ZOOPLANKTON STRUCTURE AND DYNAMICS IN TWO CONTRASTING SODA LAKES.

(DEBRE ZEIT CRATER LAKES: ETHIOPIA)

By

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June, 1992.

Addis Ababa.

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ABSTRACT

Studies on the species composition, age structure, sex ratio, pattern of abundance and measurement of body size and brood size was performed on the zooplankton community in Lakes Bishoftu and Arenguade from January, 1991 to December, 1991. The former is inhabited by planktivorous fish, *Aplocheilichthys sp* and *Oreochromis niloticus* while the latter is devoid of fish.

The species composition of the zooplankton community in both lakes is poorly diverse and share a dominant calanoid, *Lovenula* (*Pardiaptomus*) *africana* (Daday, 1908) and one dominant rotifer genus *Brachionus*. Additionally Lake Bishoftu is inhabited by the cylopoid *Mesocyclops aequatorialis*.

Body size and brood size of ovigerous females of *L.africana* from these lakes were significantly different both in body size and mean brood size (P <0.001). The frequency distribution of the adult size classes is negatively skewed in Lake Bishoftu as opposed to Lake Arenguade.

Body size and brood size were positively related in both lakes and strongly positive (R = 0.447)in the population under predation pressure than with no predation (R = 0.297). Most size classes of Lake Bishoftu's copepods bear significantly different mean brood size (GT2 test).

Sex ratio were also significantly different from the expected one to one ratio in both lakes (P < 0.001) and the ratio is strongly skewed in favour of females in Lake

Arenguade. Also a higher proportion of adults to juveniles was observed in the latter. Seasonal variation in body and brood size were also observed in relation to the mixing period (November - February) and fish kill. The differences in body and brood sizes were attributed to size selective predation by fish in Lake Bishoftu, in the absence of intense competition, food limitation and temperature differences between the two lakes.

One factor ANOVA revealed that zooplankton abundance differed significantly between months ($P < 0.001$).

Except for rotifers, zooplankton biomass showed clear seasonality with population collapse during the mixing period coinciding with upwelling of anoxic water and H_2S. Recovery and peak abundance were observed during the stratification period (July - September). Rate of recovery was variable for different species and stages. Phytoplankton and major nutrients showed less pronounced seasonality in both lakes, with nitrogen rather than phosphorous being more limiting.

CHAPTER I

1. INTRODUCTION

Historically, community ecologists have characterized organisms primarily by taxon with little regard for other potential characterization, save perhaps for trophic position or nutrition.

Taxonomic approach to community structure may not be the most useful, for it is becoming increasingly apparent that energy flow within aquatic systems is more a function of size of organisms than it is of their taxonomic status (Kerr, 1974; Sheldon et al., 1977; Dickle et al.,1987). For this reason cell size or body size of aquatic organisms is a broadly useful scaling factor for comparisons of basic metabolic processes, growth rates, production rates, reproduction commitments, and constraints on shape and mechanical design. Scaling by size also permits comparisons among ecosystems of gross structure or energy and carbon transfer efficiencies.

In aquatic ecosystems, zooplankton populations can be considered, to a certain extent, as a pivot of freshwater pelagic ecosystems for the simple reason that the phytoplankton-zooplankton relationships determine the nature of energy flow from the primary to the secondary producers and, on the other hand, the nature of the zooplankton community governs, to a larger extent, energy flow to planktivorous fish (and thence to top carnivores). Because of these reasons analysis of patterns in the structure of zooplankton communities alone can provide useful information about the nature of lake ecosystems. Besides due to the " cascading effect" (Carpenter et al.,1985) the size structure of zooplankton community also affect phytoplankton biomass and increase water transparency (Kitchell & Kitchell, 1980; Shapiro & Wright, 1984; Kitchell & Carpenter, 1988; Mc Queen & Post, 1988). Deliberate manipulation of the size structure of lake zooplankton by reducing planktivorous fish is becoming increasingly promising to improve the water quality (Shapiro & Wright, 1984; Kitchell and Carpenter, 1988).

It has been argued here that such analysis should be based on the functional, size-feeding ecological characterization of the zooplankton association for this reflects dynamic processes in the ecosystem much more closely than does a simple taxonomic characterization (Sprules & Knoechel, 1984). Thus a size feeding ecology characterization seems to be more fruitful basis to compare and classify lakes within regions and between geographic areas.

There is an intriguing possibility that the size structure of zooplankton communities responds to socially important stresses such as acid, thermal and nutrient and perturbation in the food webs. So it is worth determining whether changes in size structure can provide an early warning about deteriorating lake quality (Sprules & Knoechel, 1984). The rule of optimal foraging applies to man as well and when he attempts to recover prey of very small size from water, the energy invested in capture and processing rises dramatically even neglecting food preferences and cost factors. The efficiency at which we can derive protein from a pelagic ecosystem (the carbon transfer efficiency) falls rapidly as we attempt to harvest directly the second and first trophic level of a natural aquatic system (Hecky, 1984). As a result man tends to harvest the third level and if it is not yet available man intends to introduce it. Such perturbation in the food web at the higher level of the aquatic ecosystem brings certain changes in the lower level (Carpenter _et al_.,1985).

The study on the effects of such perturbation in the food web of a lake system can only be possible by creating near natural condition in the laboratory, in experimental ponds (e.g. Drenner _et al_., 1986, Threlkeld & Drenner, 1987) or delimiting part of the natural system and keeping it under certain degree of control such as limnocorrals (e.g. Mc Queen _et al_., 1986; Post & Mc Queen, 1987; Mc Queen & Post, 1988) or following changes in a single lake before and after manipulation (Warshaw, 1972; De Bernandi & Guissani, 1978; Kitchell & Kitchell, 1980; Shapiro & Wright, 1984; Kitchell & Carpenter, 1988) or comparative study on two closely related lakes with contrast for the given factor (Galbraith, 1967; Sprules, 1972; Gliwicz _et al_.,1981; Papinska, 1988) a rare chance in nature.

Extrapolation of limnocorral experiments suffer a serious deficiency because of reduced advection and vertical eddy of the system though they are relatively controlled conditions (Bloeschel _et al_., 1988). Direct manipulation of lakes requires introduction of planktivorous fish which will be impossible to eliminate afterwards without destructing the life in the lake (Turner, 1981). Result of these perturbations may also need longer time with all possible complications. The other way is to eliminate planktivorous fish from a lake which again affects the lives in the lake other than fish (Naess, 1991) and may also require time to recover. The other alternative is comparative study of two closely related lakes, though rare in nature (e.g. De Bernandi & Guissani, 1978).

Gliwicz *et al.*,(1981) indicated that different densities of two populations of the same species in two lakes should be easy to explain by food concentrations and / or predation pressures, presuming that no differences are present in two lakes with regard to physical and chemical environmental factors. The two lakes in this study are dominated by a single species of Copepoda, *Lovenula* (*Paradiaptomus*) *africana* (Green, 1986) and the phytoplankton population is predominantly blue green algae (Baxter & Wood, 1965; Green, 1986). The system is rather simple in a sense that there is one dominant blue green algae, one dominant crustacean herbivore species in both lakes and two planktivorous fish in one of the lakes. The physical and chemical conditions are also similar (Prosser *et al.*, 1968; Wood *et al.*,1976; 1984). Horizontal variation is minimum due to the small size of the lakes. As a result these lakes were found to be suitable for comparative study:

(i) on the effect of fish predation on the size structure of the zooplankton population and

(ii) the effect of physical and chemical changes throughout the year on the size of the individuals and population size.

Results of this study can generate information on the possible ecological risks following introduction of fish.

2. LITERATURE REVIEW

2.1. EFFECT OF PREDATION AND ADAPTIVE RESPONSE OF ZOOPLANKTON

Resource limitation and predation are the two major forces that act to limit animal and plant populations and hence structure biotic communities. Resource acquisition is a constant requirement of all organisms and, in a sense, provides an absolute limit to population density. Because there is little a resource-limited population can do to create more resources, evolutionary responses to resource limitation tend to be straight forward: take as fast as possible and store as much as feasible. Evolutionary responses to predation, however, are far from straight forward. Predators have evolved a variety of means to search out and stalk their prey, and many means have evolved to foil, at least partially, each predatory scheme (O'Brien, 1987).

The usual focus of the effect of predators on prey is the direct lethal effects of predators. By killing prey, predators can control prey populations, drive some prey types extinct and alter the relative and absolute abundances and species diversity of prey. Predators also, however, have potentially important indirect effects on shaping of preys' life-styles through their impact on the development of prey defence, both by selecting for well-adapted genotypes and inducing changes in morphology, physiology, chemistry, life history, and behaviour of prey (Havel,1987; Murdoch & Bence, 1987; Sih, 1987).

2.1.1. MORPHOLOGICAL RESPONSES OF ZOOPLANKTON TO PREDATION.

When one considers the visual acuity of predators which depends upon the contrast between the prey and its background, minimizing the contrast would mean reduction in the conspicuousness of the prey.

The evolution of increased transparency became one of the most important and widespread protective adaptation against visually feeding predators (Greze, 1963 cited in Kerfoot, 1980). The resulting crypsis provides an evolutionary solution to the problem of concealment against a continually changing background. As a result several notably large-bodied prey survive in pelagic regions because of their extreme transparency (e.g. Chaoborus, Leptodora, Daphnia galeata mendota) (Zaret, 1980a). Although the effects of visual predation are found even in clear arctic lakes (Kettle & O'Brien, 1978), responses would be especially pronounced in tropical latitudes because in tropical climates, fish activity is year-round, water are brightly illuminated and prey generation times are short (Zaret & Kerfoot, 1975; Kerfoot, 1980). Pigmented body parts such as eye-size, darker body regions, presence of haemoglobin, and the colour of the gut content also increase the conspicuousness of a prey.

Intense visual predation by fish in very clear tropical lakes explains the occupance of different eye-size "morphs" (not morphs in the sense of different phenotypes within a single brood, but genetically different clones) of Daphnia, Ceriodaphnia, and Bosmina. Despite its small size, Bosmina longirostris also show spatial and temporal differences in eye size associated with fish predation in Lake Gutun, Panama. (Zaret & Kerfoot, 1975; Kerfoot, 1980). Small eye size was also found to be negatively correlated with spine lengths in tropical Lake Gutun, Panama (Mort & Kerfoot, 1988).

Such association again leave a choice either to have larger body size with smaller eye size or smaller body size with larger eye size where both lead to a better inconspicuousness.

Females with darker eggs (e.g. Daphnia with ephippia and ovigerous females of diaptomids) were found to be highly selected than those without by planktivorous fish (see Mellors 1975; Tucker & Woolpy, 1984). Detailed field collections combined with experiments in a pond and laboratory showed that female Diaptomus sanguineus carrying eggs are especially visible to fish and suffer particularly high mortality in Bullhead pond, Rhode Island, (Hairston, 1987).

The other notable contrast between a transparent-bodied zooplankton and its environment is produced by the colour of the food item inside the gut and / or by the presence of high concentration of haemoglobin. Such individuals were found to be selected than their counterparts (Zaret, 1972; O'Brien, 1975).

Dodson (1974) proposed that cyclomorphosis, an annual change in morphology, may be an adaptive response to size-specific predation: small body size defend against visual predators, usually fish, and spines, neck teeth, and helmets defend against tactile predators. Cyclomorphosis, as an adaptation to predation, is a well documented phenomenon both in experimental and field studies. The two invertebrate predators, Anisops calcaratus and the larvae of Chaoborus americanus, release water-soluble morphogens that affect Daphnia exoskeleton (Grant & Bayly, 1981; Krueger & Dodson, 1981; and Herbert & Grewe, 1985). A. calcaratus induced crest enlargement in two of the three subspecies in the D.carinata complex. Chaoborus induced enlargement of a toothed crest or helmet in several Daphnia species (Krueger & Dodson, 1984; Herbert & Grewe, 1985). These spined morph of D.pulex were absent in ponds without Chaoborus, and the spined forms were replaced by typical morphs in a few weeks after the removal of the predator (Havel, 1985).

Lengthening the antennules and mucrones was also found to be protective in Bosmina against invertebrate predators by keeping the main and delicate body part at a distance and during manipulation, the elongated antennules may break off and allow the prey to escape (Kerfoot, 1975).

