ZOOPLANKTON COMMUNITY GRAZING RATES IN SOME LAKES AND A RESERVOIR IN ETHIOPIA

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To my mother, Wayassee Guta Ula, a corner stone and pillar of my education since elementary until the present day.

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Abstract

Zooplankton community grazing rate as % of algae grazed per day was determined in five lakes and one public water-supply reservoir from March, 1993 to October, 1993. Physical and chemical measurements (Temperature, Secchi depth, alkalinity, salinity etc.) were taken at the same time. Radio-labelling and change in chlorophyll A (chl.a.) methods were used. Zooplankton community grazing rates ranging from 0-95% day^{-1} were obtained. In size fractionated community grazing always, the larger size zooplankters showed higher $\%G.day^{-1}$. Increase in ambient density of zooplankton resulted in increased $\%G.day^{-1}$ in all cases except for Lake Bishoftu in which the reverse took place. Two regression models relating $\%G.day^{-1}$ to temperature (Temp.), mean zooplankton biomass (SD), total zooplankton biomass (ZB), large size zooplankton biomass (LZB) and total chlorophyll a (chl.a.) were tested. Backward deletion procedure resulted in three models which explained 27 - 64% of the total variation in $\%G.day^{-1}$. In both the regression models and the correlation matrices, chl.a. concentration was negatively related to $\%G.day^{-1}$. In the later case, temperature was negatively related to $\%G.day^{-1}$ and all types of zooplankton biomass. The regression coefficients were not significant at 5% significant level. Grazing results are compared with other works in temperate and tropical regions and discussed.

INTRODUCTION

In modern times both surface and sub-surface waters are becoming increasingly affected by human activities leading to the development of a number of adverse phenomena that call for ecological emergencies (Lang, 1979; IFE, 1991). Among others, organic pollution of natural waters or man-made reservoirs from the discharge of domestic sewage and industrial wastes including the intentional use of fertilizers in catchment area is now one of the great menaces both to the environment and public health (Beadle, 1981).

Eutrophication - natural or artificial addition of nutrients to bodies of water - though natural can be greatly accelerated by man (Taub, 1984). Common problems that occupied much of the limnological effort of the last three decades are excessive growth of algae and larger aquatic plants (Andersen *et al.*1978; Briand & McCauley, 1978; Henrickson *et al.*1980; Klapper, 1980; Nicholls *et al.*1980; Goad 1984; Shapiro & Wright, 1984; Lampert *et al.*1986; Benndorf, 1988; Shapiro, 1990; IFE, 1991; Lazzaro *et al.*1992). When such problems occur in public water - supply reservoirs or lakes that are important for commercial fishery, it draws much attention.

Man has tried to combat the problem of accelerated eutrophication a long time ago. However, earlier workers left aside the importance of internal ecological dynamics and stressed upon engineering techniques or chemical methods to overcome water quality deterioration due to algal blooms (NAS, 1969). Rather a complete understanding of interactions among piscivores, planktivores, herbivores and phytoplankton may provide a control strategy to combat eutrophication problems (Carpenter *et al.*1985). The evidence is that the knowledge of primary productivity alone can never give a complete explanation for eutrophication.

A fast growing science, biomanipulation, deals with such complicated interactions in lakes and man-made reservoirs. Biomanipulation - a series of approaches aimed at reclaiming lakes by manipulation of their trophic structure - can be exemplified by reduction of planktivorous fish in a lake to allow an increase in the size and grazing pressure of herbivorous zooplankton, with a consequent reduction in the abundance of algae (Shapiro & Wright, 1984). The importance of biomanipulation is clear, since conventional methods of controlling algal blooms such as harvesting or chemical treatment are either economically unaffordable or ecologically destructive (Hawkins, 1988; Mesfin & Belay, 1989). The development of nuisance planktonic algae in reservoirs built for public water supplies such as Lege Dadi reservoir incur additional expenses for both cleaning the filter beds of the reservoir and treating the water for consumption (Mesfin & Belay, 1989).

The trophic status of lakes as explained by earlier workers (Gulati *et al.*1982; Gulati, 1984; Shapiro & Wright, 1984) and recently by the trophic cascade interaction theory (Carpenter *et al.*1985; Vanni & Findlay, 1990) depends on zooplankton grazing capacity to a large extent.

The basis of this fact is the size-efficiency hypothesis proposed by Brooks & Dodson (1965). According to this theory planktivores and piscivores can be called "food selectors" because they continuously make choices in large part on the basis of size where as herbivorous zooplankters are named "food collectors" because the size range of their food is more or less automatically determined. The ecological implications of size-dependent predation upon the planktonic food collectors (*i.e.*, herbivorous zooplankters) were outlined in what Brooks & Dodson (1965) called the "Size-efficiency" hypothesis. The premises of this hypothesis are

1. Planktonic herbivores all compete for the fine particulate matter (1-15 µm) of the open waters;
2. Large zooplankters do so more efficiently and can also take larger particles;
3. Therefore, when predation is of low intensity the small planktonic herbivores will be competitively eliminated by larger forms (dominance of large cladocera and calanoid copepods);
4. But when predation is intense, size dependent predation will eliminate the large forms, allowing the small zooplankters (rotifers, small cladocera) that escape

predation to become the dominant;

5. When predation is of moderate intensity, it will, by falling more heavily upon the larger species keep the population of these more effective herbivores sufficiently low so that slightly smaller competitors are not eliminated.

The probable reason given for the greater effectiveness of the larger zooplankters in collecting the nanoseston is the fact that in related species (with specially identical food-collecting apparatus) the food collecting surfaces are proportional to the square of some characteristic linear dimension, such as body length. Accordingly whenever predation by planktivores is intense, the standing crop of small algae will be high because of relatively inefficient utilization by small planktonic herbivores, and that of large algae will also be high since this cannot be eaten by the small herbivores. In other words, the biomass of both small and large algae depends on the abundance of the larger zooplankters. Carpenter *et al.*(1985) reviewed case studies with consistent conclusions. These studies show that planktivore removal from lakes results in greater densities of larger zooplankton, which impose greater grazing pressure on the phytoplankton; increased frequency of grazing resistant phytoplankters; reduced chlorophyll a (chl.a.) concentration and total algal densities; increased Secchi disk transparency and reduced total nutrient concentration in the epilimnion.

There is a strong evidence for the water clearing capacity of zooplankton (Bogdan & Gilbert, 1982; Shapiro & Wright, 1984; Post & McQueen, 1987; Mazumder *et al.*1990; and see also Gulati, 1990). An important explanation of this fact can be inferred from biomanipulated lakes.*e.g.* Lake Lilla, Sweden (Henrikson *et al.*1980) and Round lake, Minnesota (Shapiro & Wright, 1984). The overall effect of biomanipulation was to increase zooplankton biomass and decrease phytoplankton biomass. The objective was achieved by decreasing planktivorous fish biomass by addition of rotenone to the lakes. This increased potential grazing pressure of zooplankton community and reduced chl.a. concentration and algal abundance. At the same time average Secchi disc transparency increased considerably. Concentrations of nutrients, both total nitrogen and total phosphorus, declined.

Zooplankton biomass can also be increased by stocking of piscivores which could decrease the biomass of planktivorous fish and hence decrease phytoplankton biomass that result in pronounced water clarity (Carpenter *et al.* 1985). Extensive studies on experimental removals of planktivores and simultaneous release of piscivorous fishes in Lake Trummen, Sweden, resulted in complete reduction of total P and N and showed that fish directly affect the biomass of their prey and indirectly influence trophic level interrelationships, mineralization process and nutrient availability (Anderssen *et al.*1978). Extermination of planktivorous fish by poisoning the whole lake is not an appropriate way to minimize predation on herbivorous zooplankton on a long-term scale. The reason is that predation on large carnivorous zooplankton is also automatically minimized in this way and the final result of such an extermination of fish could be a rather low density of herbivorous zooplankton due to large population of invertebrate predators (Lynch & Shapiro, 1981). To avoid such a problem, there should be a method that could maintain an optimum density of planktivorous fish and enable one to decouple abundance of large herbivores from that of planktivores and allow the herbivores to exist even in the presence of their vertebrate predators. Shapiro (1990) proposes a new idea to deal with these problems. He states that a buffer is needed which might be sought in a refuge or refuges by which the herbivores can maintain themselves. These refuges could maintain herbivore populations on a long-term bases with less attention to and management of the fish population. A suitable refuge or a combination of several refuges should allow the zooplankton to remain abundant and to graze on algae even in the presence of planktivorous fish. The possibility of these refuges include: light refuges, temperature refuges, oxygen refuges, macrophyte or other physical refuges, open water interference refuges, behavioral refuges, predator inefficiency refuges. These refuge types are broadly explained in Shapiro (1990).

It is thus theoretically feasible to improve water quality deterioration due to algal blooms through deliberate manipulation of zooplankton (Lynch & Shapiro, 1982; Carpenter *et al.* 1985; Benndorf, 1988; Shapiro, 1990; Mazumder *et al.*1990; France & Welbourn, 1992; Lazzaro *et al.*1992). However, the contribution of the zooplankton community in a particular water body must be studied and hence the measure of grazing rate should be known before corrective measures are anticipated.

While there is an overwhelming literature concerning zooplankton grazing rates in temperate regions, very little is known of zooplankton grazing pressure in tropical lakes and reservoirs. A few of the temperate studies include: Heart lake, West of Toronto, Canada (Haney, 1973), Loosdrecht lakes, the Netherlands (Gulati, 1984), two lakes in Ontario and two ponds in Southern Michigan (Haney, 1985), Great lakes North America (Ross & Munawar, 1987), Lake St.George in Ontario (Mazumder *et al.*1990), Lake Rotongio, New Zealand (James & Forsyth, 1990), 16 lakes in three states of North America, New York, Connecticut and Pennsylvania (Cyr & Pace, 1992) and numerous others. Zooplankton grazing rates in tropical lakes are seldom found in the literature (e.g., Jarvis, 1986; Hart, 1988).

Even though different workers came out with different results, grazing rates as low as 2% (Cyr & Pace, 1992) and as high as 464% day^{-1} (Haney, 1973) have been recorded. Under eutrophic conditions high grazing pressure has little effect on phytoplankton biomass (Gulati, 1984; Jarvis, 1986). Grazing rate is positively related to zooplankton biomass and negatively related to food concentration in most of the previous works (*e.g.,* see Cyr & Pace, 1992). Some workers argued that apart from phytoplankton, bacterioplankton contribute a considerable amount of zooplankton food (Borsheim & Andersen, 1987 ; Riemann & Bosselmann, 1984). In such studies low grazing rates are expected when only phytoplankters are considered. Haney (1985) found that in eutrophic lakes the rate of phytoplankton production is equivalent to the rate of their removal by zooplankton. However, Vareschi & Jacobs (1984) found that in Lake Nakuru, Kenya, the rate of production is less than the rate of consumption.

Zooplankton grazing rate (G) refers to the effect of per capita consumption of zooplankton on algae. More specifically G is defined as the volume of food suspension from which a zooplankter would have to remove all cells in a unit of time to provide its measured ingestion (Peters, 1984).

The first laboratory experiment considering grazing rate traces back to 1937 (Fuller, 1937 cited in Burns & Rigler, 1967). Later various laboratory techniques evolved which range from the cell count method (Guald, 1951 cited in Downing & Rigler, 1984) to radio-tracer technologies that utilize electronic liquid scintillation counters (Haney, 1971; 1973; Jarvis, 1986; Mazumder *et al.*1990). To maintain the natural conditions during the experiment Haney

(1971) developed the so called *in situ* method. The system employs radio-isotope tracers in a specially designed water sampler, the grazing chamber. The grazing rate in such experiments was determined by either measuring the radio-activity in the entire sample for the total grazing rates of the zooplankton community or by picking animals from the sieve for individual grazing rates (Peters, 1984). This finding came out with an enormous number of advantages apart from its naturalness. The high sensitivity gained by using radio-isotopes, enabled measurement of the grazing rates of sparse populations of zooplankton as well as bacterioplankton and short experimental time, unseen until then, without disturbing the grazer organisms made this method an elegant way of measuring zooplankton grazing rate. Its serious disadvantage is leaching or loss of isotope associated with preservation of zooplankters. The other disadvantage is the shift in the species composition during the long labelling period of the food organisms (Gulati *et al.*1982).

