	58.4	9000	-0.152	-13308.36	-15.2
	[food]4x	Open water	94.52	104	-0.331	-4,437,56.8	-33.1
24/03/06	[food]1x	Open water	29.46	3125	0.0042	283.3	0.42
	[food]2x	Open water	31	2800	-0.019	-2889.9	-1.9
	[food]4x	Open water	34.05	2450	-0.07	-6639.5	-7

Appendix 4 Grazing rate values for diluting food concentration studies

Date	Sample name	Study site	Chl a	N	F	I	%G
13/12/05	[food]1x	littoral	62.55	11,140	0.201	23419.5	20.1
	[food]1/2x	littoral	51.43	5,616	0.508	52456.1	50.8
	[food]1/4x	littoral	34.75	5000	0.802	69645.6	80.2
18/1/06	[food]1x	littoral	34.055	3384	0.284	8184.8	28.4
	[food]1/2x	littoral	25.02	3383	0.719	48661.9	71.9
	[food]1/8x	littoral	27.8	9000	0.214	13126.7	21.4
	[food]1x	Open water	41	4980	0.451	98660.76	45.1
	[food]1/2x	Open water	36.835	5000	0.524	309,89.36	52.4
	[food]1/8x	Open water	41.7	4644	0.472	50824.96	47.2
2/2/2006	[food]1x	littoral	56.99	4575	0.241	17964.14	24.1
	[food]1/2x	littoral	42.39	2695	0.847	93729.02	84.7
	[food]1/8x	littoral	50.04	3257	0.497	57483.02	49.7
	[food]1x	Open water	65.48	3180	0.021	984.06	2.1
	[food]1/2x	Open water	58.38	4820	0.102	15544.8	10.2
	[food]1/8x	Open water	64.79	4400	0.031	5290.46	3.1
1/3/2006	[food]1x	Open water	47.9	1000	-0.28	-25200	-28
	[food]1/2x	Open water	26.4	1766	0.33	19780.2	33
	[food]1/8x	Open water	40.1	1783	0.017	1371.2	1.7

Appendix 5. Zooplankton size gradient grazing rate

Date	Sample name	Study site	Chl a	N	F	I	%G
13/12/05	>250	Open water	10.43	1602	0.26	14019.2	26
	<250	Open water	15.28	1380	-0.115	-3245.3	-11.5
9/1/2006	>250	Open water	22.935	1100	0.251	9588.2	25.1
	<250	Open water	24.325	1100	0.102	4062.15	10.2
18/1/06	>250	Open water	52.125	2300	1.081	-136276.8	108.1
	<250	Open water	39.1615	14850	0.283	-25109.48	28.3
2/2/2006	>250	Open water	46.56	4,420	0.335	8756.9	33.5
	<250	Open water	48.65	4560	0.286	25093.64	28.6
17/3/2006	>450	Open water	36.835	2800	0.301	10146	30.1
	>250	Open water	36.14	1200	0.779	32912.2	77.9
	<250	Open water	32.08	3680	0.385	12200	38.5

Appendix 6. Statistical test for difference of grazing rate among sites

	t	df	Sig. (2-tailed)	Mean Difference	95% Confidence Interval of the Difference	
				Lower	Upper	
Littoral						
4.389	6	.005	64.2143	28.4157	100.0128	
Openwater						
5.171	6	.002	70.4857	37.1306	103.8408	

Appendix 7. Statistical test for the difference between Ci and Cp

ONE-WAY ANOVA

	Sum of Squares	df	Mean Square	F	Sig.
Between Groups					
668.003	1	668.003	1.281	.277	
Within Groups					
7302.288	14	521.592			
Total					
7970.291	15				

Appendix 8. Statistical test for effect of grazing rate on chlorophyll 'a'

Open water

The regression equation is
Chl 'a' = 36.9-0.146%G

Predictor	Coef	SE Coef	T	P
Constant	36.920	9.286	3.98	0.003
%G	-0.1461	0.1407	-1.04	0.326

S =15.8547 R-sq = 10.7% R-Sq (adj) =0.8

Littoral water

The regression equation is
Chl ‘a’ = 29.2 + 0.086%G

Predictor	Coef	SE Coef	T	P
Constant	29.2	19.01	1.53	0.176
%G	0.086	0.2686	0.32	0.759

S = 38.92 R-sq = 1.7% R-Sq (adj) = 0.0%