Since feeding rates of Notonecta increase with increased Daphnia body size (Scott and Murdoch, 1983), reduction of body size for the youngest adults may be adaptive in the presence of these invertebrate predators. In the absence of such predators, optimal body size should be larger in order to maximize fecundity and minimize losses from smaller invertebrate predators. Similar effects have been observed due to fish predation both in macrocosms and in natural water bodies for the last four decades (see Brooks & Dodson, 1965; Galbraith, 1967; Zaret, 1980a; 1980b; Culver et al., 1984). Brooks &

Dodson (1965) were the first to document the effect of fish in bringing about a reduction in body size of zooplankton by selectively preying on larger species or larger individuals of a given species.

Green (1967) also distinguished two morphs of Daphnia lumholtzii in a tropical Lake Albert : a small, inconspicuous horned morph found in regions of high fish predation and a large, more visible unhorned morph found in regions lacking fish.

Morphological changes induced by predators is also a strategy in zooplankton other than crustaceans. The predatory rotifer Asplanchna brightwelli releases morphogen which induce the formation of longer spines in Brachionus calyciflorus (Gilbert, 1980). A well developed postero-lateral spines of B. calyciflorus was established as a result of predation pressure of Asplanchna sieboldi in Lake Pawlo (Ethiopia) population, where it attains the longest mean spine length (Green, 1986).

When some soft-bodied rotifers, such as Synchaeta and Asplanchna are contacted by invertebrate predators, they retract their corona, making their bodies swollen and turgid. This turgor makes them difficult to grasp and hence capture by some copepods (Williamson, 1983).

2.1.2. BEHAVIOURIAL RESPONSES OF ZOOPLANKTON TO PREDATION

Noncryptic prey can persist locally with predators by limiting their activity to relatively predator-free situations. Reduced activity per se is a typical anti predator response that presumably reduce the frequency of contact with predators and the likelihood of detection and recognition as prey. Further, prey often restrict their activity to microhabitats where predators are less effective, i.e., use refuges; and restrict activity to times of the day or seasons when predators are relatively inactive. These mechanisms for "coexisting in hiding" are potentially costly to prey in terms of lost opportunities to feed or mate (Sih, 1987).

The diel vertical migration of pelagic preys is another instance of behaviourial response of zooplankton to predators. The diurnal movement to a lesser productive and cool hypolimnion decelerate growth rate and lower reproductive commitment as a result of low food availability and increased egg development due to lower temperature (Wright et al.,1980; Lampert, 1987).

Such temporal shifting of habitat in pelagic prey species show certain natural pattern depending on the age class of organisms, i.e., the smaller size/age class (less vulnerable groups for visual predators) remain relatively on the surface while the adults do migrate to a depth depending on their relative size (Zaret & Suffern, 1976; Zaret, 1980a).

The amplitude of migration in turbid lakes (with reduced penetration of light) is fairly slight, often only a few meters; whereas in oligotrophic lakes and seas, where the light intensity gradient is less, the amplitude of migration of the same species is quite marked. (Hutchinson, 1967; Zaret & Suffern 1976; Wright et al., 1980). Sex differences were also observed, whereby the females migrate deeper than the males

(Hutchinson, 1967).

Strickler and Twombly (1975) were the first to suggest diapause as a predator-avoidance adaptation. They noted that immature Cyclops scutifer entered diapause when the predatory copepod, Epishura nordenskioldi became abundant in Bauline Long Pond, NewFoundLand. Nilssen (1980) found in his study of Cyclops abyssorum in Lonavatn, Norway, that fifth instar copepodites entered diapause and rested in the lake sediments during the period when predation by fish (arctic char) was focused on the zooplankton. Hairston (1987) also found comparable temporal correspondences between the diapause of Diaptomus sanguineus (adult females switching from producing subitaneous eggs to diapausing eggs) and fish predator activity in two small water bodies in Rhode Island.

One interesting trick played by some prey species after being detected by the tactile predators is "playing dead" (akinesis). During this response the prey Bosmina or Chydorus fold their vulnerable second antennae and clamp their ventral carapace margins securely and become difficult to handle so the predator will be forced to reposition, which will increase the probability of falling of the prey species from the appendages of the predator, Cyclops, and freely sink. These passively falling Bosmina or Chydorus produce such a different signal, or so little disturbances to be relocated by the predatory Cyclops. (Kerfoot et al., 1980; Stricker, 1980). Many slow-swimming rotifers also display "Playing dead" response when contacted by a predator or large cladocerans. The corona retract into the body, and the rotifer sink passively to reduce the swimming disturbances which may endanger the prey (Stemberger & Gilbert, 1987).

One of the counter moves of zooplankton against predation is the speed and pattern of swimming. Fast swimming can save for infrequent contacts with the predator, otherwise the energy cost as calculated by Stricker (1977) for highly accelerated hopping of marine copepod, Labdocera trispinosa, is evidently larger as compared to the energy needed for normal swimming movements. Thus direct escape response appear to be a high-cost strategy for escaping predators, greatly limiting their frequency. Further, the direct escape response is effective against smaller invertebrate predators than the much larger and more agile fish. Zaret (1980b) invoked differential motion of zooplankton in lake Gutun, Panama, to account for selective predation on one of the species, which, though smaller, moved considerably more, because motion does increase the likelihood of being located. As a result daphnids continually move and thus they are highly vulnerable to fish predation than similar size copepods.

2.1.3. REPRODUCTIVE RESPONSES OF ZOOPLANKTON TO PREDATION.

The lethal effect of predation would lead to extinction unless there is a means whereby some of the adults could survive and reproduce or replace those which have been predated or dead naturally.

There is a great deal of variation in the way that rotifer oviposit. Vulnerable species like Synchaeta often release their eggs directly into the water rather than carry them attached to their bodies. Such behaviour may reduce the probability of the eggs being eaten with the parental female. In the absence of predation some population of the species, like Synchaeta lackowitziana, may carry their eggs attached by mucus thread (Stemberger & Gilbert, 1987) or the eggs remain loosely attached in case of Polyarthra sp to be easily detached when the mother is attacked.

Some prey species, such as cyclopiod copepods are found to bear resistant eggs which can get hatched after passing through fish gut (see Gliwicz & Rowan, 1984). Splitting of copepod populations in fractions of annual and biennial has been suggested by Nilssen (1977) as having an adaptive significance against size - selective predation by fish. In Cyclops scutifer, the biennial fraction reproduce first, exhibits larger female body sizes, and larger clutch volumes in an environment usually absent of predators and competitors for the offspring. The annual fraction reproduces later, when more competitors and predators are present, having smaller body size and smaller volume per clutch (Nilssen, 1980).

Eggs oviposited free in the environment could sink to deeper waters that are low in dissolved oxygen or have low concentration of food; such sedimentation might reduce the survivorship of newborns. The colder temperature of the deep waters also may increase egg development times. Additionally, freely suspended eggs could be susceptible to Asplanchna predation and to ingestion or damage by filter-feeding cladocerans (Gilbert &

Stemberger, 1985).

Some species such as B. calyciflorus carry more eggs and Conochilus keeps its larva attached to adulthood to increase their effective size against invertebrate predators. Also live-bearing rotifer may increase the survival of young by giving birth to relatively large-size, and hence well protected, individuals (Stemberger, 1985 cited in Stemberger & Gilbert, 1987).

Higher reproductive output (greater number of eggs per clutch) and remaining in habitat whereby the developmental time of the offspring can be shortened, is also a means of antipredatory response in some non-migrating Daphnids, Daphnia galeata (Stich & Lampert, 1981).

Size selective predation by fish on zooplankton eliminate larger size groups, those which have the greatest reproductive output per individual. But under various instances of fish predation pressure such as Daphnia were found to increase per capita reproduction output unless and otherwise the predation pressure becomes sufficiently great to eliminate most of the adults and collapse the population (Culver et al., 1984). Certain copepods such as Diaptomus sanguineus, also switch from making subitaneous eggs to diapausing eggs in the seasonal catastrophic increases of fish predation (Hairston, 1987).

3. DESCRIPTION OF THE STUDY AREA

The Bishoftu crater lakes occupy the principal member of the extensive series of volcanic explosion craters in the vicinity of Debre Zeit, Ethiopia, which is situated 47 Km South East of Addis Ababa at an altitude between 1870 to 1900 m, at about 9°N & 39°E (Prosser et al., 1968; wood et al., 1984) (Fig.1).

The Bishoftu region shows extensive evidence of volcanicity, numerous cinder and lava cone craters being present in addition to the explosion craters (Prosser et al., 1968). Mohr (1961) recognized thirteen craters and grouped them separately than other volcanic craters because they are basin-shaped depressions wholly below ground level except for their rims. They have steep sides and diameters close to 1 Km and are not directly associated with lava flows. Eleven of these craters are aligned North by East and South by West. The remaining two, one of which contains Lake Kilotes, lie east of the general alignment. The entire system is on the ill-defined western margin of the main Ethiopian Rift (Prosser et al., 1968).

The catchments of the five lakes are formed from volcanic rocks of basalt, rhyolite and tuff. Although their relative amounts vary,there are no large differences between the catchments (Mohr, 1961). The maximum distance between the lakes is 20 Km. They have small catchment areas and rainfall, varying around 850 mm per year, appear to be the major source of water (Rippey & Wood, 1985). Both Lakes :Bishoftu and Arenguade are well sheltered from wind effect by the deep crater rims.

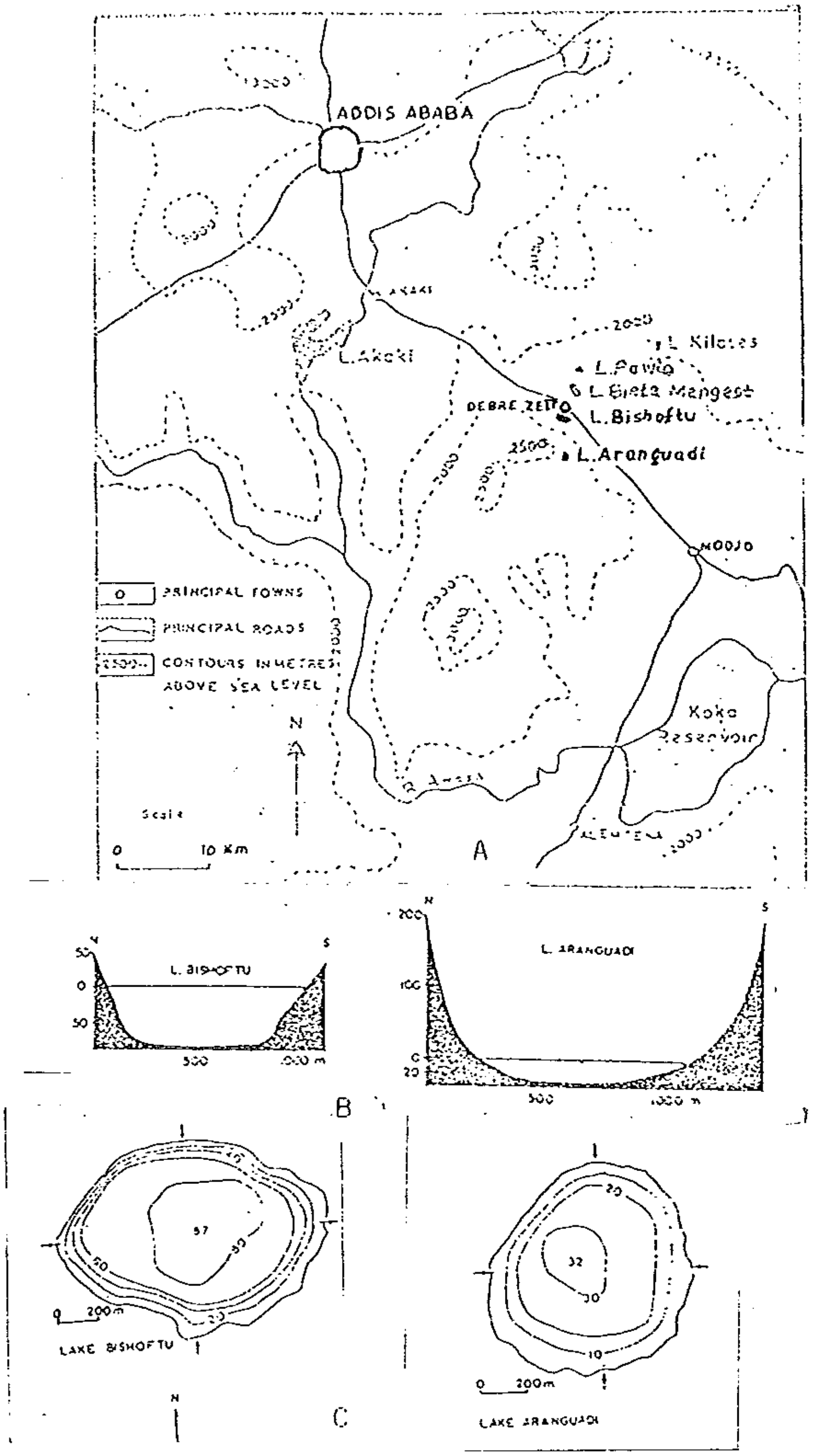

Fig. 1. A. Map showing the location of Lake Arenguade and Bishoftu.
B. North to South profile of Lake Arenguade and Bishoftu.
C. Bathymetric maps of Lake Arenguade and Bishoftu.
(After Prosser *et al.*, 1968)

None of the lakes has an obvious inflow; evaporation is apparently balanced by direct rainfall on the small catchments and by seepage. These lakes are chemically dominated by sodium and bicarbonate or carbonate ions (Wood et al.,1984). The major constituents of surface water from these lakes are shown in Table 1. The weathering of the predominant basaltic rocks forming the craters coupled with concentration by evaporative of possible underground seepage water containing minerals dissolved from more distant sources, has resulted in mineral-rich inflows and the lakes are rich in inorganic nutrients (Wood <u>et</u> <u>al</u>.,1984).