In his long experimental time (5-14 hours), Frost (1972) developed a valuable formula relating the grazing rate of zooplankton to cell growth rate in controlled experiments. This formula is represented as

$$C_2 = C_1 e^{(k-g)(t2-t1)}$$

where C_1 and C_2 are cell concentrations in a beaker with grazers at time t_1 and t_2 respectively and k is a constant for algal growth calculated from a control experiment and g is the quantity of algae disappeared due to grazing.

When experimental times are short, k approaches zero and the initial cell concentration is less than the cell concentration at which the maximal ingestion rate is first achieved (critical concentration), Marin *et al.*(1986) developed a model equation which is useful in calculating grazing rate. The equation is $dc/dt = -gc$, where g is the grazing coefficient and c is the initial cell concentration at time t. The drawback of this method is that in a mixed species it is difficult to detect the point of food critical concentration since this condition differs for different species, while in nature organisms exist in such a way. Recent workers use the cell count method in some modified forms. Cyr & Pace (1992) extrapolated cell concentration as chl.a. which is measured spectrophotometrically to quantify the concentration of chlorophyll pigment present in the sample. This method of chlorophyll quantification was first introduced by Talling & Driver (1963).

Several studies indicate that grazing rate of zooplankton may be strongly influenced by many intrinsic and extrinsic factors. To note a few of them, Burns & Rigler (1967) showed that filtering rate increases with increasing body length and temperature up to 20°c. This idea amends to the size-efficiency hypothesis for the filtering apparatus possesses an area equivalent to the square of the body length of that specific species. So the longer the organism the larger the filtering apparatus thus filtering large volume of water according to this theory. Even though grazing rate increases with temperature up to certain temperature limit, there is no single explanation for the reason of such a linearity. Haney (1973) detected that the dominant filter-feeding zooplankton species in Heart Lake had population maxima in summer and population minima in late-winter, which corresponded with grazing rate maxima and minima recorded during the same period. From this finding temperature induces reproduction thus increasing population size that may contribute to increased grazing. It was Vijverberg (1980) who explained this fact more explicitly. He stated that the growth in length is mainly a function of temperature, age, food conditions and maximum size of the species concerned. He also remarked that the lower the temperature the poorer the growth-rate and the smaller the maximum length achieved. Since grazing rate is related to body length, temperature indirectly affects zooplankton grazing pressure. Gulati *et al.*(1982) summarizing this fact, states that the rise in temperature contributes significantly in causing the increased rate of egg production and instantaneous growth and decreased duration of egg development. It is also generally believed that egg duration time for a particular species of zooplankton depends only on temperature (Vijverberg, 1980).

High food concentration decreases grazing rate because the food level may lead to superfluous feeding. That is above the incipient limiting level the assimilation rate reaches a plateau thus there is no more increase in grazing rate (Gulati *et al.*1982). From physiological point of view, the food particles can be ingested only after falling from a feeding current onto the sieve-like second maxillae in the case of filter feeding copepods. Ingestion rate for such a feeder increases in direct proportion to increase in concentration of food up to a saturation point above which ingestion may be determined by the passage rate of food through the alimentary canal (Frost, 1972). In a laboratory experiment Vareschi & Jacobs (1984) also found a highly significant and steep negative correlation in adult copepods of *Lovenula africana* between algal concentration and clearing rate. They claimed saturation or clogging effect at higher concentration as the main reason.

In connection with biomanipulation, recently it has been found that top carnivores affect grazing rate considerably. In their broad explanation Carpenter *et al.*(1985) have clearly pointed out how piscivores affect indirectly the grazer zooplankters and hence the grazing rate. That is piscivore stocking reduces the biomass of planktivore fishes thus increasing the biomass of zooplankters that result in decrease of phytoplankton biomass.

Our knowledge of the methods used to mitigate eutrophication processes, besides classical restoration procedures, involves almost exclusively engineering techniques. There is now an alternative approach (in order to avoid high economic associated costs and/or common irrelevance of more conventional approaches) consisting of flexible ecological shifting of trophic state balances. At present extensive literature is devoted to the feasibility of biomanipulation approaches to restore lakes and reservoirs (*e.g.*, Shapiro & Wright, 1984; Goad, 1984; Lazzaro, 1988; Benndorf, 1988; Shapiro, 1990).

Benndorf (1988) proposed integration of two strategies to have a better water quality and lower cost/benefit ratio in the management of water resources. These are

1. The strategy of reducing the external load of nutrients, toxic substances, organic matter or acid precipitation.
2. The strategy of controlling internal ecological processes (ecotechnology)

If one considers the second solution, it is clear that zooplankton grazing rate is one of the internal dynamics regulating water clarity. Implementation of this solution requires, as its first step, having some idea of percentage zooplankton community grazing rate per unit time and zooplankton biomass in each lake or reservoir.

In Ethiopia cultural eutrophication is leading to accelerated water quality deterioration. Among the Bishoftu crater lakes Lake Hora and Lake Bishoftu are the two most affected lakes due to recreation, livestock watering, laundering and dumping of domestic sewage directly into the lakes.

Lege Dadi reservoir is one of the two main water-supply reservoirs for the Addis Ababa city. In this reservoir copper sulphate is used to control algal blooms (Mesfin & Belay, 1989). This practice is still going on. However, copper sulphate has been found to be toxic at higher concentration to every organism (Hawkins, 1988). Mesfin & Belay (1989), have recommended that copper sulphate should not be applied in public water supply reservoir as algicide. The maximum tolerated concentration of copper in water basins is 0.1 $mg.L^{-1}$. Doses of copper salts 0.2-0.5 mg.L-1 caused vomiting, and 1-2 g lethal cases of poisoning (Gruzdyev *et al.*1988).

Elizabeth *et.al.*(1992) reported cultural eutrophication and/or addition of planktivorous fish species, *Tilapia,* as possible reasons for the increase of phytoplankton biomass and consequent mass fish kill in Lake Hayq.

Lake Awassa is bordered on one side by the town, Awassa, but exposed on the other side to rural farm-lands. It is thus liable to both domestic and industrial wastes from the town and fertilizers from the farm-lands (if any).

Compared to any of the lakes treated in this study, Lake Arenguade is highly protected due to its location and steep slope. The lake is entirely found in the rural area and its catchment is totally unsuitable for cultivation or settlement. The two activities observed in the basin are livestock watering and laundering. Due to the belief that peasants developed from experience, intensive livestock watering is observed every saturday and sunday. Peasants believe that livestock watered from Lake Arenguade are many fold fatter than when fed on other fodder. This may have a scientific value since Lake Arenguade is full of *Spirulina platensis*, which is proved to be highly rich in protein.

These water bodies were chosen among other Ethiopian lakes and reservoirs due to their accessibility and their exposure to human influences, and documented cases of eutrophication. It was anticipated that zooplankton grazing would also show contrasting rates in these lakes of different trophic status. To this end, the zooplankton community grazing rates were measured in these five lakes and the reservoir during 1993.

The objectives of this study are

I. To estimate zooplankton community grazing rates in some lakes and Lege Dadi reservoir and determine the contribution of zooplankton grazing to water quality improvement.

II. To determine which size fractions of the zooplankton community are more efficient grazers.

III. To contribute to the type of values that are typical for tropical lakes and water bodies of varying trophic status, (since no comparative work has been done in other tropical lakes except a few).

2. DESCRIPTION OF STUDY SITES

2.1. MORPHOMETRY OF STUDY SITES

The study was performed in five lakes and one public water-supply reservoir. These include the three Bishoftu crater lakes-Hora, Bishoftu and Arenguade; Lake Awassa in the southern rift valley and Lake Hayq in Northern Ethiopia, Wollo administrative region. Lege Dadi reservoir is one of the main water-supply reservoir of the Addis Ababa city. The morphometric data and bathymetry of the study sites are given in Table.1. and Figures 1-3. respectively. Sampling stations are numbered 1 to 3 in the maps depending on the number of stations studied.

Table.1. Morphometric data of the lakes and reservoir studied.

Lakes/reservoir	Area (Km^2)	Max.depth(m)	Mean depth(m)	Alt.asl(m)
Bishoftu(1)	0.929	87	55	1870
Hora(1)	1.029	N.Crater 38 S.Crater 31	75.5	1850
Arenguade(1)	0.541	32	18.5	1900
Awassa(2)	90	22	10	1600
Hayq(3)	23.2	88.2	37.37	2030
Lege Dadi(4)	5	30	1.88	2450

Source: (1) Prosser *et al.*(1968); (2) Mengestou (1989); (3) Baxter & Golobitch (1970); (4) Mesfin & Belay (1989) and Addis Ababa Water and Sewerage Authority (1980).

2.2. DRAINAGE CHARACTERISTICS OF THE STUDY SITES

2.2.1. THE BISHOFTU CRATERS

Among the sixteen-explosion type craters in the vicinity of Bishoftu, recognized by Mohr (1961), only three from the five permanent crater lakes were included in this study (Fig.3.a, c and d). The Bishoftu explosion craters constitute a system of lakes with similar surface area and common origin. These lakes are characterized by their confined and circular catchment area, steep slopes, flat bottom and protective rims (Mohr, 1961; Prosser *et al.*1968). Lake Hora loses the circular nature of the crater lakes because it is made of two intersecting crater lakes (Mohr, 1961). All the three lakes considered here, Bishoftu, Arenguade and Hora have no any visible inlet or outlet but the latter possesses underground springs on the western side of its northern crater (Mohr, 1961). Earlier workers also observed spring line near the shore of Lake Arenguade (Prosser *et al.*1968). So these lakes appear to conserve the major part of their water from the relatively small basins of their own craters.

2.2.2.LAKE AWASSA

Lake Awassa, located at lat.6°33'-7°33'N and Long.38°22'-38°29'E is the smallest of the southern rift valley lakes (Fig.3.e). It is fed by Tikur Wuha, eight other seasonal streams and shallow swamps partly (Wood & Talling, 1988; Seyoum Mengestou, 1989). There is no any outflow mentioned any where. The details of this lake is found in Seyoum Mengestou (1989).

2.2.3.LAKE HAYQ

Situated at 11°15'N lat. 39°57'E long.and at altitude of 2030 m asl, Lake Hayq is one of the few Ethiopian high land lakes. No geological work of this lake exists in the literature. It is visible, however, that it is not an explosive crater lake unlike any of the Bishoftu craters. The lake surface is totally exposed to wind action because of the absence of crater walls or mountain ridges. Lake Hayq is nourished by a single temporary stream Anchercah. The stream flows into the lake at its Southeast corner. Lake Hayq has no visible outlet (Baxter & Golobich, 1970). Due to the long drought time in the past two decades the water level of the lake has decreased and an area once considered as an island has become part of the mainland

(Fig.3.b).

2.2.4. LEGE DADI RESERVOIR

Unlike the lakes mentioned, Lege Dadi reservoir is relatively a dynamic system in which the residence time of the inflowing water is so short because of the constant outflow for consumption. It is located to the east of the Addis Ababa city 9°20'N, 38°55'E, 2450 m asl, with a useable capacity of 47 million m^3 and treatment facility designed for a rated capacity of 50, 000 m^3 per day (Fig.2). Its catchment area covers 225 km^2 and is drained by two rivers Sendafa and Sokoru (Mesfin & Belay, 1989). The surrounding area of the reservoir is bare land with no vegetation and cultivated fields at times. It is fully exposed to wind due to the absence of wind breaks such as mountain or vegetation.