The seasonal pattern of the dynamics of the chemical constituents are related closely to the pattern of thermal stratification and mixing.

Table 1. Chemical and Physical feature of Lake Arenguade and Lake Bishoftu

	Lake Bishoftu	Lake Arenguade
Area (Km^2)	0.929	.541[1]
Maximum depth(m)	87	32[1]
Mean depth (m)	55	18.5[1]
Total volume(m^3 X 10^6)	52	10[1]
PH (Mean value)	9.2	10.3[1]
Alkalinity (meq/l)		
(CO_2 + HCO_3)	20	51.4[1]
Total dissolved		
solids (g l^{-1})	1.88	5.82[2]
Total cations(meq/l)	23.6	75.7[1]
Total anions(meq/l)	24.4	74.1[1]
Calcium "	0.37	0.67[1]
Magnesium "	5.8	<0.6[1]
Sodium	16.0	67.0[1]
Potassium "	1.5	8.1[1]
Chloride "	4.0	22.0[1]
Sulphate "	0.35	0.7[1]

[1] Prosser _et_ _al_.,(1968).

[2] Rippey & Wood (1985).

4. MATERIALS AND METHODS I

Net samples were collected from the central site of Lake Arenguade and Lake Bishoftu using #25 plankton net with mouth diameter of 25 cm. The nets were hauled vertically from the depth of 10 m. Samples were collected (ca.250 ml) and preserved with 4% formaldehyde solution. In the laboratory ovigerous females with their intact clutch were sorted out in Bogorov's counting chamber under stereomicroscope and transferred to vials. samples were kept for a month to avoid variability which might result due to the action of the preservative on organisms which were not relaxed prior to preservation.

Cephalothoracic length was selected as the core body of copepods (after Jamieson, 1980; and Drenner & Mc Comas, 1980; Miller et al., 1992); this also remains stretched and intact after preservation or during the detachment of egg clutch.

All ovigerous females with intact clutches were sorted and transferred to a slide with a drop of water and the cephalothoracic length was measured using calibrated ocular micrometer under stereomicrscope (Wild M8) to the nearest 36 um (Mag. 100X.) Clutches were detached from the respective mothers and checked for intactness, i.e., looking for any pocket left by detached eggs. The complete clutches were counted and recorded along with the cephalothoracic length of the mother.

On two occasions an attempts were made to collect fish using beach seine but the slope and the ground of the shore in lake Bishoftu was not suitable for beach seine. As a result, only about 50 Aplocheilichthys sp and 10 juveniles of Oreochromis niloticus could be collected. These fish were preserved with 10% formaldehyde and transported to the laboratory. In the laboratory the gut contents were removed under stereomicroscope and searched for the contents.

Measurements of the food size were not possible because in most cases the copepod were found tightly packed with compressed and deformed carapace as the collection hours were not during the active feeding hours of the fish.

Collection of samples were possible only for the months of January, February, and July - December from Lake Arenguade and January - April and July - December for Lake Bishoftu.

Statistical analysis

Multiple comparison of means were used to compare mean brood size of different body size classes using MCPAIR programm of BIOM package (Rolf, 1985). All measurement of dispersion around the mean, regression analysis, measurement of skewness and chi-square test were done using SYSTAT package (Wilkinson, 1986).

5. RESULTS I

I. BODY SIZE OF OVIGEROUS FEMALES.

The body size of 558 ovigerous females of Lovenula africana from lake Arenguade ranges from 2304 um to 2952 um. The mean size for each month shows a maximum at the end of the mixing period, February, and a second maximum in September with a minimum in November (Fig.2A). The percentage composition of the size groups also show a similar pattern. More and more smaller-sized individuals started to appear during the stratification period with more than 63% of them lying under 2700 um and a mean size less than 2625 um, with the exception in September. In September, where the second peak was observed, only 48.2% of the total ovigerous females have a body size lower than 2700 um (Fig 3). In the mixing period, though there were no adult in the sample collected in January, they started to appear in February with few but larger individuals. More than 80% of the February population have body sizes greater than 2700 um (Fig.3).

The Lake Bishoftu population of L.africana were smaller, having a body size ranging from 1260 um to 1980 um (Fig. 2B). The mean size of each month vary with larger individuals appearing in March (mean size = 1738 um) followed by a drastic decrease in April and further in July (mean size = 1575 um and 1448 um respectively). A slight increase was observed from the minima of July by August which kept creeping up until October, the last month of the year where adults appeared in the samples (Fig.2B).

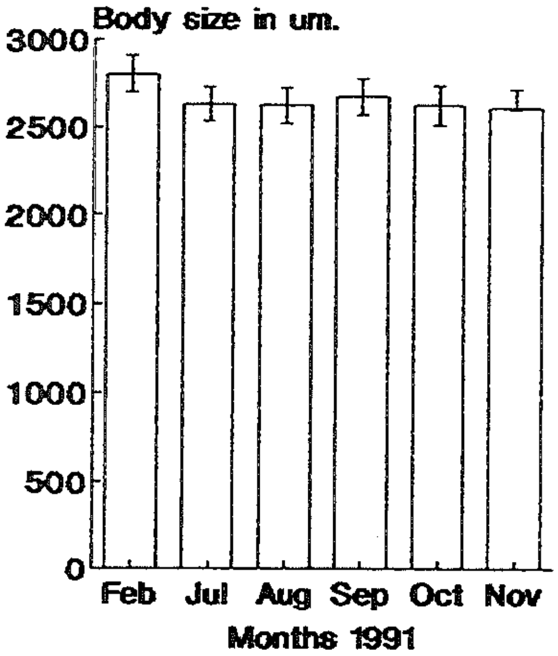

Fig. 2A. Mean body size of L. africana in Lake Arenguade.
Values are means + S.D.

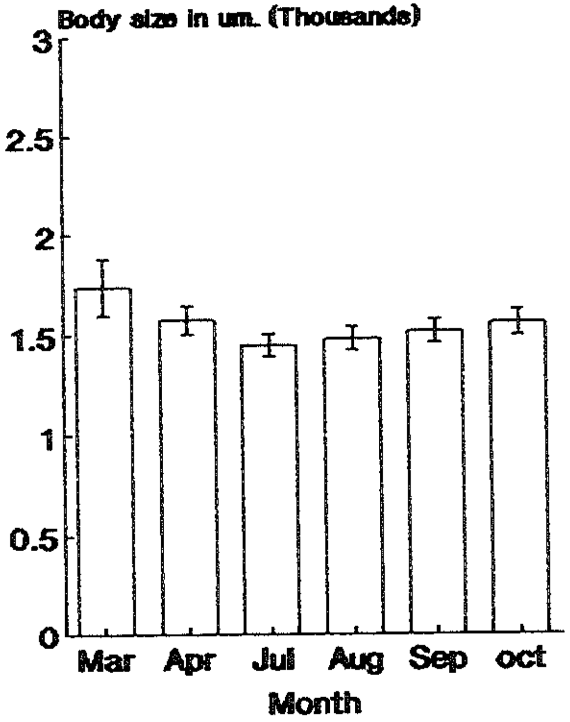

Fig.2B Mean body size of L. africana in Lake Bishoftu.
Values are mean + S.D.

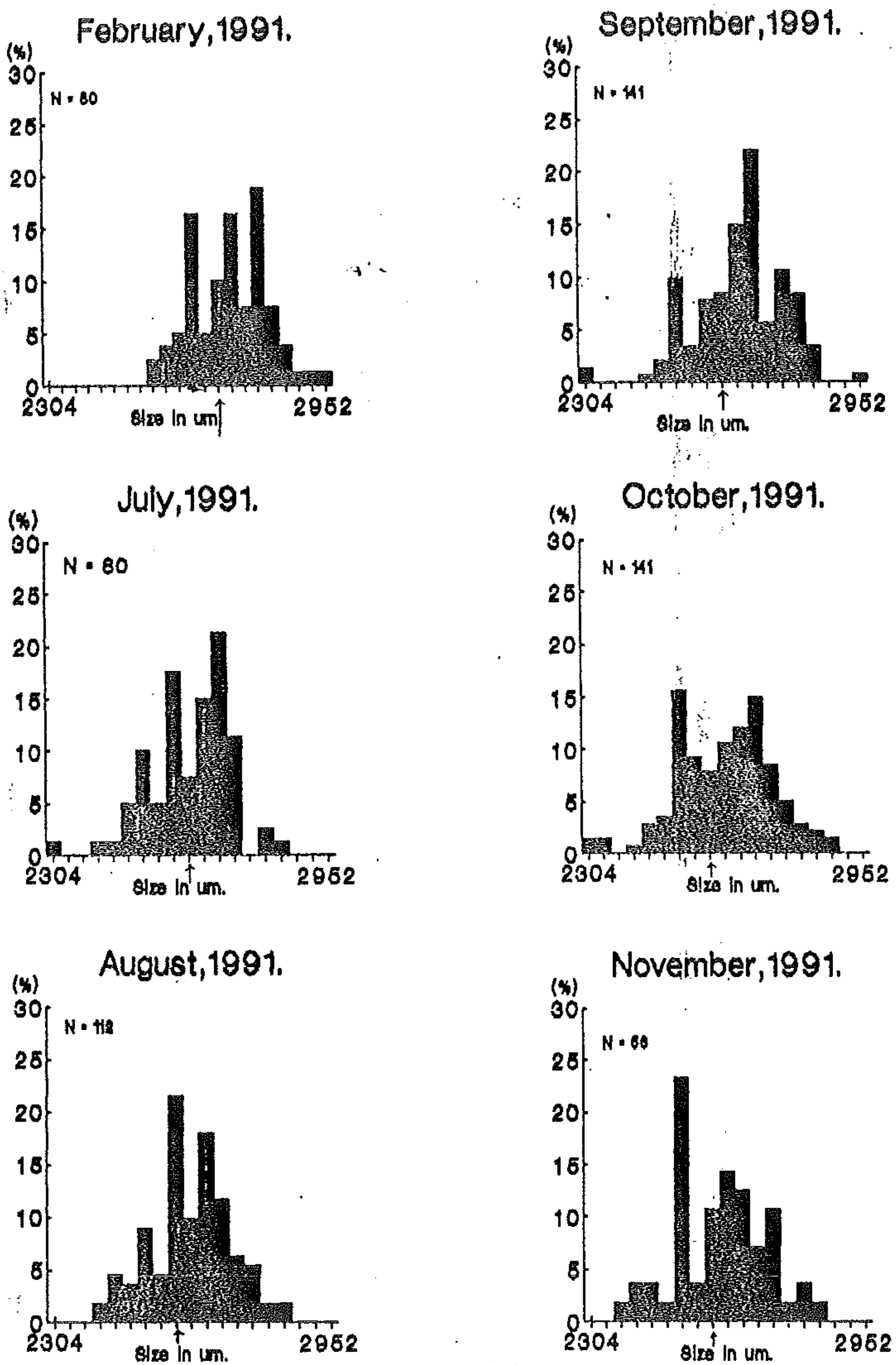

Fig.3. Seasonal frequency distribution (%) of size classes in L. Arenguade.
(Arrows indicate mean sizes)

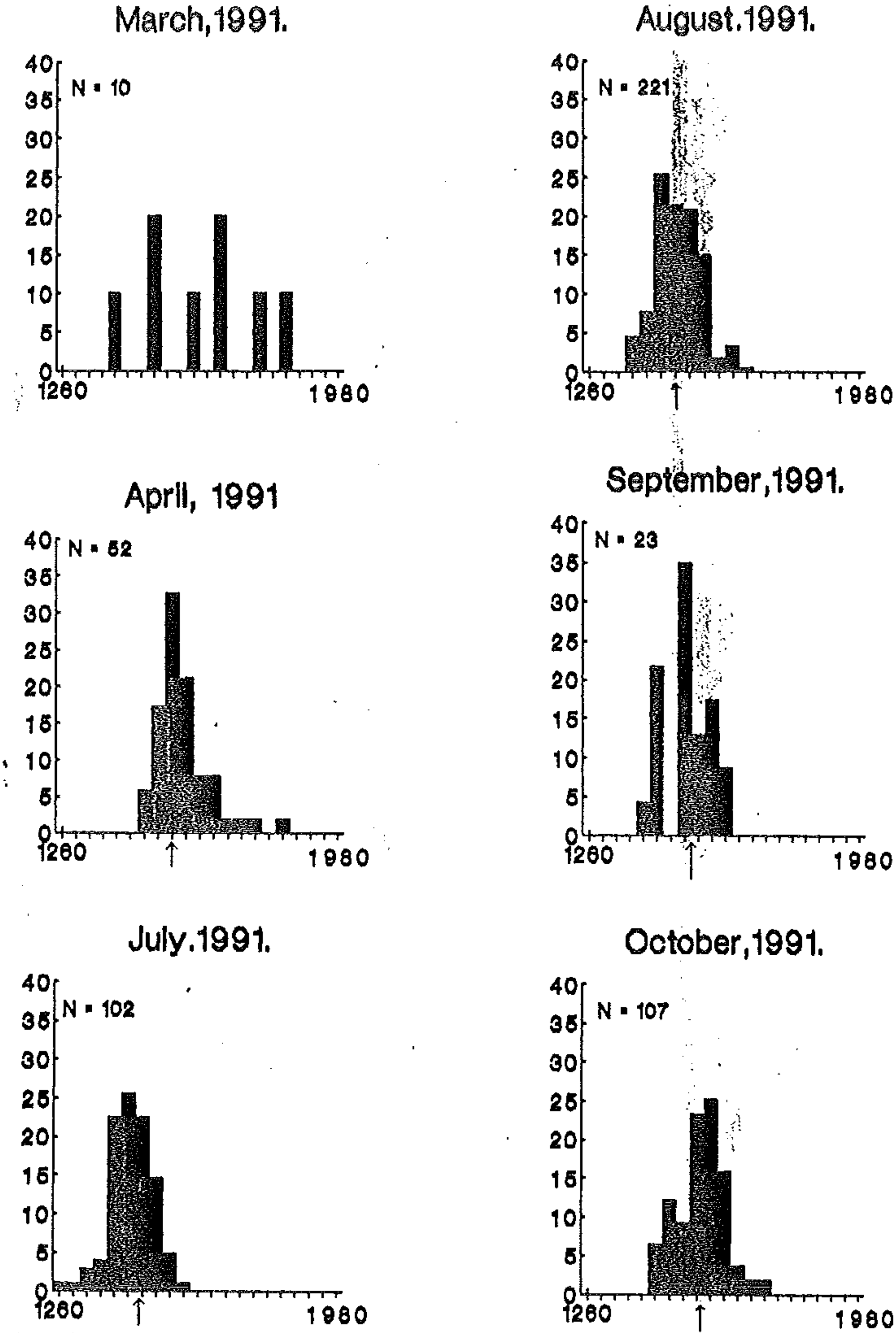

Fig.4. Seasonal frequency distribution (%) of size classes in L. Bishoftu

(Arrows indicate mean sizes).

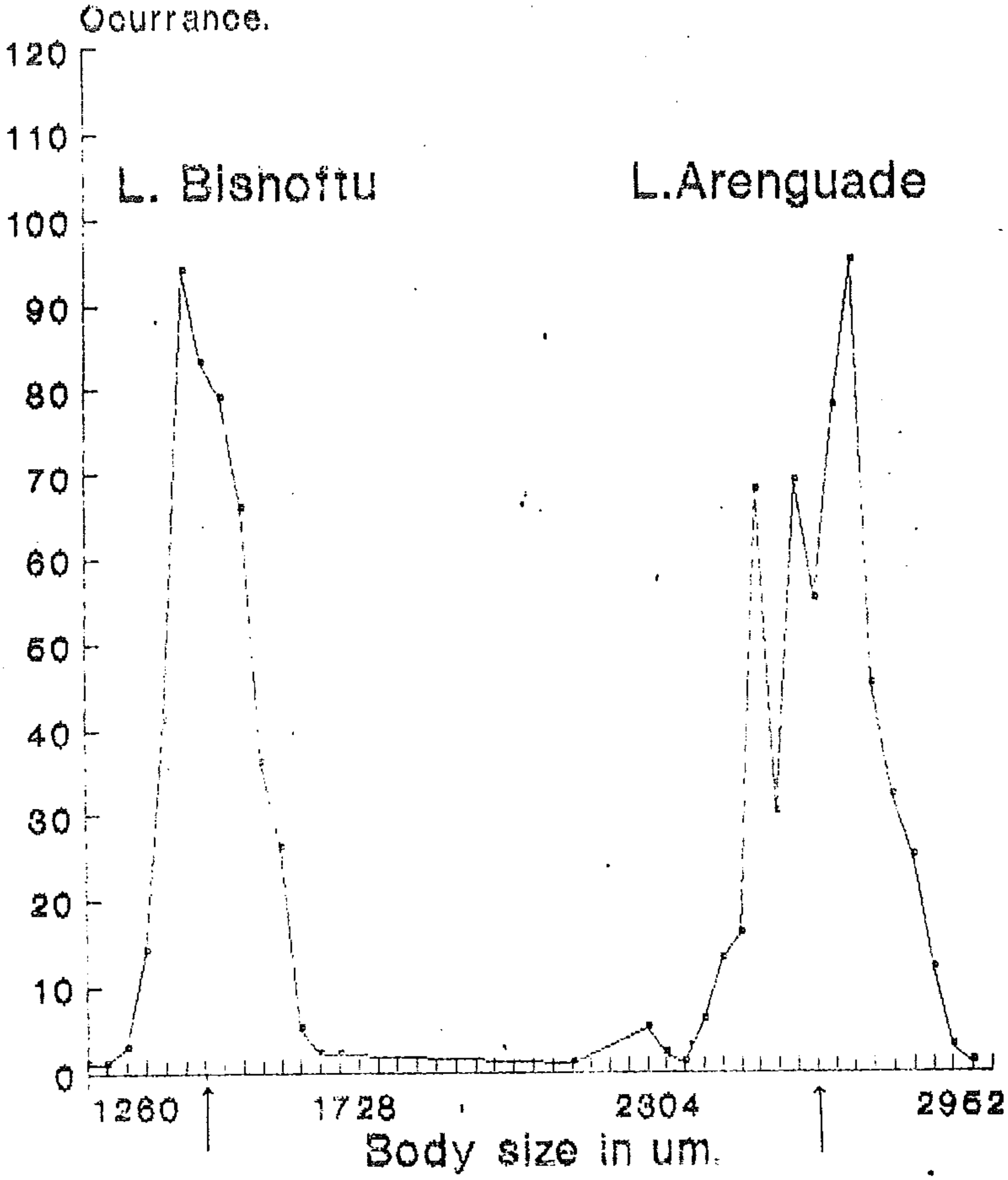

Fig. 5. Frequency distribution of body size classes.
(Arrows indicate mean sizes).

The shifting of body size from larger individuals of the mixing period to a smaller individuals of the stratification period is rather pronounced in Lake Bishoftu's population, where by greater than 70% of the individuals fall below 1512 um during this period whereas no individual was observed to have a body size of less than 1512 um in March and only 5.3% in April. A progressive increase was observed starting the July minima to October.

The size frequency distribution in lake Arenguade shows asymmetric distribution , i.e., the distribution is positively skewed (skewness = -0.439, Median size = 2592) as opposed to the frequency distribution of Lake Bishoftu's population (skewness = 0.258, Median size = 1494) (Fig.5).

II. BROOD SIZE

Ovigerous females of L.africana from Lake Arenguade and Lake Bishoftu bear brood sizes ranging from 21 to 72 with a mean size of 39, and from 5 to 18 with a mean size of 10, respectively.(Fig. 6A & B)

The population of Lovenula africana from Lake Arenguade has got significantly different brood size as compared with the population from Lake Bishoftu (ANOVA : F = 5.158, DF = 505, P < 0.025) (Fig.7). There was one peak season in September with an average of 44 eggs per clutch followed by February having slightly greater number of eggs (39) than the rest of the months (fig.6A).

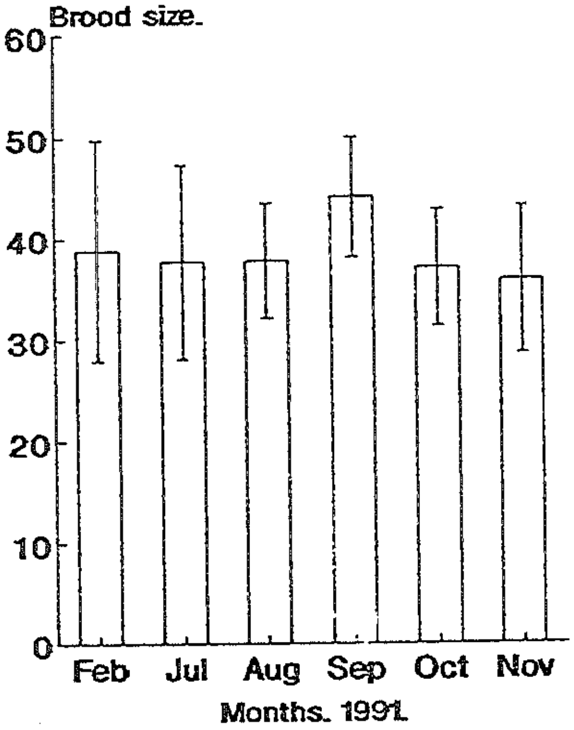

Fig. 6A. Mean brood size of L. africana in Lake Arenguade.
Values are means ± S.D.

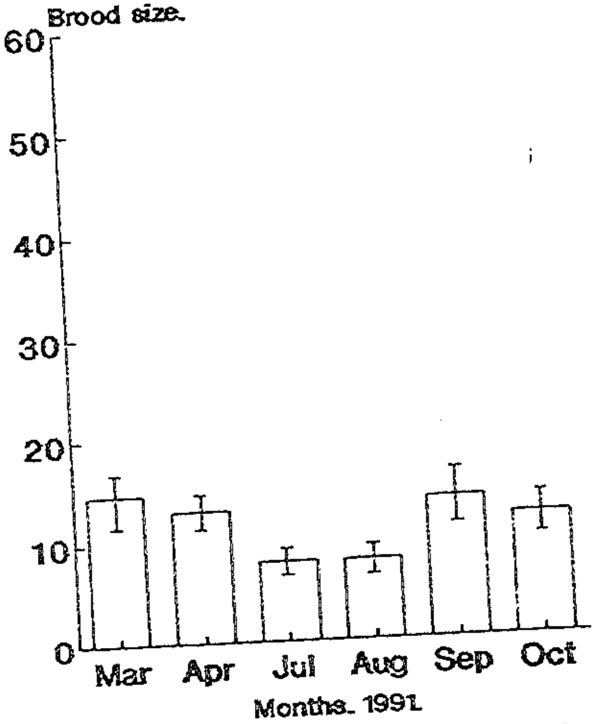

Fig.6B. Mean brood size of L. africana in Lake Bishoftu.
Values are means ± S.D.