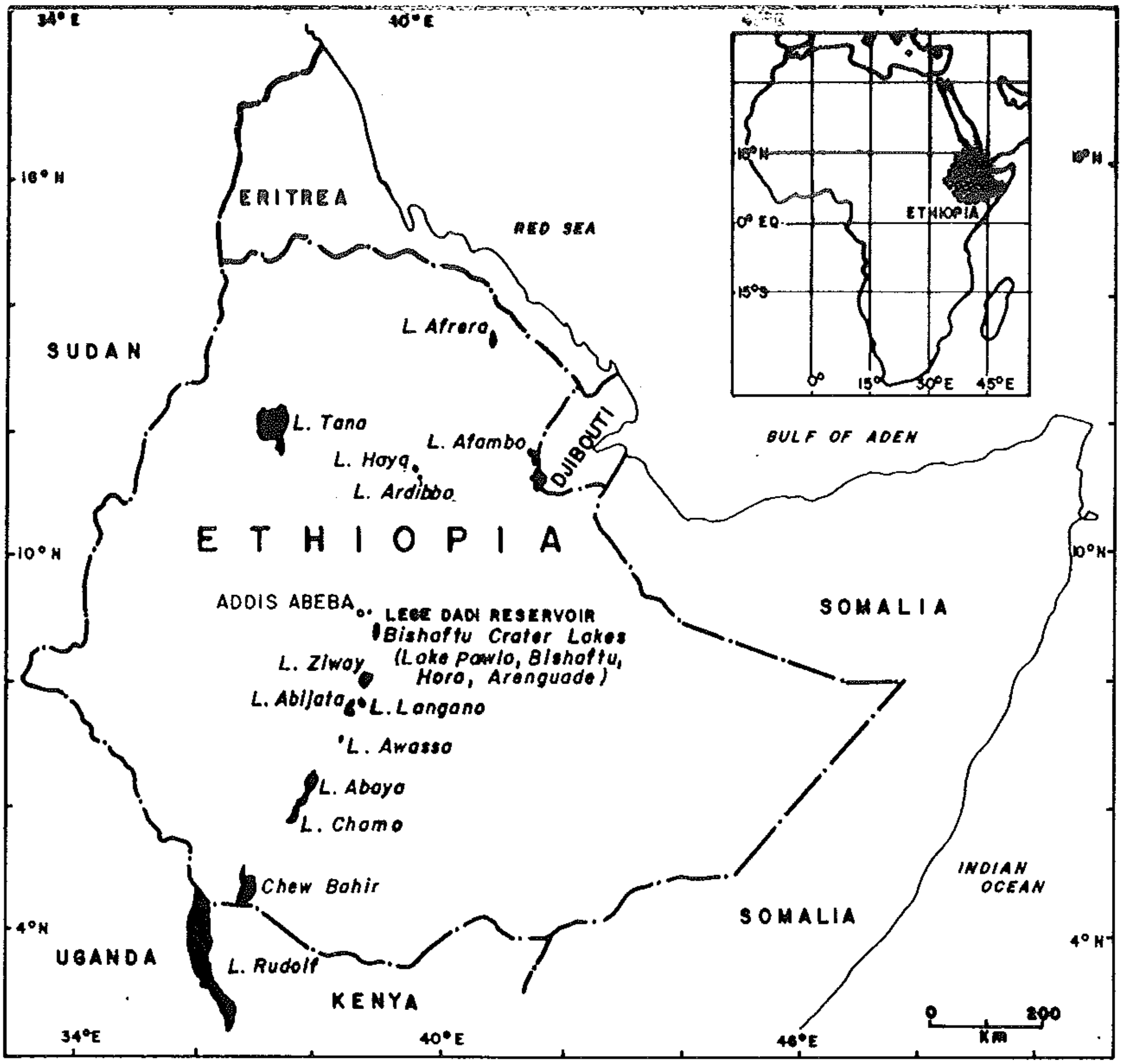


Fig.1. The Location Of Study Lakes.

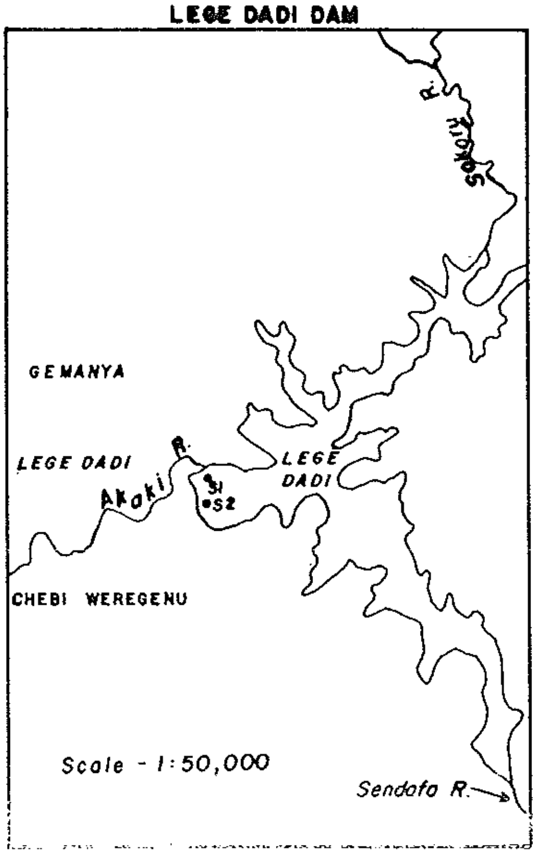


Fig.2 The Morphology of LEGE DADI Reservoir & Study Sites (Inset)

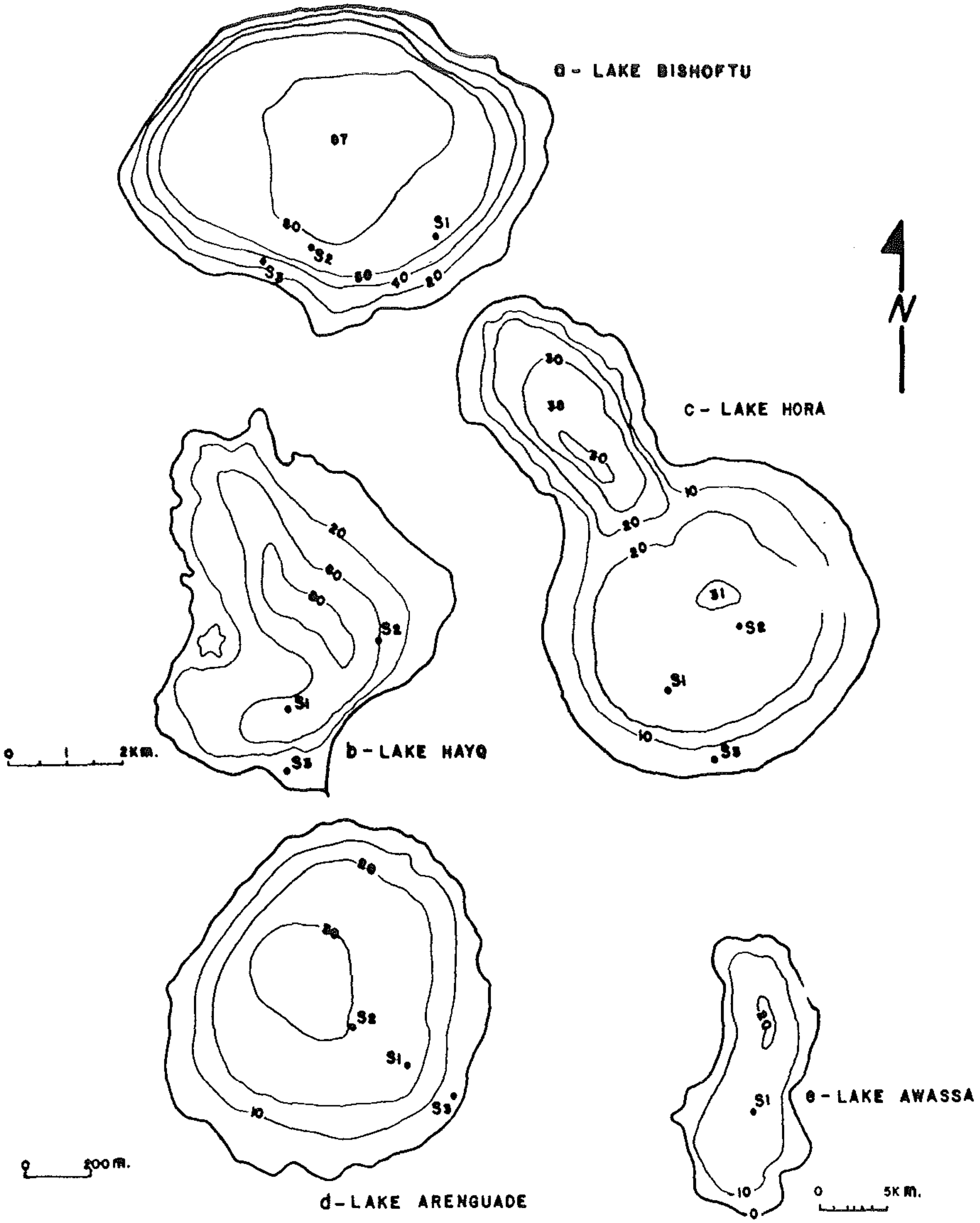


Fig. 3. Maps Showing The Bathymetry Of Study Lakes & Sampling Stations (S1 to S3). Lower left Scale is for Lakes a, c, and d.

3. MATERIALS AND METHODS

3.1. COLLECTION OF PLANKTON SAMPLES

Zooplankton and phytoplankton samples were collected from 5 meter vertical depths by hauling #25 (64µm mesh) net and phytoplankton net from each station. Three replicates were collected for each zooplankton and phytoplankton sample and preserved in whirlpak bags with 4% formalin and Lugol's iodine, respectively. These samples were analyzed in the laboratory for plankton composition and biomass.

3.2. PHYSICO-CHEMICAL MEASUREMENTS

Physico-chemical feature of each lake was considered in some detail because these features govern biological communities and their interactions.

Water samples for chemical analysis were collected from the upper 0.5 m in opaque plastic bottles. In all cases, HACH kit (HACH chemical company, model DREL/1C) was used for the determination of chemical parameters. Total hardness and total alkalinity as $CaCO_3$ were measured by the titration method. Total alkalinity was measured by titrating 1.6N sulfuric acid standard solution against a sample after phenolphthalein indicator was added. Total hardness was measured by titrating 0.8M EDTA solution with the sample after a buffer and indicator solution were added to the sample. In both cases the concentration was read as $CaCO_3$ in $mg.L^{-1}$ directly from the digital counter following the procedures in the HACH manual.

Chloride was measured by Mercuric Nitrate method, Ammonia and Ammonium nitrogen by Nessler's method, Sulphate by the turbidimetric method, Silica by the Hetropoly blue method, Nitrite by the Diazotization method and Soluble reactive phosphate by the ascorbic acid method. Temperature and dissolved oxygen (DO) were measured with a YSI model 57 oxygen meter, salinity and conductivity with a YSI model 33 S.C.T. meter, pH with a digital pH-meter model 607 (Canlab) and Secchi depth with a Secchi disc. Most of the chemical analyses were completed at shore sites.

3.3. PLANKTON COMPOSITION

Phytoplankton samples were observed under an inverted microscope (magnification 1000x) while zooplankton were counted under a wild stereoscope (magnification 100x) according to the methods recommended in Edmondson & Winberg (1971). The dominant zooplankton and phytoplankton in each lake and Lege Dadi reservoir were determined according to their numerical abundance based on Mengistou (1989) and Prescott (1970), respectively.

3.4. ZOOPLANKTON BIOMASS

Zooplankton biomass was determined from length-weight regressions as in Culver *et al.*(1985). In all cases except for Lake Arenguade, only length was measured and dry weight was obtained from regression equations. Since there was no length-weight regressions for *Paradiaptomus* (=*Lovenula*) *africana*, dry weight was determined using a sartorius digital balance (sensitivity = 100 µg). The length of each stage of species was measured under an inverted microscope. Dry weight was determined by counting a number of individuals (usually more than 10) and drying at 60°C for 2 hours in an oven (Culver *et al.*1985). After desiccation for 24 hours over calcium chloride, the animals were weighed in mass on tiny aluminum foils on a sartorius balance. The observed dry weight was then regressed against the observed length and the prediction length-weight regression was obtained (see Table.6).

3.5. ZOOPLANKTON GRAZING RATE STUDIES

The measurement of zooplankton community grazing rate was done by two methods: radio-labelling and change in chlorophyll method.

3.5.1. RADIO-LABELLING METHOD

Radio-labelling method was used based on the technique developed by Haney (1971). The natural food of zooplankton was used, as this work was intended to measure community grazing rate under natural condition. Algal food was obtained by filtering a known volume of lake water through a 38 µm mesh sieve. To one litre of filtrate 2 µCi of $NaH^{14}CO_3$ (Amersham International) was added and placed under the bank of florescent lamp (36 watt), at room temperature, for 24 hours. The sample was refrigerated overnight at about 5°c and the supernatant was decanted. The remaining few millilitres of the concentrate was then resuspended in 100 mL of 0.45 µm Whatman filtered lake water. This was then filtered through a 38 µm sieve and transferred to a cylindrical glass and left for about 4 hours. The last step was repeated twice to remove all the radioactive carbon not bound to the algal cells. Two mL of the aliquot was filtered through a 0.5 millipore membrane by a pump harvester and the disc with the algal food was added into a scintillation vial containing 10 mL scintillation cock-tail (Beckman) for the determination of radioactivity of the food.