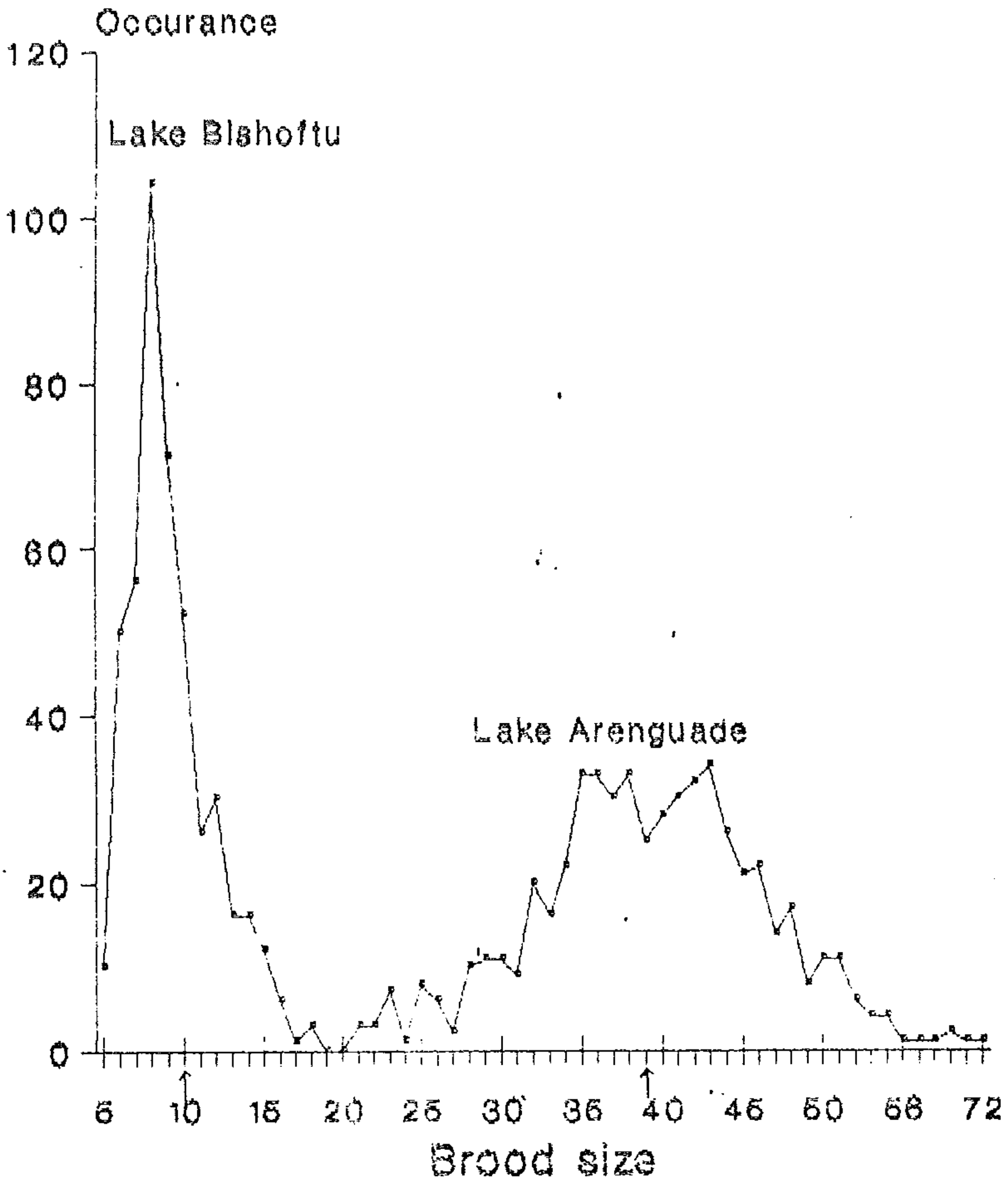

Fig. 7. Frequency distribution of brood sizes.
(Arrows indicate mean sizes).

Roughly the seasonal pattern of mean brood size of the Lake Bishoftu's population coincided with the seasonal pattern of mean body size, i.e., the highest peak was also in March and April, the lowest in the stratification period of July and August and a second peak in September (Fig.6A & B).

The frequency distribution of brood size in both lakes were also asymmetric but with greater differences:

Skewness = 0.132, Mid size = 40.5 in Lake Arenguade and
Skewness = 0.924, Mid size = 11.5 in Lake Bishoftu (Fig.7).

III. BODY SIZE - BROOD SIZE RELATION.

Mean brood size of both populations of L.africana was found to be a positive function of their mean body size by the linear expression:

$$BrS = 0.020KS - 13.836 \quad (R = 0.297,\ n = 558,\ P < 0.001)$$

for Lake Arenguade population (Fig. 8A) and

$$BrS = 0.014KS - 15.271 \quad (R = 0.447,\ n = 453,\ P < 0.001)$$

for Lake Bishoftu population (Fig. 8B).

(Where BrS = Brood size, KS = Body size.)

The coefficient of determination (R) for brood size against body size in both lakes were rather low. The seasonal variation confound the R value which otherwise could have been comparable to the other results using the mean rathre than total brood size

(R =0.95 for Lake Bishoftu and R= 0.86 for Lake Arenguade).

Differently sized groups tend to produce significantly different brood sizes in Lake Bishoftu (Table 2) whereas in

Lake Arenguade body size classes with great differences produced similar brood size though they have broader range in body size than Lake Bishoftu's population.(GT2 test) (Table 2).

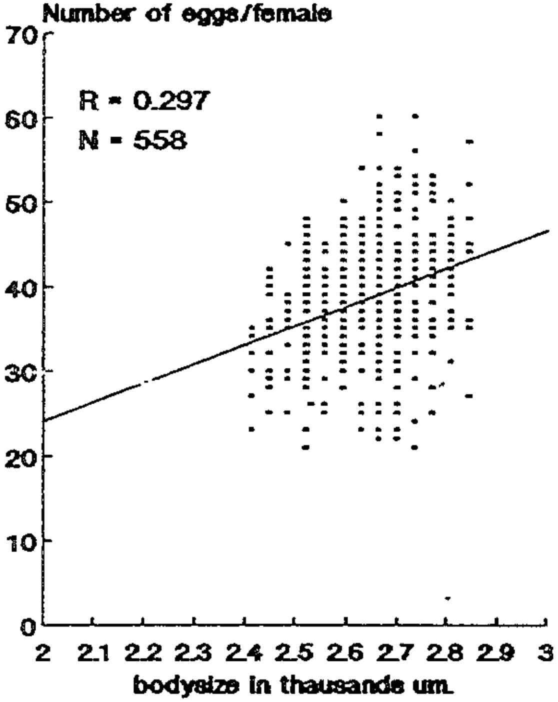

Fig.8A. The relation between body size and brood size of L. africana in Lake Arenguade.

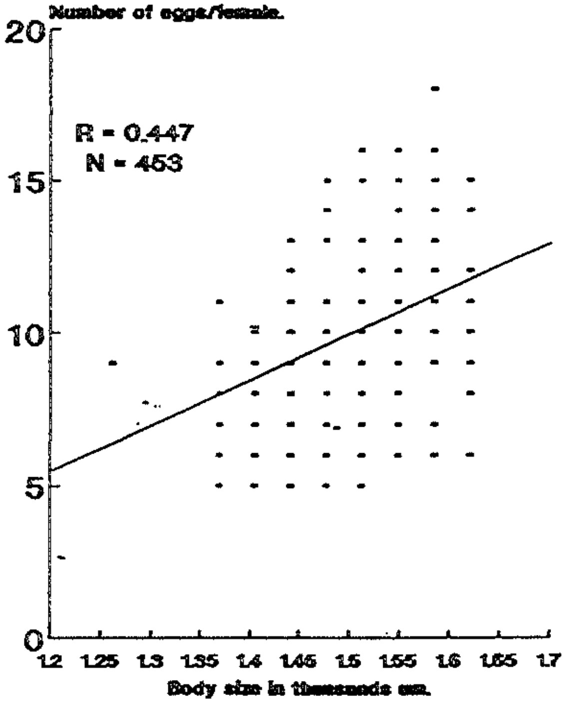

Fig. 8B. The relation between body size and brood size of L. africana in Lake Bishoftu.

Table 2 . multiple comparison of mean brood size between size classes for ovigerous female <u>Lovenula</u> <u>africana</u> from Lake Bishoftu and Lake Arenguade.

Lake	Size classes*												
Bishoftu	1	2	3	4	5	6	7	8					
Arenguade	1	2	3	4	5	6	7	8	9	10	11	12	13

* Size classes in Lake Bishoftu starts with 1250 um.

Size classes in Lake Arenguade starts with 2304 um

Size class increment is by 36 um in both lakes.

There is no significant difference in the mean brood size between size classes that are connected by the same line (see Sokal & Rohlf, 1981)

IV. FISH GUT CONTENTS.

Aplocheilichthys sp (Pisces: Cyprinidae), and juvenile stage of *Oreochromis niloticus* (Pisces: Cichlidae) are the two zooplanktivorous fish in Lake Bishoftu. Gut contents of *Aplocheilichthys sp* were mainly dominated by two prey organisms, namely *L. africana* and chironomid larvae. The percentage occurrence of *L. africana* in the gut contents was found to be 46%. In 30% of *Aplocheilichthyts sp* the guts were entirely packed with *L. africana*, whereas the juvenile stages of *O. niloticus* were not able to collect.

6. DISCUSSION I

Although there have been some studies of body size at maturity and its correlate brood size in field populations of Copepoda from the temperate zone by Revera & Tonolli,(1956; cited in Allan & Goulden, 1980), few tropical and sub - tropical works (Burgis, 1971; Hart, 1981; 1983; Burns 1979) paid attention to the effect of predation as a major factor determining the size structure of zooplankton and phytoplankton, and the cascading effect of size-dependent trophic interactions (Carpenter et al.,1985). But works on single species of Cladocera (Brook & Dodson, 1965; Galbraith, 1967; Kerfoot, 1974; De Bernandi & Guisani, 1978; Kitchell & Kitchell, 1980; Zaret, 1980b; Dodson, 1988; and Mort & Kerfoot, 1988) highlighted that populations of a given species of Cladocera under fish predation shift towards smaller individuals and get matured at a relatively smaller size. The absence of large cladocerans from tropical lakes is well documented (Green, 1967; Fernando, 1980) and often attributed to the high selective pressure exerted by planktivorous fish upon large prey. The pressure is assumed to be higher in more eutrophic lakes, because planktivorous fish seem to be more abundant there as a result of vast littoral area offering spawning grounds and shelter (Kerfoot, 1974).

Copepods show no increment in size after maturity due to their determinate growth pattern (Taylor, 1980). All energy intake in excess of maintenance needs after maturity is channelled into egg production; as a result, the total production comes closer to the egg production (Lampert & Much, 1985). Thus brood size-body size comparisons in copepods are only between individuals since there is no variation within an individual in its body size and brood size after maturation due to age unlike cladocerans (Allan & Goulden, 1980; Taylor, 1980). As a result measurements obtained from body sizes of adult copepods are not subjected to age after maturity and hence form convenient subjects for comparative study of changes in body size due to size selective predation (Brooks & Dodson, 1965) or food limitation (Herbert, 1985), temperature (Hart, 1981) or any combination.

Based on the above concept, measurements done on body size of ovigerous females of Lovenula africana (Daday) from Lake Bishoftu, a lake with two zooplanktivorous fish, are significantly smaller than the population from the neighbouring fishless lake, Lake Arenguade (ANOVA: $F = 1807.3$, $DF = 504$, $P < 0.001$). The body size ranges from the two lakes were not continuous. This indicates that these two populations are of two different size groups.(Fig. 5). Such significantly high reduction in the body size (by half) as a result of size selective predation of fish was demonstrated in populations of Daphnia compared to another population in a similar water basin with minimum or absence of fish predation from eutrophic temperate crater lake of Lago Di Annone, Italy, by De Bernandi & Giussani (1978) and in Lake Peter, Wiscosin, by Kitchell & Carpenter (1988). Earlier Galbraith (1967) also observed a 30% decrease in the adult size of Daphnia after introduction of planktivorous fish.

The other observed effect was the replacement of larger cladocerans such as daphnids by smaller cladocerans such as *Bosmina* after fish introductions (Brook & Dodson, 1965; Kerfoot, 1974b; Gliwicz, 1985). Also it was observed that as large prey become scarce, smaller prey have a greater chance of appearing large, and the fish tend to eat more prey from smaller size classes (Jakobsen & Johnsen, 1988).

In Lake Kariba, six years after the introduction of the planktivorous fish, *Limnothrissa miodon*, Begg (1974 cited in Turner, 1981) noted that this planktivorous fish exerted a high predatory pressure on the zooplankton because there was an obvious decline in the large zooplankton particularly *Ceriodaphnia*, *Diaphanosoma*, and *Diaptomus*. In 1973/74 about 80% of the food items ingested by *L. miodon* were *Bosmina*. Afterwards this small-sized Cladocera rapidly disappeared and the major food item for this fish became dominated by small cyclopoid copepod *Mesocyclops leukarti*, a situation approaching that in Lake Tanganyika (Turner, 1981). The absence of cladocerans from the pelagic water of Lake Tanganyika was also attributed to the intense predatory pressure by the endemic clupeid fish, *Limnothrissa miodon* and *Stolothrissa tanganyicae* (Green, 1967).

In Lake Kivu the zooplankton community was composed of large, distinctly pigmented copepods and cladocerans. In 1981, after 21 years of introduction of planktivorous fish, *Limnothrissa*, Reynlijens (1982 cited in Dumont, 1986) found that the size structure of zooplankton had changed completely, the previous cyclopoid species had reduced in body size by half (from 1.003 mm to 0.55 mm). The large *Daphnia*, however, had disappeared. Later in 1983, Dumont (1986) found no zooplankton of such size but zooplankton with body size less than 0.2 mm. This condition is typical of heavy size-selective predation on the zooplankton by fish, and evidently predation by the introduced *Limnothrissa*.

The large species, *Daphnia magna* were reported from lake Hayq (Ethiopia) before the introduction of *O. niloticus* in 1978 (Cannicci & Almagia', 1947 cited in Elizabeth *et al*., submitted for publication; and Baxter & Golobitsch, 1970). Later in 1984 *Daphnia magna* was eliminated and replaced by Cyclopoids (Dr. Seyoum Mengistu pers.comm). This was primarily attributed to the size-selective predation of *Daphnia* by juvenile stages of *Oreochromis niloticus* (Elizabeth *et al*.).

Temperature is one of the factors which determine body size. The inverse effect of temperature is evident in lakes with greater annual range of temperature such as the sub - tropical Lake Sibaya (Chapman, 1973; Hart, 1981) temperate, and arctic lakes (Herbert, 1985; and Ohman, 1985; Uye, 1988). But the annual range of temperature in Lake Arenguade and Lake Bishoftu is not big enough to bring about such significant size variation. If at all temperature is large enough it will equally affect both populations of Lake Arenguade and Lake Bishoftu because the annual and diurnal temperature changes in these lakes is about the same (Wood *et al*.,1976).

The other factor which is responsible for determination of body size of calaniods is the concentration of available food.

Studies mainly in marine habitat reveal that the change in the cephalothoracic length of *Temora longispina* (Calanioda: Copepoda) have been attributed to food concentration (Klein Breteler & Gonzales, 1982 cited in Razoules & Razoules, 1988). Miller *et al.*, (1992) also account changes in mean prosomal length of *Neocalanus plumchrus* and *N. flemingeri* to variations in temperature or food availabilty or both in the gulf of Alaska. But as compared to cladocerans, calanoid copepods are less affected by food limitation because they have developed a complex and selective feeding strategies based on chemoreception which fits them well to a nutritionally dilute environment (Koehl & Strickler, 1984). Besides certain species or stages of growth in calanoid copepod facing shortage of food such as marine forms store large amount of lipids and are less affected by food changes or decrease in nutrition (Mayzaud & Mayzaud, 1985). Also calanoid copepods withstand starvation better than cladocerans : the group most of our understanding on effect of food limitation is generated from (Gliwicz, 1980; 1985; 1990). Limitation of food in the eutrophic lakes of Lake Arenguade and Lake Bishoftu will be negligible so long as the copepods graze on the dominant phytoplankton as was observed from the gut content of *Lovenula* which was full of chopped pieces of the dominant filamentous Blue Green algae, *Spirulina*, in Lake Arenguade (personal observation). Goldman (1981) and Burgis (1978) indicated that raptorial cyclopoid adults and copepodites feed on colonies of *Microsystis aeruginosa* in Lake George. It was also reported, that calaniods fed on small colonies of (20 - 50 cells) *Microsystis aeruginosa* (De Bernardi *et al.*, 1981). At times, the bloom of *M. aeruginosa* coincided with maxima of copepods, in the eutrophic tropical Lake Valencia (Infante & Riehl, 1984). Another calanoid copepod, *Eucalanus crassus*, was reported to break colonies of algae, like *Rhizosolenia indica* and *Lauderia borealis* before ingesting (Alcaraz *et at.*, 1980). So it seems that calanoid copepods in Lake Bishoftu can also feed upon the available *M. aeruginosa* and in doing so the population will not be in short of food supply.

As opposed to the nearby lake, Lake Langano (Ethiopia), Taylor & Zinabu (1989) found that large plankton crustaceans were absent from the epilimnitic zone and remained confined in the hypolimnion of Lake Awasa, and accounted this to hypolimnetic refuge from vertebrate predation. Large-bodied daphnids dominate the nearby Lake Langano because of its high turbidity due to colloidal suspension and hence reduced visibility leading to reduced predation pressure by visual vertebrate predators. Shapiro *et al.*, (1982) predicted that oxygenated hypolimnia might provide a refugia for large-bodied *Daphnia* from warm water fish populations. This was what has been observed in Lake Awasa (Taylor & Zinabu, 1989). Limnocorral studies also indicated that when the hypolimnitic oxygen concentrations began to decrease *Daphnia* began to shift to the epilimnion as a result they will be more exposed to predation but in the presence of oxygenated hypolimnia the biomass of planktivorous fish required to eliminate the large-bodied *Daphnia* should rise in three fold as compare to anoxic hypolimnia (Mc Queen & Post, 1988). Such spatial segregation are minimum in small and eutrophic lakes such as Lake Arenguade and lake Bishoftu with their anoxic hypolimnion. It was also observed from depth samples that water samples from 15 m and 20 m were devoid of calanoids. At these depths the presence of Hydrogen Sulphide is more evident by the strong rotten egg smell of the water which could be detrimental to the survival of L. africana. So in both lakes the hypolimnia is not oxygenated to provide refugia and depth samples also revealed the absence of L. africana below 10 m depth. The biomass of planktivorous fish needed to eliminate large - bodied zooplankton was found to be lower as compared to zooplankton in oxygenated hypolimnia (Kitchell & Carpenter, 1988). The Secchi depth of both lakes is always very low, 5 cm and 60 cm respectively, so preys in these lakes have no advantages of migrating far below the euphotic depth to reduce their visibility.

It seems likely that fish predation is the main explanation for the observed absence of larger individuals in Lake Bishoftu despite its close proximity, similar climate, general chemistry and topography with fishless Lake Arenguade.

The effect of fish predation on L. africana population in Lake Bishoftu was also traced from the gut content of the main predator fish, Aplocheilichthys sp. Though the fish were collected from the littoral zone, their gut content included greater proportion of L.africana (46% in number) and more than a quarter of the guts (30%) were packed exclusively with L.africana. From such observation it seems possible to expect greater proportion of L.africana in the gut content of the fish from the pelagic zone where L.africana is the dominant zooplankton, and the smaller biomass of chironomid larva (the second major food item in the littoral zone) could amplify the effect of fish on L. africana. Greater number of cladocerans were also reported in the gut of Aplocheilichthys from another Rift Valley Lake Awasa (Taylor & Zinabu, 1989, Sisay, 1991) and Lake Gorge, Uganda (Beadle, 1981). Dune (1972 cited in Beadle, 1981) reported that Aplocheilichthys is dominant in number and prey on zooplankton in Lake Albert (Uganda).

We were not able to collect omnivorous stages (size: 10 mm - 15 mm) of O. niloticus as was recorded by Tudorancea et al., (1989) for lake Awasa where it was reported that copepods frequently occurred (18%) in the gut of juvenile fish and contribute more by volume (Tudorancea et al., 1988). Likewise juveniles of O. niloticus in Lake Bishoftu are expected to prey upon the available large sized zooplankton in the pelagia such as L. africana to the same extent and in doing so affect the size distribution of the copepods especially after the peak spawning season of the fish when the abundance of the juvenile fish increase.

Comparative study on the age structure of L. africana from both lakes indicate that the adult stages in Lake Bishoftu have higher mortality rate, which could be aggravated by fish predation, because the adults contribute less to the population size in Lake Bishoftu as compared to the share of the adults in Lake Arenguade. By virtue of their large size the adults and particularly the females are vulnerable to the size selective predation by fish and are able to sustain the high losses because the adult stage was subsided by recruitment from earlier, less vulnerable developmental stages (Saunders & Lewis, 1988, Gophen, 1988). Hence, though sex ratio (Male:Female) in both lakes is significantly different from naturally expected one to one ratio ($X^2 = 79.9$, $P < 0.001$ in Lake Bishoftu and $X^2 = 1325.72$, $P < 0.001$ in Lake Arenguade) the proportion of males to females in Lake Bishoftu is smaller (1: 1.1) as compared to Lake Arenguade (1: 1.5). This also indicates that fish selectively prey upon larger individuals among the existing small sized prey (see Jakobsen & Johnsen, 1988). The relatively large body size of the females and their egg sacs made them more conspicuous and vulnerable for size selective predation by fish (Gophen, 1988).

Frequency distribution of the body size in Lake Bishoftu's population of L. africana is in general skewed to the right in favour of smaller sizes (skewness = 0.258) whereas Lake Arenguade's population size classes frequency distribution is skewed to the left in favour of the larger sizes (skewness =-0.439) (Fig 5). Such skewness of body size distribution can also be an indication of ongoing size selective predation (e.g. Warshaw, 1967; Post & Mc Queen, 1987). This is because vertebrates prey mainly upon larger zooplankton species when all sizes are abundant until densities of large prey are greatly reduced, then the diet can include smaller species or individuals (Hall et al., 1976; Jakobson & Johnsen, 1988).

Seasonal variation in the body size of Lake Bishoftu population was also observed, with greater mean size during March -

April following the vertical mixing of the lakes which could bring up nutrient from the bottom and favour the cropping of appropriate size food organisms (nanoplankton). This enhances the growth of the naupliar stages ultimately producing larger adults shortly after the mixing season. In contrast to this, adults in the season of stratification were found to be smaller than the adults immediately after mixing season except in September.

The second peak in body size obtained in September may result from the similar effect of increasing nanoplankton during the rainy months of July and August caused by runoff and partial mixing due to cold runoff introduced to the lake. As the result of the increase in body size the population show an increase in brood size in September.

On top of the above reason the population in lake Bishoftu will get rid of the intense predation pressure as a result of mass mortality of fish caused by anoxia and upwelling of H_2S during vertical mixing (November - February) of the lake . Such event were reported from the neighbouring lake, Lake Pawlo during the same season (Baxter et al.,1965; cited in Talling, 1969), and is also an annual experience of the local people around lake Bishoftu. Annual lake turnover also happens every year in another eutrophic tropical lake, Lake Valencia, Venezuela where it kills both fish and zooplankton (Infante, 1982; Saunders & Lewis, 1988). Similar catastrophe was also reported from another tropical crater lake, Lake Nkugute, Uganda (Beadle, 1966). Mass mortality of inshore fish was also reported from Lake Tanganyika in July 1961, and the eastern shore of Lake Malawi. This was due to the rapid upward migration of fish to escape oxygen depletion and consequent loss of hydrostatic control, but may have been also due to poisoning by hydrogen sulphide or by direct asphyxia (Eccles, 1976).

The seasonal variation in body size in Lake Arenguade was not as pronounced as in Lake Bishoftu. There is a slight increase in February and September for the same reason as in Lake Bishoftu except for the absence of predation.