In situ grazing rate was measured using Haney's grazing chamber (Haney, 1971) as modified by Mazumder *et al.*(1990). In the field 5 mL of the tracer food was injected into three 4.13 L chambers. The experimental feeding time was set at 8 minutes, less than the gut passage time of most crustacean zooplankton (Jarvis, 1986). After the grazing time the chamber was withdrawn from the lake and the contents were drained out through 63 µm mesh sieves. Zooplankters were then washed back into marked whirl pack bags and preserved in 4% formalin, brought to the laboratory and stored at 5°C. Radioactivity in zooplankton was counted by transferring 10-20 individuals to a pyrex flask containing 15 mL of 10% KOH. The zooplankton were boiled until digested. Four mL of the solution was added into each scintillation vial to which scintillation cocktail was added. Radioactivity was counted by a digital liquid scintillation counter (Beckman). Three replicates were counted for each sample. Quench curve correction was based on external standard ratio (ESR) and counting efficiency, employing a computer programme to calculate the disintegration per minute (DPM) via the third degree polynomial regression. Percentage grazing rate per day was calculated using the formula of Haney (1973)as follows :

$$\%G=\frac{(DPM_a \times 60 \times 24)}{(DPM_f \times t \times V)}100$$

where, %G = zooplankton community grazing rate as % day^{-1}

V = volume of the chamber in litres

t = experimental time (8 minutes)

DPM_a = radioactivity in animals

DPM_f = radioactivity in food

3.5.2. CHANGE IN CHLOROPHYLL METHOD

Zooplankton grazing rate as % per day was calculated as in Cyr & Pace (1992) based on the original formula of Lehman (1980) assuming that loss is attributed only to grazing. In calculating the initial and final chlorophyll "a" (chl.a.) concentrations the monochromatic method in Wetzel & Likens (1979) was adopted by substituting a factor 11.3 by 13.9 for cold methanol extraction method. The initial chl.a. concentration (C_0) was determined by filtering a known volume of water (usually 250 mL) with GF/C filter papers which were put in a 15 mL basic methanol (2 mL of 0.5 M NaOH per litre of methanol) (Cyr & Pace, 1992) and transported to the laboratory in an ice box. All samples were processed in about 24 hours except that of Lake Hayq which was processed in about 72 hours. The extract was crushed with a mortar for a few seconds and centrifuged in a tapered centrifuge glass for 5 minutes. The supernatant was then used for reading in a spectrophotometer (Spectronic 1001) with 1 cm cuvette light path. Final chl.a. concentration (C_1) was measured after draining the contents of the three chambers. Zooplankters were removed with 63 or 75 µm mesh sieve and the water was filtered with GF/C filter papers. C_1 was measured in the same way as C_0 above. In both cases more than two reapts of the same measurement was done.

3.6. MANIPULATED ZOOPLANKTON GRAZING RATES

Zooplankton percentage grazing rate per day was also done under manipulated condition, that is by altering their natural density or fractionating into different size groups. This was done to detect if there is any difference in percentage grazing rate due to zooplankton size difference or different density gradient. Zooplankton density was manipulated in relative units. When zooplankters were concentrated from 5 meter vertical depth by hauling the net once it was designated as 1x, when twice, 2x and so on up to three in most cases. When 1x concentration was divided by four it was designated as 1/4x, and when by two as 1/2x. In each case the concentrated zooplankters were added into 38µm filtered lake water which was then poured into labelled chambers. The grazing chamber was then incubated in the euphotic depth (usually <2m) for the time period determined to allow grazing (3 hours).

Zooplankton size fractions were obtained by filtering sampled lake water using different size sieves. For example, when zooplankton size less than 300µm were required the sampled lake water is passed through 300µm mesh sieve and added directly into the grazing chamber to be incubated. When zooplankton size greater than 500µm are required the water sample is passed into 500μm mesh sieve at the air-water interface at a minimum time possible to reduce the number of deaths due to exposure out of water.

In all cases, final chl.a. concentration was measured after draining the contents of the three chambers into three different buckets. Zooplankters were removed with 63 or 75 μm mesh sieve and the water was filtered with GF/C filter papers. These were used to measure final chl.a. concentration (C_1) accordingly. From the logarithmic difference of the final and the initial chl.a. concentrations, the grazing coefficient (g) was calculated. The incubation time was three hours except few which was 2 hours (*e.g,* L.Hayq). This time limit was chosen to avoid long experimental time so that the net reproduction of phytoplankton will be undetectable. From the experiments done at Lege Dadi reservoir long experimental time resulted in distorted grazing rate due to high degraded pigment products. Furthermore the model used in this particular work supports minimum experimental time at which grazing rate could be determined without any net growth of phytoplankters (Marin *et al.*1986). Incubation was always in the euphotic depth or on shore. For each reading of spectrophotometer the reading was corrected for phaeopigments by adding 40μL 4N HCl per cell of acid (0.01 mL of acid per mL of extract). This was done in order to find out the amount of phaeopigments and subtract the result from the total absorption before acidification. This step also helps to know the magnitude of degradation products before and after grazing experiment.

Calculation of percentage grazing rate per day for the change in chlorophyll method was done using the model of Marin *et al.*(1986) with some modifications. When integrated and rearranged the model equation dc/dt = -gc will be equal to $(1 - e^{-gt})$ where, g = grazing coefficient, t = experimental time in days and e = the base of the natural logarithm. Therefore percentage grazing rate per day at the community level is $(1 - e^{-gt})100$ (See Appendix I for more explanation).

3.7. STATISTICAL METHODS

The results were analyzed using statistical packages for social sciences ($SPSS/PC_{TM}$), Version 4.0+. Two regression models were tested to seek for relationships between grazing rate (%G day^{-1}) and characteristics of the zooplankton communities (biomass, size distribution) and of the environment (food concentration and temperature)(Table. 2). The coefficients (b_n) were fit by multiple regression analysis using backward elimination procedure. Logarithmic transformation was performed to fulfil the normality and homoscedasticity assumptions of regression analysis as suggested by Sokal & Rohlf (1981). Both models 1 and 2 were also developed by Cyr & Pace (1992) but were used in this case after some modifications. Finally zooplankton community grazing rates predicted from the models developed were compared with measured rates and published results in the literature.

Table.2. Models tested in search of predictive equations for zooplankton percentage community grazing rate (%G.day^{-1}). ZB is total zooplankton biomass (mg.L^{-1}), MZ is mean zooplankton biomass, chl.a.is total chlorophyll A concentration, T is water temperature at 1 m depth (^{o}C), and LZB is zooplankton biomass excluding nauplii and copepodite (mg.L^{-1}).

Model	Equations
1.	$\log_{10}(G) = b_1\log_{10}(ZB) + b_2MZ + b_3\log_{10}(chl.a) + b_4T + b_o$
2.	$\log_{10}(G) = b_1\log_{10}(LZB) + b_2MZ + b_3\log_{10}(chl.A) + b_4T + b_o$

The study sites and method of study at each lake is given in Table.3.

Table.3. Study sites and methods used.

Lakes	Date of study (Mo/d)	Method of studies	Types of studies
Arenguade	03/14	RLM	ZCGR
	05/31	chl.a.	ZCGR
	09/19	chl.a.	ZDGR, ZSGR, ZCGR
Bishoftu	03/13	RLM	ZCGR
	05/29	chl.a.	ZCGR
	09/18	chl.a.	ZDGR
Hora	03/12	RLM	ZCGR
	06/01	chl.a.	ZCGR
	08/09	chl.a.	ZCGR, ZSGR
	09/20	chl.a.	ZDGR, ZCGR, ZSGR
Awassa	10/12	chl.a.	ZCGR, ZDGR
	10/13	chl.a.	ZCGR, ZSGR
Hayq	07/16	chl.a.	ZCGR
	07/17	chl.a.	ZSGR, ZDGR
	07/18	chl.a.	ZDGR, ZSGR, ZCGR
Lege Dadi	05/07	chl.a.	ZCGR
	05/08	chl.a.	ZCGR

Legend:

RLM = radio-labelling method; chl.a.= change in chlorophyll method; ZCGR = zooplankton community grazing rate; ZSGR = zooplankton size gradient grazing rate; ZDGR = zooplankton density gradient grazing rate. Year of study is 1993.

4.RESULTS

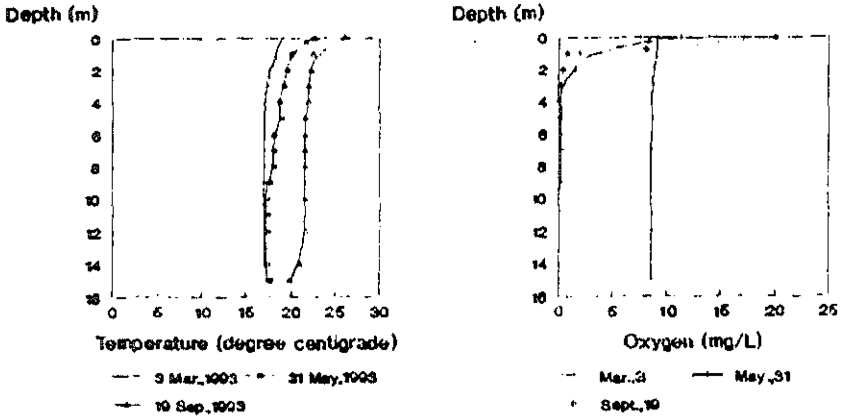
4.1. CHEMICAL COMPOSITION

The chemical composition of the study lakes are listed in Table 4. An average of two measurements were done at each study lake.

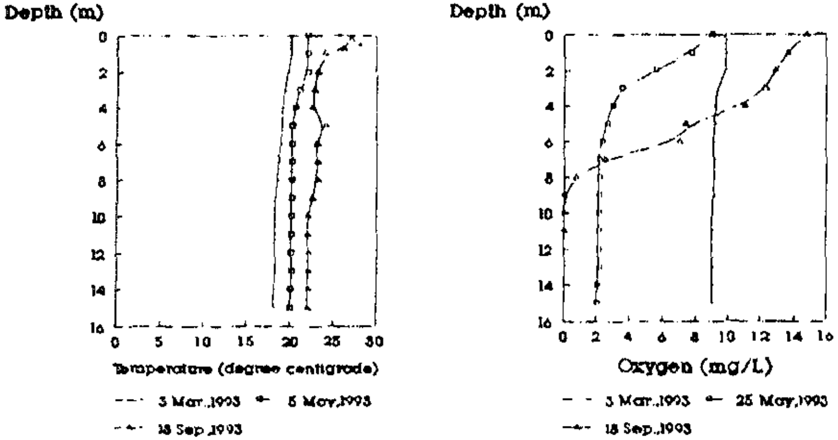
Depth-temperature and depth-oxygen profiles for the lakes during the study period are shown in Figures.4. a-f.

Table.4. Chemical composition of the study lakes (all units in mg.L^{-1} unless otherwise stated).

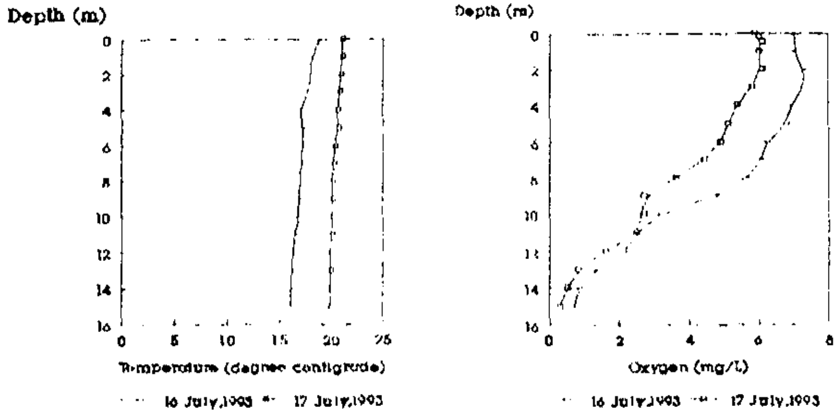
	LAKES					
CHEMICALS	Arenguade	Bisshoftu	Hora	Hayq	Awassa	Lege Dadi
Total alkalinity	650	176	1050	482	352	58
Total hardness	170	166	190	282	45	116
Total carbon-dioxide	0	95	176	0	---	33
Chloride	612	83	193	40	---	16
Ammonia-nitrogen	2.44	1.10	0.12	0.67	1.10	>2.44
Ammonium-nitrogen	2.58	1.16	0.13	0.71	1.16	>2.58
Ortho-phosphate	5	0	0	100	---	0.30
Sulphate	7	6	0	---	---	45
Silicate	35	36	>40	5.5	>40	>3
Nitrite-Nitrogen	0.10	0.20	0.07	---	---	0.13
Conductivity (µs.cm^{-1})	6133	1000	1347	785	700	70
Salinity (ppt)	3.60	2	1.40	0.50	0.20	0
pH	9.48	8.13	8.38	7.70	8.37	7.32
Secchi depth(m)	0.23	0.50	1.34	1.57	---	0.20



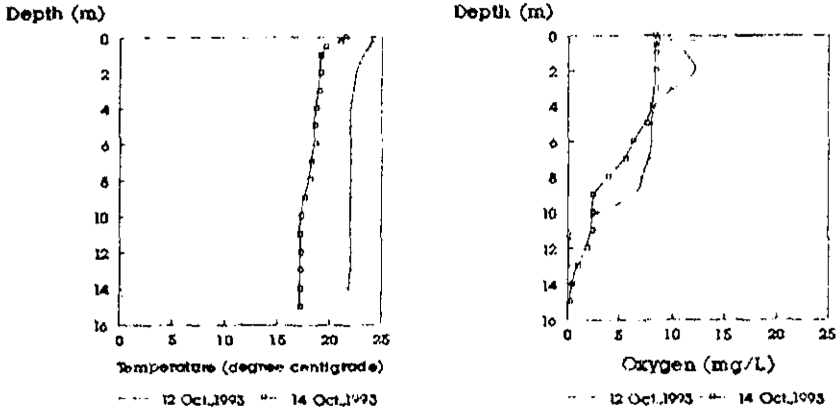
(a) Lake Arenguade



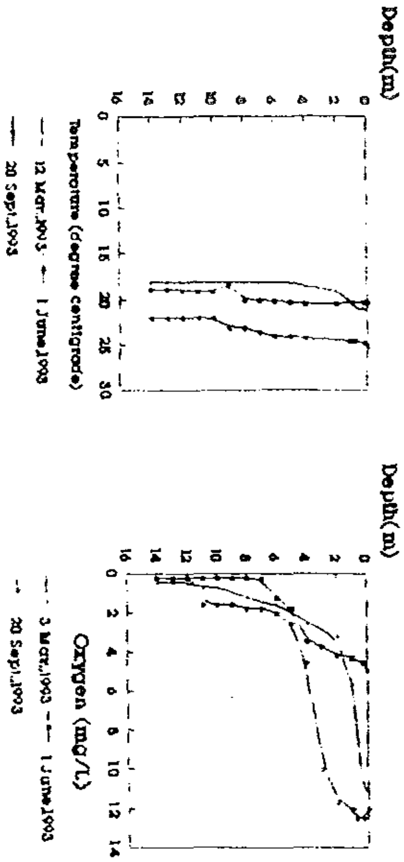
(b) Lake Bishoftu



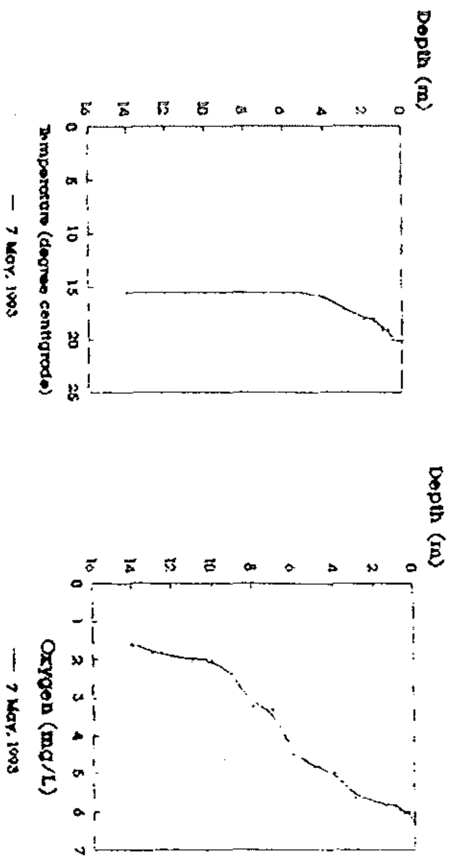
(c) Lake Hayq



(d) Lake Awassa



(e) Lake Hora



(f) Lake Pedi reservoir

Figure 4. Depth-temperature and depth-oxygen curves for the lakes studied during the study period (includes a to f).

4.2. ZOOPLANKTON AND PHYTOPLANKTON SPECIES COMPOSITION

From the six study lakes five genera of crustacean zooplankton were identified. Out of these two were cyclopoid copepods, two calanoid copepods and the remaining one is a cladoceran. The two cyclopoid genera are *Mesocyclops* and *Thermocyclops*, while the two calanoid genera are *Lovenula*(=*Paradiaptomus*) and *Metadiaptomus*. The only cladoceran copepod encountered during this work was *Diaphanosoma exisum* in lakes Awassa and Hayq.

Regarding the phytoplankton, four genera of the blue-green algae (Cyanophyta) and one genus of green algae (Chlorophyceae) were identified. The blue-green algae include: *Spirulina*, *Microcystis*, *Oscillatoria*, and *Gloeocapsa* while the remaining genus of green algae is *Botryococcus*.

Rotifers were not considered in this study. Also, only the most abundant plankton are enumerated in Table 5. and the less common forms are omitted.

Table.5. Dominant crustacean zooplankton and phytoplankton in the study lakes and reservoir.

Lake/Reservoir	**Dominant zooplankton**	**Dominant phytoplankton**
Arenguade	*Lovenula africana*	*Spirulina platensis*
Bisshoftu	*Mesocyclops sp.*	*Microcystis aeruginosa*
	L. africana	*Oscillatoria sp.*
Hora	*L. africana*	*M. aeruginosa*
	Mesocyclops sp.	
Hayq	*Thermcyclops ethiopiensis*	*Gleocapsa sp.*
	Diaphanosoma exisum	*Oscillatoria sp.*
		Spirulina sp.
Awassa	*M.aequatorialis similis*	*Botryococcus sp.*
	D. exisum	
	Thermocyclops consimilis	
Lege Dadi	*Metadiaptomus colonialis*	diatoms

4.3. ZOOPLANKTON BIOMASS

Zooplankton biomass of each species was calculated according to their respective regression equations from literature values. The biomass of *Mesocyclops* was calculated using the regression equation $DW = 2.257L^{2.252}$ ($r^2 = 0.85$) where, DW = dry weight (mg) and L = total length (mm). Similarly, the biomass of *Diaphanosoma exisum* was extrapolated from the mean values calculated for juveniles and adults (see Mengistou & Fernando, 1990). The same regression equation developed for *L. africana* was also used for *M. colonialis* since these two species were found to be highly related (see Hutchinson, 1967). The regression equation developed was $DW = 50.103L^{1.520}$ ($r^2 = 0.89$); where DW and L are as defined previously. Results are given in Table.6.

Table.7. Zooplankton community grazing rates in study lakes and reservoir (values are given in range whenever measured more than one time).

Lake/Reservoir	Arenguade	Bishoftu	Hora	Awassa	Hayq	Lege Dadi
Range of %G day^{-1}	4.2-95.5	59.37	7.10-77.08	0	62.5-81.7	5.0-56.8

Table.8. Zooplankton size fraction %G day^{-1} in some of the study lakes.

	Lakes		
Size fraction (μm)	Arenguade	Hora	Hayq
<300	71.1	38.8	58.3
>300	---	---	100
>500	100	69.1	---

Note:

< = less than

> = greater than

--- = no data

Density gradient grazing rate studies were performed in lakes Bishoftu, Hayq, Arenguade and Hora. Grazing stayed constant or decreased after an increase of 1.5x (Lake Hayq), 2x (Lake Hora) ambient zooplankton density. For Lake Arenguade, grazing increased with threefold increase in ambient zooplankton density while in Lake Bishoftu, a sharp decrease in %G day^{-1} was observed with slight increase of the natural ambient density (Fig.5).

Table.9. Selected models relating grazing rate (%G.day^{-1}) to characteristics of zooplankton communities and of the environment (see Table.2. for clarification).

Models	equations
1.	$\mathrm{Log}_{10}(G) = 0.023MZ + 0.994T - 2.242\log_{10}(chl.a) + 1.023\log_{10}(LZB) - 19.149$, $R^2=0.64$
2.	$\mathrm{Log}_{10}(G) = 0.023MZ + 0.948T - 2.253\log_{10}(chl.a) + 0.992\log_{10}(ZB) - 18.259$, $R^2=0.51$
3.	$\mathrm{Log}^{10}(G) = 0.033MZ + 0.399T - 2.218\mathrm{Log}_{10}(chl.a.) - 5.498$, $R^2=0.27$

From these models it is clear that chl.a. is negatively related to grazing rate while the other three factors are positively related to it (see also Appendix III).

From the correlation matrics (Appendix III) it was observed that mean zooplankton biomass (MŻ) has significant positive association with Chl.a. ($P<0.01$). Each of the above three models show that grazing decreases by more than 2.2 units for a unit increase in chl.a. concentration while Models 1 and 2 show grazing increases by more than 0.9 for a unit increase in lake water temperature at a given depth. Large size zooplankton biomass (LZB) shows strong positive association with grazing rate than total zooplankton biomass (ZB). That is grazing rate increases by more than one unit for a unit increase in LZB while it increases by less than one unit for a unit increase in ZB. Mean zooplankton biomass, in these terms, has the least contribution to grazing rate from all the three models(Table.9).

5. DISCUSSION

5.1. CHEMICAL COMPOSITION OF THE STUDY LAKES

A good deal of summary concerning the chemical and algal relationships of Ethiopian inland waters is compiled in Wood & Talling (1988). In this work, lakes were arranged in a salinity series and treated according to their drainage characteristics. The three Bishoftu crater lakes Hora, Arenguade and Bishoftu fall in a closed-basin type lakes. The persistence of such lakes require that the annual water inflow should equal the annual evaporation loss minus direct rain-fall on the lake. However, this water budget is sometimes distorted by underground inflow, outflow, or seepage. The chemical composition of such lakes depends mainly on their drainage characteristics. That is apart from the internal regeneration of elements, inputs from the external environment also affects the chemical concentration of each lake. Saline inflows induce salinity while dilute springs cause dilution of lake waters. On the other hand when the evaporative loss of the water balance exceeds gain through rain-fall the salt concentration of the lake water tends to rise. The rather low salinity of Lake Hora is probably due to its subterranean spring inflow but the salt concentration of the inflowing spring is not known.

The shallow papyrus-dominated swamp to the north-east of Lake Awassa was estimated to be contributing some 40% of the total inflow and had a conductivity of 50 $\mu s.cm^{-1}$ and the other 60% of inflow from eight other streams averaged around 100$\mu s.cm^{-1}$ (Wood & Talling, 1988). If this situation still hold true, the dilution of Lake Awassa may be a cumulative effect of these inflows. In Ethiopia, the time variation of salinity is dominated by the alternation of wet and dry seasons. That is conductivity increases during the dry seasons and decreases during the wet seasons. These situations are forced by the evaporative concentration and dilution by the incoming water, respectively. If this is the case and high salinity is accompanied by high conductivity, as it is theoretically known, lakes Arenguade, Bishoftu, Hora and Hayq follow the usual trend proposed by Wood & Talling (1988). High salinity is not accompanied by high conductivity in Lake Hora. This could be for the fact that alkalinity increases as solubility of calcium carbonate increases (Wood & Talling, 1988). Therefore solubility of calcium carbonate may be higher in lake Hora than the other two lakes (Arenguade and Bishoftu). Alkalinity is usually lost from Lake Arenguade by precipitation of calcium carbonate. During the grazing experiment the grazing chamber was found encrusted with calcium carbonate. This condition was also observed by Prosser *et al.*(1968). In this work most of the chemical measurements were taken during the rainy season (see Table.3.). All the study lakes are well buffered except Lege Dadi reservoir which cannot be classified with these lakes since it is constantly replaced. One of the exceptional characteristics of Lege Dadi reservoir is its high ammonia and ammonium nitrogen content. The source of these chemicals is uncertain but intense bacterial decomposition is expected to contribute much. If the peasants around the reservoir use nitrogen fertilizers, the chemicals can also be imported by flood. Apart from these alternatives, excretion from fish and zooplankton can also result in the same situation. The very high level of sulphate in Lege Dadi reservoir is obviously from the added copper sulphate to control algal blooms. Copper sulphate is added at a given interval of time into Lege Daidi reservoir but the interval of time and dosage is not known (Mesfin & Belay, 1989). The present measured value (45 $mg.L^{-1}$) is sufficient to cause vomiting to human beings and it is well above the maximum tolerable concentration (0.1$mg.L^{-1}$). However, this concentration may not occur in the finally treated water.