In most observation of cladocerans and copepods (Revera & Tonolli, 1956 cited in Allan & Goulden, 1980; Burgis, 1971; Herbert, 1985) and particularly the sub-tropical Diaptomids (Hart, 1981) a positive relationship between the brood size and body size is exhibited. The present observation in both lakes also exhibit a positive relationship between body size and brood size (R = 0.297, N = 558, and R = 0.447, N = 453 for body - brood size regression in Lake Arenguade and Lake Bishoftu respectively). The smaller R values are due to seasonal confounding, and variances were not minimized by using averages, which otherwise would have raised values of R to 0.86 and 0.95 for Lake Arenguade and Lake Bishoftu, respectively. These values are comparable with other studies done in the Arctic (Herbert, 1985).

It is particularly clear that an increase in vertebrate predation leads to a decline in optimal body size. In that case, there would be an advantage of initiating reproduction at a smaller size and to maximizing reproductive effort in subsequent age classes. In addition to maintaining a reproducing population, this will defer growth to the larger and more vulnerable sizes (Lynch, 1977). This relationship is confounded in the presence of stress such as predation and is highly correlated only under steady state conditions with food not limiting as can be seen from the relation of body size to brood size in the two contrasting lakes. Results of multiple comparison of mean brood size between body size classes indicate that there is a strict size-dependent brood size resulting in significant differences in the brood sizes of the lower size classes; as a result individuals with small differences in size bear significantly different brood size in Lake Bishoftu whereas in Lake Arenguade population, individuals bear broods of the same size even though they have greater body size differences (Table.2). In extreme case in tropical cladocerans, the small-sized helmeted D. lumholtzi, under strong predation pressure, produce more eggs per female than the large monacha form in Lake Albert (Green, 1967).

In general large planktonic herbivores have relatively reduced metabolic demands per unit mass, permitting more assimilation to go to egg production (Brooks & Dodson, 1965). They are superior competitors for resources, being able to grow and reproduce at lower food concentrations, i.e., food threshold concentrations are lower in larger species than smaller species (Gliwicz, 1990). Besides, calanoid copepods' maximum filtering rate is best expressed as a power function of body length with an exponent between two and three. Thus small differences in body length can have large effects on filtering rate (Hall et al., 1976). Both greater efficiency of food collecting and somewhat greater metabolic economy explain the demonstrably greater reproductive success of the larger among related species (Brook & Dodson, 1965; Hall et al., 1976). Similarly the size differences observed in the two population of L. africana from the two lakes bear significantly different mean brood size (F = 8364, N = 2, P = <0.001). The asymmetric frequency distribution of body size were also reflected in the brood size strongly though it is negative in both cases. The frequency distribution of brood size in Lake Bishoftu is more negatively skewed (skewness = 0.924) than Lake Arenguade population (skewness = 0.132). This asymmetric distribution also indicates that females are in favour of having smaller clutch size under fish predation where otherwise they become more vulnerable to fish predation by being less mobile and more visible.

The highest peak of mean brood size in Lake Arenguade in September could also be explained in terms of the increase in body size which could result probably due to the increase of nanoplankton of the previous rainy months of July and August.

The peak brood size in March for Lake Bishoftu population could be attributed to the relatively large body size caused by relaxation from predation pressure caused by fish kill during mixing period, which would also allow larger brood size. Other wise it would have increased vulnerability by increasing their conspicuousness.

The July minima of both body size and brood size could be attributed to the increased predation pressure by emerging juvenile stages of O. niloticus. Inferences from other nearby rift Valley lakes points that the spawning activity of

O. niloticus increase during the small rain of February - April (Tudorancea et al., 1988), because rain stimulates reproduction in Tilapia (Sundraraj, 1980).

Elimination of excess algae that result from eutrophication is a topic of continuing interest. However, despite the success of conventional methods, such as nutrient diversion, alternative methods are being sought. These alternatives are needed to circumvent the high costs and frequent inapplicability of conventional methods. Among the alternatives proposed is Biomanipulation - a series of approaches aimed at benefiting lakes by manipulation of their trophic structure (Shapiro & Wright, 1984).

Improving water quality caused by eutrophication can make use of zooplankton as a target population in aquatic food web to control phytoplankton both by grazing and reducing nutrient resource simultaneously (Shapiro & Wright, 1984; Kitchell & Carpenter, 1988). Commonly an increase in water transparency follows the elimination or reduction of planktivorous fish after winter fish kill (Schindler & Comita, 1972; Bashier et al., 1973) or after manipulation through application of toxic chemicals such as rotenone (Galbriath, 1967; Herikson et al., 1980; Shapiro & Wright, 1984) or introduction of piscivorous fish (Benndorf et al., 1984; Berthelmes, 1988). From the cascading trophic interaction pattern outlined by Carpenter et. al.,(1985) introduction or increase in planktivory can cause a decline in large-bodied grazers (zooplankton) which favours the increase in phytoplankton population and deterioration of water transparency (e.g. lake Hayq). Further studies in this line could be one way of tackling problems of unnecessary phytoplankton blooming in some tropical reservoirs such as Legedadi and blooming of toxic algae causing death of wild life in Lake Chamo (Ethiopia) (Amha & Wood, 1982).

However, the introduction of a new species into a large aquatic environment is a one way event and the decision to do so must be a difficult one. It is easy to introduce them but impossible to eliminate them if they do not produce the desired results. For every successful introduction by man, there are as many or more failures which have sometimes had a detrimental impact on some highly valued fisheries For example the introduction of Lates in lake Victoria affected tilapia fisheries (Ogutu-Ohayo, 1984; Goudswaard & Witte, 1984). The sudden fish kill everywhere in tropical lakes (Beadle, 1981) such as lake Hayq is very common. The practical management of lakes must be based on knowledge not only about nutrient loading or fish yield but also about the structure and functions of the biotic feedback systems. Much work is, however, still needed to make this knowledge a precise tool in lake management.

CHAPTER II

7. SEASONALITY IN TROPICAL ZOOPLANKTON

The factors influencing seasonality in the tropical lakes are attributed mainly to water body circulation and hydrological cycles. The relative significance of vertical mixing for lake biology is likely to be enhanced in a tropical climate, in which seasonal variations in temperature and solar radiation are minimal. Talling (1969) traced regularities in the seasonal timing of vertical mixing, and also some consequences in the productivity of some tropical lakes.

In temperate lakes the annual stratification and overturn is primarily dependent on a wide temperature swing which is by far minimized in tropics. At first sight it seems that this comparatively small seasonal variation in tropical temperature would be less conducive to stable stratification than in temperate lakes. However, slight increase in the gradient of the elevated temperature in a tropical lakes can maintain the same stability as the much steeper gradient of temperate lakes. Conversely, a much smaller drop in temperature at the surface is needed to obliterate stratification. On further cooling, the same reversed gradient would cause greater stability in tropical lakes than in a temperate lakes (Beadle, 1981).

Within the broad context of African limnology, some Ethiopian highland lakes provide valuable systems for study. Although situated within tropics and subjected to comparatively small overall annual variations in temperature, they can experience considerable diurnal fluctuations of temperature because of their relatively high altitude as well as great seasonal variation in rainfall, humidity, cloud cover, and solar radiation (Wood _et_ _al_., 1976).

Heat fluxes and thermal stability depends on a delicate balance principally between solar inputs and evaporative heat loss, so that cooling and mixing are more likely to follow cloudless periods with low humidity. Cloud cover and high humidity, although associated with low solar influx, typify period of warming leading to stratification. Daily increments in long - term heat gains and losses may represent as little as 3% of the diurnal heat fluxes and small changes in weather conditions can easily reverse cooling and prevent mixing from being a regular annual phenomenon. Thus cooling may occur during periods of highest solar input and vice versa. However, meteorological conditions could easily reverse the cooling process before the seasonal overturn so that complete mixing is by no means a predictably regular annual event in the Debre Zeit crater lakes (Wood _et_ _al_., 1976).

However seasonal cycles in the physical and chemical limnology of most tropical lakes are well documented, especially of the Rift Valley lakes (Wood _et_ _al_., 1976; 1984). Data on the dynamics of some tropical lakes often imply that zooplankton populations remain relatively constant over time,the reason behind such conclusion is that tropical zooplankton often breed continuously and species composition does not vary seasonally (e.g. Burgis, 1971; 1978; Lewis, 1979), particularly when compared with high seasonal patterns of temperate populations. This impression persist, in part, because the dynamics of tropical zooplankton are poorly known and conclusions were drown from a single equatorial Lake George, (Burgis, 1971; 1978) where constancy is attributed to its unique features (shallow and less protected) than the rest of tropical lakes. In the least sheltered and shallow Lake George with sufficiently frequent winds at all seasons the circulation of nutrients is more or less continuous and moreover, what is more remarkable of this lake is the very constant water level controlled by Lake Albert (Beadle, 1981). Thus the ecological stability of Lake George is controlled by a combination of fortuitous circumstances which is not common for most tropical lakes.

Contrary to earlier conclusions based on Lake George, a growing body of data have accumulated on the seasonal variations in the abundance of tropical zooplankton populations from other tropical lakes (Green, 1967; Robinson & Robinson, 1971; Litterick et al., 1979; Infante, 1982; Kassahun & Amha, 1984; Hart 1981; 1985 for review; Semeneh, 1987; and Seyoum & Fernando, 1991).

In lakes sufficiently deep to stratify, the period of low surface temperatures is likely to be that in which vertical mixing, partial or complete, is most readily induced. Such mixing bring detectable changes in the phytoplankton population due to upwelling of nutrient from the depth which is previously sunk and accumulated in the hypolimnia or resuspension of phytoplankton especially filamentous algae which are otherwise prone to sink rapidly (Talling, 1969).

The zooplankton in tropical lakes are frequently dominated by microphagus herbivores, whose seasonality is partly influenced by the availability of phytoplankton food. The magnitude of these seasonal fluctuation is often large in lakes throughout the tropics. On the other hand the magnitude and duration of mixing periods have a negative effect by reducing phytoplankton population as in the case of Lake Kariba (Hart, 1985) and Lake Lanao (Lewis, 1987). Transient, aperiodic events may be survived by algae and zooplankton drawing upon stored energy reserves (Hart, 1985). Direct effect on the survivorship of the zooplankton is introduced by creating anoxic epilimnia and surfacing of toxic chemicals such as Hydrogen Sulphide (Beadle, 1981) which are lethal to plankton beyond certain limit, as was frequently reported from Lake Valencia (Infante, 1982) Lake Chilwa (Kalk, 1979) and Lake Edward (Beadle, 1974; after Verbeke, 1957). The effect of anoxia on mass mortality of fish is well known in tropical inland waters (Beadle, 1981) but its effect on zooplankton population directly, or indirectly by reducing predation pressure was not investigated in most of the lakes.

The other seasonal change in zooplankton population size corresponds with the seasonal rainfall. Tropical lakes that receive a large proportion of their total volume from seasonal rains and inflowing streams increase nutrients concentration during rainy season and zooplankton peaks follow this nutrient input (Robinson & Robinson, 1971; Kalk, 1979; Infante, 1982; Kassahun & Ameha, 1984; Semeneh, 1987). In lakes where stream discharge is extremely large, zooplankton populations often decline in size as in Lake Chad (Gras et al., 1967 cited in Hart, 1985) due to increased turbidity affecting the phytoplankton production.

Both periods of vertical mixing and the seasonal rainfall coincide and lead to an increase in zooplankton abundance (e.g. Seyoum & Fernando, 1991).

Physical factors strongly influence seasonality, but parallel deterministic influences of direct biological effects and interactions undoubtedly exist; the influence of food availability and of algal growth-zooplankton growth interactions; the influence of predation and its feed-back upon zooplankton abundances and composition, etc. With respect to the biological effect on seasonality of zooplankton abundances and composition in tropical lakes, few reports are available. The decrease in abundance of zooplankton in June was attributed to greater predation pressure of fish in Lake Valencia (Infante, 1982) and Chaoborus (Saunders & Lewis, 1988). The decline of cladocerans coincide with the annual bloom of the troublesome filamentous algae (Infante & Riehl, 1984). In Lake Chilwa increase in zooplankton abundance is often disrupted by increased predation pressure (Kalk, 1979).

Water level fluctuation which is a seasonal phenomenon directly related to the amount of rainfall is known to have important effects on zooplankton populations. Fernando & Rajapaksa (1983) observed a reduction in the proportion of large zooplankton as the water level decreased.

Generally knowledge on seasonality of tropical zooplankton from various water bodies imply that factors controlling seasonality are highly variable, highly local and least uniform as compared to temperate water bodies.