Some other chemical anomaly particularly concerning soluble reactive phosphate is observed in Lake Hayq. It is known that unlike that of copepods the faecal pellet of cladoceran is flocculent and remains in the upper layer of the lake being soluble. Since large number of them are found in Lake Hayq, the faecal pellet of cladoceran might have contributed to such a high level of ortho-phosphate observed. In general diel vertical migration and excretion can also induce such effects (Wright & Shapiro, 1984).

Since the lakes considered are dominated by Na^+, total hardness is a reflection of carbonate and bicarbonate concentrations of each water body. It is previously reported that the Bishoftu crater lakes contain sodium as a major cation and carbonate and bicarbonates as major anions (Prosser *et al.* 1968).

Chlorine is considered to be generally conservative and the best measure of evaporative concentration (Wood & Talling, 1988). The high level of chlorine in the Bishoftu crater lakes compared to the other study lakes could be a result of high evaporative loss since they are closed basin type lakes. Lake Arenguade is relatively smaller than the other two lakes

(Bishoftu and Hora) and is more affected by direct human interference. Therefore livestock watering and washing of their bodies directly in the lake and laundering by the local peasantry may contribute a considerable chlorine input.

The plant nutrients such as silicate, phosphate and nitrogen in the Bishoftu crater lakes are within the range of values recorded by other workers (Wood *et al.*1984; Wood & Talling, 1988). Measured phosphate concentration in Lake Arenguade is similar to that of Wood *et al.*(1984) for the period between December-January but a bit higher. Ortho-phosphate could not be detected in surface waters of lake Bishoftu and Lake Hora during the study period. This is not a new phenomena since it is known that ortho-phosphate is normally present in very low concentrations in surface waters of Lake Bishoftu and Lake Hora (Prosser *et al.*1968). An exceptional case of Lake Hayq requires special explanation. An ortho-phosphate record of 100 $mg.L^{-1}$ is extremely high. Even range of values 3-7 $mg.L^{-1}$ in surface waters are indications of surplus ortho-phosphate (Wood *et al.*1984). Since Lake Hayq is well mixed from the surface deep to 15m during the study period (Fig.4c), ortho-phosphate might have been released from the sediment up to the epilimnion. Furthermore, the yearly mass-fish kill can also contribute in two ways. Firstly, it is observed that chl.a. concentration has decreased ten fold. This can result in reduced ortho-phosphate uptake since the phytoplankton population is so much declined. Secondly, phosphate can be released from the decomposed body of dead fishes and then transformed to ortho-phosphate through some reactions.

Though it is difficult to find nitrite-nitrogen records in its own respect, the measured values in this work are quite above the detection values while most workers argue that nitrite or nitrate nitrogen are seldom detected in surface waters (Prosser *et al.*1968; Wood *et al.*1984; Wood & Talling, 1988). In general the alkalinity, pH and conductivity are less than previously measured values (Wood & Talling, 1988). This may be due to dilution by rain water or the time change of the chemical situation.

Concerning dissolved oxygen (Fig.4) all the study lakes and Lege Dadi reservoir show oxygen stratification. This stratification can be a result of an intense hypolimnetic bacterial decomposition or intense epilimnetic photosynthesis. In the former case oxygen is consumed while in the later case it is released (Wood *et al.* 1984).

The depth-oxygen profiles are in accordance with other similar works. *e.g.* dissolved oxygen concentration of Lake Arenguade on 3 March, 1993 is exactly the same as that of 6 October, 1964 (Wood *et al.*1984). It seems that comparison of these results is irrelevant because of the time elapsed. The authors, however, have expressed that it was a rainy season during that year which has an almost similar climatic condition to the time when the measurement was taken in this work. This value (20 $mg.L^{-1}$) at surface and total depletion of oxygen at about 2.5m is the very reason why fish cannot survive in Lake Arenguade but exist in the other lakes studied.

Total carbon dioxide in Lake Arenguade and Lake Hayq could not be detected. This could be due to active photosynthesis during the measurements or methodological error since carbon dioxide is highly sensitive, even, to slight shaking of the sample during the experiment. However, it is known that at very high pH, active phytoplankton populations would be expected to raise the pH by several units and soon exhaust the available carbon dioxide (Talling *et al.*1973). Depletion of carbon dioxide was expected to occur relative to the content at air-equilibrium.

Thermal stratification is not observed in any one of the lakes studied (Fig.4). The unpredictable nature of thermal stratification in Ethiopian lakes is prevalent also in this work (Prosser *et al.*1968; Wood & Talling, 1988). The effect of each of these chemicals on grazing rate is related to the trophic status of the lakes. It is known that eutrophic lakes are rich in their chemical concentration. This condition is discussed below in relation to zooplankton grazing rate in each lake.

5.2. NATURAL ZOOPLANKTON COMMUNITY GRAZING RATES

In this study zooplankton community grazing rate ranging from 0-95.5% day^{-1} was measured. The high photosynthetic capacity and biomass of the phytoplankton in the lakes studied in comparison with their counterparts located in the temperate zones (Serruya & Pollingher, 1983) are not accompanied by high grazing rates as expected. Various reasons could be pointed out for such a result. Before going into the details of the explanations, it may be helpful to look into the trophic states of the study lakes. Based on the classification system proposed by Reckhow & Chapara (1983) cited in Stephen *et al.*(1989), lakes could be grouped into four, according to their mean chl.a. concentrations:

Oligotrophic < 4 $\mu g.L^{-1}$
Mesotrophic 4-10 $\mu g.L^{-1}$
Eutrophic 10-25 $\mu g.L^{-1}$
Hyper-eutrophic > 25$\mu g.L^{-1}$

Depending on this classification, lakes Bishoftu, Hora, and Lege Dadi reservoir could be categorized as mesotrophic while Lake Awassa is eutrophic, Lake Arenguade is hyper-eutrophic and Lake Hayq is oligotrophic (see Appendix II).

Apart from elevated chl.a. concentrations eutrophic lakes are characterized by high nutrient concentrations and increasing incidence of nuisance algal blooms (Stephen *et al.*1989). Regarding the chemical concentrations of the study lakes, only Lake Arenguade could be considered as saline having salinity value in excess of 3 $g.L^{-1}$ (Wood & Talling, 1988). Their silica content is very high, greater than 40 $mg.L^{-1}$ in some cases (Table 4). This may result in part from the relatively insignificant contribution which diatoms make to the phytoplankton of the lakes with high silica concentration in this study (Prosser *et al.* 1968). Recent workers argue that phosphate and nitrate concentration, but not other chemicals, determine chl.a. concentrations to a large extent (IFE, 1991/1992). The same authority claimed that limiting nutrients are different for different lakes. In other cases it is evident that as the ratio of inorganic nitrogen to phosphate phosphorus become smaller, nitrogen-fixing blue-green algae will become dominant (Kanninen *et al.* 1982) as these are capable of utilizing inorganic nitrogen.

When average values of each lake are compared an inverse relationship between the trophic status and %G day^{-1} is observed. That is grazing rate decreases with increasing trophy. Since grazing rate decreases with increasing food concentration (Gulati *et al.*1982; James & Forsyth, 1990; Cyr & Pace, 1992) this observation is in agreement with theoretical expectations. Based on the trophic classification used above, eutrophic lakes are characterized by high chl.a. and nutrient concentration. Accordingly, in such lakes grazing rates are expected to be low. However, this order is sometimes complicated by the types of crustacean zooplankton present in each lake. For example, the average grazing rate of mesotrophic Lake Hora (75%) is even higher than that of oligotrophic Lake Hayq (72%) (see Appendix II). This may be due to the calanoid copepod *L.africana* in Lake Hora and cyclopoid copepods and cladocera in Lake hayq. It is known that calanoids are more efficient grazers when compared to cladoceran and cyclopoid copepods (Cyr & Pace, 1992). Whenever calanoid copepods are the dominant grazers high grazing rate is expected; concurrently when cyclopoids or cladocerans are dominating the reverse situation should prevail. However, the trophic conditions of the lakes but not the type of zooplankton present determined grazing rate at large. In other words good grazers were hindered by the high food concentrations of eutrophic lakes and poor grazers were favoured to do well by the low food concentration of oligotrophic lakes. *e.g.* consider the cases of Lake Arenguade and Lake Hayq (Appendix II). In some cases grazing rate could be hampered by some physical hindrances such as turbidity *e.g.* Lege Dadi reservoir.

In Lake Hayq where soluble reactive phosphate is extremely high (100 µg. L^{-1}) nitrogen may be a limiting element. Such a chemical anomaly may be due to a flocculent nature of cladoceran faecal pellets (Shapiro & Wright, 1984). In the tropics where the temperatures of the water and surface sediments are very high, nitrate is rapidly lost from the water column while the flux of soluble reactive phosphate from the sediment into the overlying water is enhanced (IFE, 1991/1992). It is also possible that the time of measurement might have coincided with a high flux of ortho-phosphate from the sediment to the upper layer of the water column or by the force of mixing. The water temperature of Lake Hayq on 17 July, 1993 was 20^{0} C up to 14 m depth (Fig.4.C). Under such conditions chl.a. concentration will be very low if there are non-nitrogen fixing algae. This means non-nitrogen fixing algae may be excluded by competition since they are unable to use inorganic nitrogen. So the case of Lake Hayq is in agreement with this conclusion. However, it is difficult to elucidate such facts without having sufficient data of these chemicals at hand.

In any case the measurements obtained using both the radio-labelling and change in chl.a. method are higher than most published temperate percentage zooplankton community grazing rates. This is evident from Cyr & Pace (1992) who plotted frequency distribution of published measurements versus %G.day^{-1} and found that 51% out of 365 observations were less than 25%.day^{-1}. Few of the temperate community grazing rates much higher than the present measurements are also notable (Haney, 1973, Gulati *et al.*1982). %G.day^{-1} in this work is less than that of tropical African measured values (*e.g.*, Jarvis, 1986). Several reasons could be pointed out for such values. Radio-labelling method is more sensitive than change in chl.a. method on the whole (Peters, 1984). However, in this work change in chl.a. method was applied almost all the times. Comparison of tropical grazing rate values with those of temperate results is misleading for various reasons. For one thing temperate zooplankters whenever mentioned are usually cladoceran, especially *Daphnia*; secondly there is great difference in temperature as well as mixing pattern. When there is complete mixing, particularly in eutrophic lakes, regions of low food concentration are not available. That is the food available in the lake is evenly distributed and when it is highly concentrated grazing rate decreases. It is also possible that high temperature may result in higher grazing rate, for respiratory rate increases more rapidly at higher temperatures, but the magnitude of the acceleration of the metabolic rate determined by the value of Q_{10} (Lampert, 1984). Finally, zooplankton grazing rate studies are highly concentrated in temperate regions; especially tropical Africa is in severe lack of literature in this field. Therefore comparison of individual lakes studied in this work seems to be most appropriate.

The lakes studied were all dominated by the blue-green algae and only one genus of green algae , *Botryococcus sp.*, in Lake Awassa. Lower grazing rates were recorded by the radio-labelling method, though zero %G.day^{-1} was observed by the change in Chl.a. method in one case. The lower %G.day^{-1} obtained by radio-labelling method could be due to the loss of the isotope from the zooplankton by leaching in the preservative fluid (Gulati *et al.*1982). *Botryococcus*, a single phytoplankton species in Lake Awassa was found to be among the lipid producing buoyant green algae and characterized by mucilage production. Under conditions of extreme nitrogen deficiency, the cells become buoyant with simultaneous increase in carotenoid content (Reynolds, 1984). From this definition it can be deduced that since carotenes cannot contribute to chl.a. content, the loss in chl.a. when measured can inevitably be zero. On the other hand the zooplankton and the *Botryococcus sp.* will be spatially separated during the day when the measurement was taken. This separation is due to the fact that zooplankton migrate downwards against visual planktivory (Lazzaro, 1988) or to exploit less concentrated environment (Haney, 1985), while the *Botryococcus* floats. In all cases whether they feed on *Botryococcus* or not, measurable chl.a. difference was not obtained. Gelatinous green algae were also found to be actively rejected by zooplankters (Porter, 1973).

It is well known that adult *Mesocyclops* are carnivores (Burgis *et al.*1973). The biomass of adult Mesocyclops in Lake Awassa during this experiment was 1.92 mg.m^{-3} while that of *Thermocyclops* and *Diaphanosoma* were 0.79 and 2.38 mg.m^{-3} respectively. These values are very small compared to the 1987 october result of Mengistou & Fernando (1991). In their study this month was a moderately high production season (see Figures 2-5 in their work). Apart from carnivory by adult mesocyclops, vertebrate planktivory might have kept the population size of these herbivores very low. On the other hand, cyclopoids are found to be poor grazers even if they were present in large numbers (Cyr & Pace, 1992). These all may contribute to small grazing rate but by any means cannot result in negligible %G.day^{-1}. Therefore this result shows complete rejection of the *Botryococcus* by the zooplankton most probably due to its inedible nature. If *Botryococcus* is edible and all these possibilities fail to explain the reason of obtaining lowest result in Lake Awassa, conditions of temperate regions may operate also in the tropics. To find measurable grazed phytoplankton, nutrient addition, longer experimental time or larger chambers may help to increase phytoplankton biomass as in the case of Cyr & Pace (1992).

In Lake Arenguade where highest %G.day^{-1} was observed, the largest calanoid copepod *L.africana* was the only crustacean zooplankter found. The phytoplankton was a uni-algal culture of *Spirulina platensis*. This result is comparable with that observed by Vareschi & Jacobs (1984). In a laboratory experiment they found that both the copepods and adult stages of *L.africana* feed on *Spirulina* and obtained clearing rate of 92 ± 7 μL.L^{-1} in 73 repeated experiments, though the unit of measurement are different. In this lake *Spirulina platensis* has successfully out competed all other phytoplankters and now exists as a pure culture. The probable reasons for the competitive ability of the blue-green algae was explained by Keating (1978). Among these factors allelopathy was considered to be the most prominent. *L.africana* could have cleared more but the gut analysis under an inverted microscope shows that large number of coccoid bacteria were consumed too. Some workers found that bacterioplankton contribute a considerable amount to zooplankton food (Riemann & Bosselmann, 1984; Borsheim & Anderssen, 1987). The *Spirulina* ingested was also found to be fragmented showing raptorial feeding. One may wonder comparing the chl.a. concentrations of Lake Arenguade in 1964-1966 (Wood & Talling, 1988) (chl.a. concentration 400-5000 $\mu g.L^{-1}$) and this work (292 $\mu g.L^{-1}$). While most of the lakes studied and the worlds' lakes are accelerating towards eutrophication (Benndorf, 1988; Shapiro, 1990) this lake is moving to oligotrophic condition. Actually it is not striking since in alkaline-saline lake, Nakuru, of similar ecological characteristics production is by far less than consumption. Further more self shading limits algal production (see Vareschi & Jacobs, 1984). In Lake Arenguade, the consumption rate of the lesser Flamingo, *Phoeniconias minor* is not known. However, Vareschi & Jacobs (1984) found the highest consumption rate (12.6 KJ.m-3.d-1) while copepods consumed only 6.5 $KJ.m^{-3}.d^{-1}$ in lake Nakuru. Therefore it is not illogical if chl.a. concentration goes on decreasing order year after year. It is well known that grazing by zooplankton in eutrophic lakes has little effect since production is found to be equal to consumption (Jarvis, 1986; James & Forsyth, 1990)

Except Lake Awassa, the other lakes are almost occupied by the blue-green algae. From the Bishoftu group Lake Bishoftu was once observed covered with scum of *Microcystis aeruginosa*. In such cases zooplankters may have little effect on phytoplankters either because of their toxic production (Stangenberg, 1968) or too large to be easily grazed. Therefore grazing rate is expected to be very low. During the bloom season *Oscilatoria* may be excluded by the inhibitory effects or allelopathy, leaving toxic *Microcystis aeruginosa* for grazers. *Oscilatoria* by itself is both mucilaginous and filamentous. Thus it is large in size and buoyant in space, being unavailable for grazers at about 1m.

Considering Lake Hayq, chl.a. concentration was lowest probably due to high grazing pressure or unproductiveness of the lake. It is possible that under low chl.a. concentration high grazing pressure can create a clear-water phase (Gulati *et al.*1982; Kleot, 1982). From all lakes studied Lake Hayq is the deepest lake. Furthermore, zooplankton density is very high in comparison to the other lakes, even though the biomass is small. This lake may be one of those lakes that regulate themselves by natural biomanipulation. That is when the biomass of planktivorous fish becomes higher and phytoplankton biomass rises, mass fish-kill occurs as a result of hypolimnetic oxygen depletion after which the phytoplankton biomass declines and so on (Shapiro, 1990). Recently fish gut analysis showed that immature forms of *Tilapia* largely feed on zooplankton in Lake Hayq. This is a new event since previously it was only known that very small sizes much less than the present forms feed on zooplankton. Thus from this finding it is observed that *Tilapia* is changing its feeding habit. However, what caused change their feeding habit is not known yet (Demeke Admassu, personal communication). In such cases it could be possible that a slight increase in fish biomass may cause a pronounced increase in phytoplankton biomass and this is true particularly during the hatching season, and thereafter until their adult stage is achieved.

An increase in number and biomass of their immature forms may be a self suicide for the fish population, since this phenomenon results in increase in phytoplankton biomass and hypolimnetic oxygen depletion which could cause mass-fish kill. Mass fish-kill was reported recently in this lake (Elizabeth *et al.*1992) and every year (Kebede personal communication). The reduction in chl.a. concentration from 15 $\mu g.L^{-1}$ in 1989 (Elizabeth *et al.*1992) to 1.5 $\mu g.L^{-1}$ in this work may be the consequence of mass fish-kill every year.

Concerning Lege Dadi reservoir, grazing rate is relatively lower than the other four lakes excluding Lake Awassa, due probably to turbidity. The reservoir water is highly turbid as a result of flood in the month of May, 1993. Since the surrounding area of the dam is farmland, there is an enormous silt accumulation. *Metadiaptomus colonialis*, the next larger calanoid copepod in this study is the only dominant zooplankter with very rare cyclopoid copepod, *Thermocyclops sp.* in Lege Dadi reservoir. In a turbid tropical reservoir, Hart (1988) observed a sharp linear decrease of consumption rate with increasing turbidity for a calanoid copepod *Metadiaptomus meridianus.* He also stated that turbidity is tolerable provided food content rises concurrently. However, high mineral turbidity and high food availability are mutually exclusive conditions. The turbidity level of Lege Dadi reservoir during this study was not measured, but Secchi depth was only 20 cm and the chl.a. concentration was 5.6 $\mu g.L^{-1}$

showing a mesotrophic condition. Certainly this low transparency is attributed to turbidity, that may be the very reason for low grazing rate observed here.

Contrary to this fact, turbidity has also a considerable importance when it is related to biomanipulation. Any factor affecting quantity or quality of light will affect visual predation rate. Therefore the frequent high turbidity of reservoirs caused by silt and/or clay will help zooplankton to exist in the immediate presence of planktivorous fish. This is one, among the seven possibilities proposed as zooplankton refuge types. It is termed as light refuge (Shapiro, 1990). Through such refuges one can maintain herbivore populations with less attention to and management of fish populations. Two benefits: water clarity and fish protein could be obtained by implementing refuge concept.

5.3. MANIPULATED COMMUNITY GRAZING RATES

Zooplankton manipulation in this work is different from that of temperate manipulations since there is no nutrient added to increase phytoplankton growth. At the same time the chambers used are smaller than that is usually used in the temperate regions.(*e.g.* see Mazumder *et al.* 1990; Cyr & Pace, 1992).

Whenever zooplankton size fraction grazing rate was performed, always the larger size zooplankters showed higher grazing rates than the smaller size classes. The fact that body size has a strong effect on grazing rate seems to be universally accepted (see Peters & Downing, 1985; references listed therein and also Mazumder *et al.*1990; Turner & Mittelbach, 1992). This is true because larger size zooplankters increase the range of energy-rich resources available to them, their disadvantage being vulnerability to predation (Burgis *et al.* 1973; Hecky, 1984). From Peters & Downing (1984) one can observe that absolute grazing rate (cells.animal^{-1}.time^{-1}) rises with grazer size, while mass- specific grazing rate (cells.mg.animal^{-1}.time^{-1}) declines with grazer size.

Zooplankton biomass gradient grazing rate showed similar linear characteristic in all lakes considered except for Lake Bishoftu (Fig.5). That is increase in biomass increased %G to a certain maximum point beyond which a plateau was attained. This is in agreement with the simulation models of Carpenter *et al.*(1985). In their simulation models when herbivore biomass was high, productivity was restrained by grazing and declined as grazer biomass rose. So the decline in phytoplankton biomass by the grazers' pressure, increases grazing rate. The plateau in one case (Lake Hora) was declined showing a downward parabola-like shape, an inverse case which the authors proposed. That is productivity was related parabolically to chl.a. This means primary production shows positive relationship with chl.a. Therefore when zooplankton biomass increases either because of piscivore stocking or planktivore removal the reverse of upward parabola should prevail, according to the theory of cascading trophic interaction (For further details see Fig.3. in Carpenter *et al.*1985). Cyr & Pace (1992) also developed allometric equations and predicted that grazing rates increase with zooplankton biomass. The plateau and break-down of the saturated curve, however, requires especial explanation. Crowding reduces the grazing rate of both copepods and cladoceran (Peters, 1984). The other reason is as zooplankton biomass increases, chl.a. concentration decreases (James & Forsyth, 1990) and a threshold reached where no more grazing rate increases after which it decreases because of shortage of food. The implication of this idea to biomanipulation is that in order to attain the required water quality there should be a desired number of herbivorous zooplankton. In other words the biomass vales of zooplankton needed to clear the daily primary production in each lake of different trophic status should be known (Gulati, 1990). From the graphs (Fig.4), it is clear that 100% removal of the daily phytoplankton biomass is only possible in Lake Hayq. Increase of zooplankton ambient density to a considerable degree (even 3x), could not remove more than 85% of the daily phytoplankton biomass in the other study lakes. In Lake Arenguade the saturation point could not be reached while in Lake Bishoftu it might have been bypassed or the phytoplankton species present may be inedible. From all these facts it is possible to speculate that biomanipulation is is highly effective in Lake Hayq rather than the other three lakes (Arenguade, Bishoftu and Hora). Even though production is less than consumption in such lakes as Lake Arenguade, it may be very high that creation of a clear-water phase is improbable. To know the effective zooplankton biomass that can create a clear-water phase one should follow seasonal characteristics of zooplankton community grazing rate and biomass of each water body.

The case of Lake Bishoftu is different since during the study season blooms of blue-green algae (*Microcystis aeruginosa*) was observed. It is known that such toxic and large sized blue-greens are actively rejected by herbivorous zooplankton (Stangenberg, 1968; Peters, 1984). Thus the increase in zooplankton biomass contributes to competition for other few available edible algae causing %G.day^{-1} to decrease. Therefore increase in zooplankton biomass has a strong negative effect on phytoplankton biomass up to a certain maximum threshold above which grazing rate decreases. This final statement holds true if and only if the phytoplankton under consideration is edible. This problem is still a challenge to biomanpulation. That is when phytoplankton under consideration is inedible by the zooplankton of that system, no solution can be found (Benndorf, 1988).

5.4. STATISTICAL MODELS

Backward elimination procedure resulted in three regression equations with adjusted R^2 ranging from 27-64%. These results are comparable with those of Cyr & Pace (1992), particularly when zooplankton biomass is considered. This is not a chance correlation because it is a well established fact that zooplankton biomass has a strong positive effect on grazing (McCauley & Kalff, 1981; Kloet, 1982; Gulati *et al.* 1982; Peters & Downing, 1984; Haney, 1985; Knoechel & Haltby, 1986; Lampert *et al.*1986). Large size zooplankton biomass has strong effect on grazing rate than total zooplankton biomass for the reasons explained previously.

The probable reason why the coefficients are not significant may be due to the small sample size (n=6). However, these models provide a basic idea that at least 64% of the variation in percentage community grazing rate is due mainly to large size zooplankton biomass, chl.a. and temperature, mean zooplankton biomass having relatively small effect. It is not clear why temperature is negatively related to grazing rate and all types of zooplankton biomass in the correlation matrics (Appendix III). Nevertheless, this correlation does not seem to be the messy-data type or chance correlation. Gulati *et al.*(1982) clearly showed the inverse relationship between the mean individual weight and temperature in Lake Vetchen, the Netherlands. They also found that the specific filtering rate of zooplankton increases up to (15-20°C) and then decreases. This means filtering rate as any biological process has a temperature optimum above which it cannot increase. In this case the temperature values observed may be above the temperature optima required by the grazers under the present condition. Chl.a. is negatively related to %G. day^{-1}, for the very reason that as food concentration increases grazing rate also decreases (Burns & Rigler, 1967; Kloet, 1982; Turner & Mittelbach, 1992).

The validity of these models is open to further research but they are of heuristic value nevertheless. The models that are available for temperate regions mainly deal with cladoceran and when they do so, they use different units such as filtering rate, ingestion rate or feeding rate (Peters & Downing, 1984; Haney, 1985; Knoechel & Holtby, 1986). Such models are actually not available for tropical zooplankton community grazing rates. It may not be appropriate to compare temperate allometric models to tropical situations where there is unpredictable stratification (Prosser *et al.*1968) an almost year round constant temperature and eutrophic lakes dominated by inedible blue-green algae (Talling, *et al.*1973; Serruya & Pollingher, 1983). The zooplankton community are also different from temperate regions in that species diversity are limited due to intolerable alkalinity and salinity (Vareschi & Jacobs, 1984), and when present are calanoid and cyclopoid copepods (Serruya & Pollingher, 1983). The variation in predicted and observed values may be the reflection of these and /or more important factors might have been missed.

It is known that apart from filter-feeding cyclopoids are raptorials (James & Forsyth, 1990) and in this work total chl.a. is considered to allow raptorial grazing. So where ever large colonial blue-greens are present the cyclopoids and calanoids spend their time in pinching off the food available but actively filter feed when there are no such giant colony. The former situation lowers grazing rate while the later facilitates and raises the magnitude of grazing rate. The gap between the lower and the higher grazing rate is determined by the type of food available in each lake. Therefore for these models to be working models the number of lakes considered should be large enough and include different geographical region of the country. Future problems identified from this work are increasing the number of study lakes and developing similar models so that comparison is possible. Effective zooplankton biomass rather than total zooplankton biomass has considerable influence on phytoplankton biomass. Therefore that effective biomass which can control nuisance phytoplankton blooms should be determined. The method used in grazing rate measurements also should be the same throughout to avoid errors due to methodological artifacts.

6. CONCLUSION

The shore lines of most of the lakes studied including Lege Dadi reservoir are dynamic resource systems providing opportunities for agricultural, residential, recreational, commercial and industrial development. Yet many reaches of these shore lines also pose hazards to the lakes' ecosystem. The trophic status of these lakes may be the reflection of such a multipurpose activity whereby the integrated effect is accelerating most of these lakes towards hyper-eutrophic condition. An interesting outcome of these cases could be that of Lege Dadi reservoir where a public water-supply reservoir shows eutrophic condition. While flood imports silt, it also adds fertilizers leaching from the farm-lands that may be necessary for the algal growth. For some of the study lakes this condition holds true. *e.g.* Lake Hayq and Lake Awassa.

As natural protection, re-vegetation of the shore lines of the lakes may be an advisable solution, though it takes time. However, control of internal ecological dynamics is recently advocated as the most approachable strategy. The applicability of this strategy depends on zooplankton community grazing rate at large. That is, if zooplankton community grazing rate in a given lake is low nutrient control may be important. However, if zooplankton grazing rate is high, biomanipulation is certainly a choice of preference. Among the study lakes Lake Hayq could be considered as an example. Even though this lake is exposed to several human interference, it seems that it is a self-controlling system against eutrophication. A condition that seems catastrophic for the fish is certainly long lasting for the lake. What one learns from this natural biomanipulation is that planktivorous fish as it is already known are destructive in terms of water quality. Therefore from Lake Hayq it is evident that total removal of fish is not necessary to enhance zooplankton biomass but there is a balance somewhere where the zooplankton and fish co exist and at the same time eutrophication is checked. This is possible because intensive fishing can control fish biomass and increase zooplankton biomass. For Lege Dadi reservoir introduction of planktivorous fish from the very beginning was erroneous, since the objective of the dam was not for fish production but water-supply. It is recommended that intensive fishing be followed to keep the fish biomass very low. Total removal may not be advisable for the fact that invertebrate predators could predominate and destroy the zooplankters in the absence of planktivorous fish.

In most of the lakes studied grazing rate is moderately high. Nevertheless under eutrophic condition high grazing rate has little effect on phytoplankton biomass. This is true because except some saline lakes like that of Lake Arenguade the rate of production is equal to the rate of consumption. Furthermore, these lakes are occupied by the blue-green algae which are not edible either because of their large size or toxicity. It is also clear that grazing rate is only important where ever edible alga are dominant. From the present work it is clear that increase in the biomass of zooplankton results in decrease in the biomass of phytoplankton. Since this work was performed under natural condition it amends to the objectives of biomanipulation. While control of internal ecological dynamics is an important factor, management of external nutrient input cannot be ruled out to control eutrophication. It is important to note that the type of zooplankton and phytoplankton species determine the application of biomanipulation. Based on the grazing rate measured it seems that biomanipulation is applicable in all of the lakes and Lege dadi reservoir except in Lake Awassa. However, it is also necessary to know that high grazing rate does not mean water clarity since high grazing rates may have no effect on eutrophic lakes. The concept of refuge could be implemented in the study lakes rather than exterminating fish. For example, open water interference refuge, macrophyte or any physical refuge can help zooplankton to survive high predation pressures by visual planktivores. This can control edible phytoplankton at a considerably lower biomass (see Shapiro, 1990 for broader explanation of refuge concept).

Finally, eight basic conclusions can be generated:

1. Percentage community grazing rate per day in the study lakes is relatively high when compared with those of temperate regions but lower than those of tropical measured values.
2. Large size zooplankton showed higher grazing rate than the small size classes.
3. Increase in zooplankton density has considerable effect on phytoplankton biomass up to a certain maximum point after which grazing has no effect on phytoplankton biomass.
4. The regression models developed could be valuable allometric models if done on large scale and many lakes or the same lake under different conditions (R^2= 27-64%).

5. Biomanipulation is promising to control eutrophication in the study lakes except Lake Awassa in which %G day^{-1} could not be detected.

6. Two alternatives could be proposed:

(1) Control of nutrient input in the lakes where low grazing rates were recorded.

(2) Enhance fish production and water clarity by refuge manipulation where high grazing rates were observed.

7. There should be shore line policies to prolong the life of the lakes studied. Otherwise some of the lakes are liable to severe degradation.

8. Stop poisoning Addis Abeba with copper sulphate!!

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APPENDIX I

CALCULATION OF PERCENTAGE GRAZING RATE PER DAY

Percentage grazing rate per day was calculated based on the formula of Cyr & Pace(1992) with some basic modifications. In their calculation Cyr & Pace(1992) used the formula $(1 - e^b)100$ to calculate percentage grazing rate per day. From the relationship of their equations (1) and (2)

$$b=[\ln C1-\ln Co/T(ZC)]-A$$

where, C_1 and C_o are initial and final Chl.a. concentrations, T is the experimental period and ZC zooplankton concentration (x natural density), A is the realized algal growth when saturated with nutrients in the absence of macro zooplankton. In order $(1 - e^b)$ greater than zero b must be less than zero. Therefore in this equation b must be always negative to satisfy the rate equation under consideration. Since b is grazing rate the negative value of b has no physical meaning. Further more in the presence of sufficient zooplankton C_1 is always less than Co and b remains negative. This situation is evident particularly when phytoplankton production is less than their consumption by zooplankton. It is thus necessary to modify this equation in order to avoid such an imbalance. In this particular work the percentage algae grazed per day was calculated as follows:

Let C_o = initial chlorophyll a (chl.a.) concentration

C_t = final chl.a. concentration

C_g = chl.a. concentration disappeared due to grazing.

Assuming that loss is only due to grazing, at any given time t

$$Cg = Co - C_t \text{ ....}(1)$$

To find C_t the first order rate equation in kinetics can be used. Since the initial concentration of chl.a. goes on decreasing order, Chl.a. concentration (C) can be written as a function of time (see Marin *et al.*1986 and compare with Miller, 1984) for further explanation.i.e.,

$$-\frac{dc}{dt}=kc$$

where k is rate constant but coefficient of grazing in this experiment. Rearranging to:

$$-\frac{dc}{C}=kdt$$

and integrating between the limits of the initial concentration C_o at time t_o and the concentration C_t at time t

gives
$$-\int_{C_o}^{C_t}\frac{dC}{C}=\int_{t_o}^{t}kdt$$

and

$$-(\ln C_t - \ln C_o) = k(t - t_o)$$

Since $t_o = 0$, we have

$$-\ln(Ct/Co)=kt$$

Inverting the concentration term to eliminate the negative sign

$$\ln(Co/Ct)=kt \ldots\ldots\ldots\ldots\ldots 2$$

From (2) $\ln C_o - \ln C_t = kt$, and

$$K=\ln Co-\ln Ct/t \ldots\ldots\ldots\ldots 3$$

where, t= experimental time in days.

Equation (3) can be written as

$$\ln Ct-\ln Co=-Kt$$

(by multiplying both sides by -1)

So,

$$\ln Ct/Co=-Kt$$

thus

$e^{\ln Ct/Co} = e^{-kt}$

and $C_t/C_o = e^{-kt}$, where,

$C_t = C_o e^{-kt}$............4

Equation (4) shows that the original chlorophyll a concentration (Co) is reduced at any given time (t) to the concentration of chlorophyll a remaining (C_t).

Therefore by combining (1) and (4)

$$C_g = C_o - C_o\, e^{-kt}$$

and

$$C_g/C_o = 1 - e^{-kt}$$

The percent algae grazed is thus

$$(C_g/C_o) \times 100$$

or

$$(1 - e^{-kt}) \times 100$$

APPENDIX II

Raw data used for the calculation of regression models. Averages of two or three measurements were only considered in developing the regression models and calculation of correlation matrics in Appendix III.

Lakes	Date (Mo/d)	Temp	chl.a.	ZB	LZB	MZ	%G ± S.E
Arenguade	03/14	18.2	291.90	1554.04	1357.85	145.52	4.26 ± 0.52*
	05/31	19.9					95.46 ± 2.53
	09/19	22.5					62.48 ± 1.06
Bishoftu	03/13	20.0	7.90	6.51	5.26	0.459	59.37 ± 0.97
	05/25	22.0					
	09/19	24.0					
Hora	03/12	20.5	5.00	15.50	10.46	6.75	7.10 ± 1.35*
	06/01	20.3					77.08 ± 2.16
	09/20	24.5					72.22 ± 3.06
Awassa	10/12	23.2	12.60	6.304	4.34	0.30	0
	10/14	19.1					0
	10/11	----					
Hayq	07/16	18.0	1.14	52.17	44.54	0.43	81.69 ± 1.90
	07/17	21.0					
	07/18						62.50 ± 2.04
Lege Dadi	05/07	19.0	5.60	969.95	889.91	19.00	5.00 ± 0.82@
	05/08	----					56.84 ± 1.76

Note: Water temperature (^{o}C) at 1m is listed.

Units and designations: Temp = temperature in degree centigrade; chl.a.= Total chlorophyll a concentration in $\mu g.L^{-1}$; ZB = Total zooplankton biomass in $mg.m^{-3}$; LZB = large size zooplankton also in $mg.m^{-3}$; MZ = mean zooplankton biomass; %G percentage community grazing rate per day and --- = not measured;* = Radio-labelling method is used; @ = Long experimental time (18 hrs).

APPENDIX III

Computer print-out of the correlation matrics used in the regression models.

Correlation	Temp	logchl.a.	log ZB	log LZB	MZ	log%G
Temp	1.0000	.0817	-.7683	-.7762	-.2322	-.1317
log chl.a.	.0817	1.0000	.4675	.4567	.8963*	-.0143
log ZB	-.7683	.4673	1.0000	.9995**	.7236	.3822
log LZB	-.7762	.4567	.9995**	1.0000	.7160	.3905
MZ	-.2322	.8963*	.7236	.7160	1.0000	.2936
log Gr	-.1317	-.0143	.3822	.3905	.2936	1.0000

N of cases: 6 1-tailed Signif: *.01 **-.001