Knowledge on the dynamics of zooplankton population of Ethiopian lakes is meagre, except for records made by Kassahun and Amha (1984), Semeneh (1987), and Seyoum & Fernando (1991).

Biological limnology of the Ethiopian crater lakes is poorly known except for few investigations made for a short period of time on the zooplankton by Green (1986), on the phytoplankton by Baxter & Wood (1965) and productivity by Talling <u>et al</u>., (1973 cited in Green, 1986).

Because of the crucial position of zooplankton in the energy transfer of lake ecosystem, proper understanding of its dynamics and its interaction with environmental conditions is a necessity. Owing to the inadequacy of our present knowledge this baseline study was initiated to monitor the seasonal dynamics of the zooplankton community in these two small tropical lakes - Bishoftu and Arenguade.

8. MATERIALS AND METHODS II

I. PHYSICAL AND CHEMICAL PARAMETERS

Hydrogen ion concentration was measured using portable Cole Parmer P^H meter and conductivity of the water was determined using portable Cole Parmer conductivty meter.

Total dissolved phosphate and oxidized nitrogen of the surface water were determined using Ammonium molybdovanadate method and Cadmium reduction method with a portable HACH Kit.

II. ZOOPLANKTON

Field sampling : Zooplankton was sampled monthly from January, 1991 to December 1991 from the central site of Lake Arenguade and Lake Bishoftu. Triplicate samples were collected as vertical hauls from 10 m to the surface using number 25 plankton net with 64 um mesh size and 25 cm mouth diameter. All samples were preserved in a 4% formaldehyde solution. Vertical samples were collected at 5 m interval using Schindler Patalas plankton trap (10l). Samples were not collected for two months (April and June) from lake Bishoftu and for four months (March - June) from lake Arenguade.

Counting : For the analysis of abundance pattern,the triplicate samples were counted. Counting was done under a Wild (M8) stereomicroscope (Mag. 100X) using Bogorov's counting chamber and a multichannel counter (interface systems). Infrequently when samples were so dense three sub-samples each containing 0.1 part of the whole sample were drawn for counting using a wide-mouthed graded glass pipette. All developmental stages of copepods were lumped to Nauplius, Copepodite, and adult count categories. Adult females, ovigerous females, males and loose eggs were identified and counted separately.

Statistical analysis : Two way analysis of variance was done to determine if the zooplankton counts were significantly different among months and replicates. The summary of these analysis is reported. The analysis were done using the MGLH module packages in SYSTAT (Wilkinson, 1986).

III. PHYTOPLANKTON

Field sampling : Phytoplankton samples were collected at the same position where zooplankton samples were collected in both Lake Arenguade and Lake Bishoftu. 100 ml of lake water from the surface were drawn from Van Dorn water sampler (2.5 L) and preserved by Lugol's Iodine solution.

Counting : 1 ml sub - sample (1 ml) was transferred to 9 ml distilled water and allowed to sediment in a settling chamber for 24 hours. The settling chamber were mounted on an inverted microscope (Nikon) and the entire content were counted at 800 times magnification.

Counting units were colonies for colonial algae and coils for filamentous algae, because cells were too small and tightly packed to be distinguished individually.

9. RESULTS II

I. Species composition.

The dominant crustacean zooplankton of these soda lakes was found to be a calanoid copepod, *Lovenula africana* identified after Defaye (1988). *L. africana* was the only crustacean zooplankton in Lake Arenguade whereas in Lake Bishoftu another crustacean zooplankton, *Mesocyclops aequatorialis* , also exist. Planktonic rotifers which belong to the genus *Brachionus* were also recorded, in both lakes (identified after Koste, 1978 and Seyoum pers. comm). In Lake Bishoftu, the rotifer population is *B. calyciflorus* and in Lake Arenguade the rotifer population is *B. dimidiatus* (Seyoum pers.comm.)

II. Statistical analysis

One - way analysis of variance for all duplicate tows counted shows highly significant differences ($P < 0.001$) between sampling months for all stages and sexes of *Lovenula africana* in Lake Arenguade (Table 3) and Lake Bishoftu (Table 4). Triplicate tows contributed insignificantly to the variance in the relative abundance of each stages and sexes. This suggested that irregular fluctuations observed in population size cannot be dismissed simply as sampling error, due to local concentration (patches) of zooplankton, but rather appear to reflect substantial seasonal changes in the abundance of each stages and sexes.

Table 3. Results of one - way ANOVA to show differences between sampling months of <u>Lovenula</u> <u>africana</u> in Lake Arenguade.Rplicates forming the error term.

Stages	Source of variation	DF	MS	F - Ratio	Significance
Nauplii	Month	7	47511000	174.995	*
	Error	16	271499.500		
Copepodites	Month	7	11162200	45.866	*
	Error	16	243366.167		
Male (adult)	Month	7	7451930	28.755	*
	Error	16	259155.833		
Female(adult)	Month	7	15200600	56.907	*
	Error	16	267113.333		
Adult(total)	Month	7	43042400	47.284	*
	Error	16	910295.042		

* = Significant at $P \leq 0.001$

Table 4 . Results of one - way ANOVA to show differences between sampling months of Lovenula africana in Lake Bishoftu. Rplicates forming the error term.

Stages	Source of variation	DF	MS	F -ratio	Significance
Nauplii	Month	9	1167071.348	135.017	*
	Error	20	8643.867		
Copepodites	Month	9	931030.83	126.615	*
	Error	20	7353.267		
Male(adult)	Month	9	377829.274	78.682	*
	Error	20	4802.000		
Female(adult)	Month	9	468946.8	63.628	*
	Error	20	6980.533		
Adult (total)	Month	9	55069.467	20.294	*
	Error	20	2713.600		

* significant at $P \leq 0.001$

III. Pattern of abundance.

The abundance of the zooplankton population was considered as relative abundance because the filtering efficiency of the plankton net was not determined using flowmeter; as a result the abundances are relative but this does not affect the discussion on the pattern of abundance.

Zooplankton population in Lake Arenguade exhibited seasonal fluctuations in population size. There were clear seasonal patterns in the abundance of L. africana's juveniles (Fig.9A & B) and adults (Fig.10). The nauplii of L. africana population were absent at the beginning of the sampling season (January, 1991) and appeared in February and attained its maxima during the rainy season in August. Again the nauplii sharply declined in September and collapsed in December (Fig.9A). Similarly the copepodite stages of L. africana were absent in January, recovered in February and steadily increased with maxima in August. After the peak in August the copepodites sharply decreased in September and remained low up to December and collapsed in December(Fig.9B). The population size of the copepodites is greatly reduced as compared to the nauplii and adults.

The adult stage of L.africana in Lake Arenguade also follow a similar pattern of abundance like the juveniles but the adults' maxima persisted longer (August to October) and a sharp decline was observed late in November followed by collapse in December (Fig.10). The adults increase about five fold from

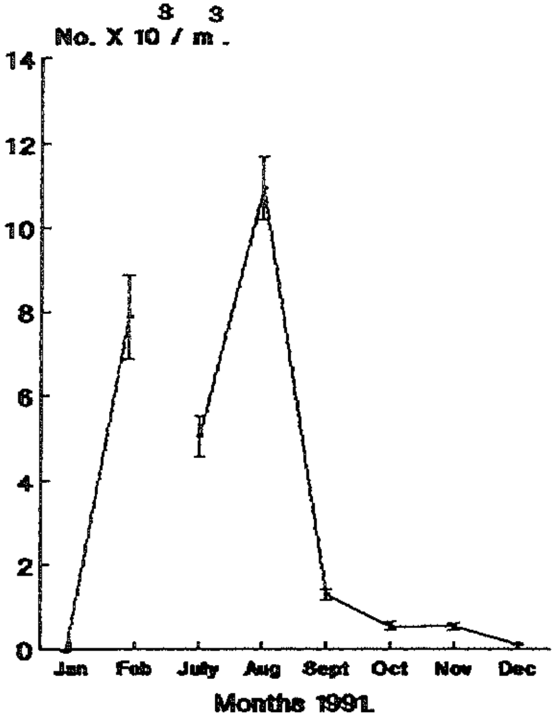

Fig. 9A. Relative abundance of Nauplii of L. africana in Lake Arenguade

Values are means + S.D.

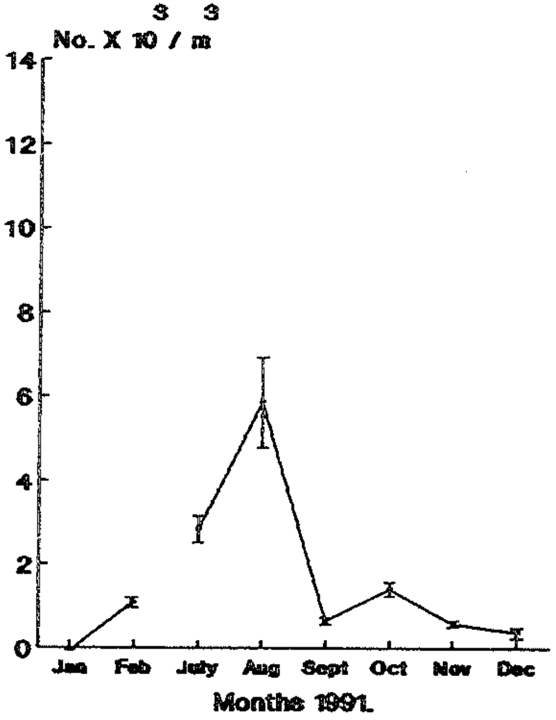

Fig. 9B. Relative abundance of Copepodites of L. africana in Lake Arenguade.

Values are means + S.D.

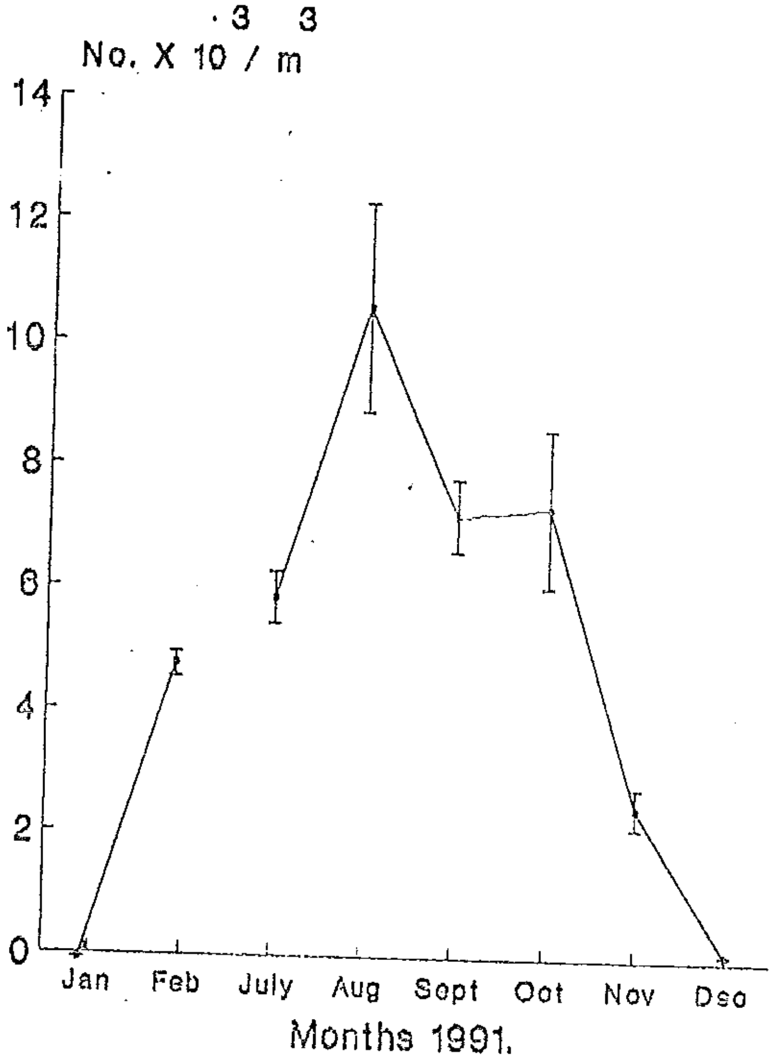

Fig.10. Relative abundance of adult L. africana in Lake Arenguade.

Values are means ± S.D.

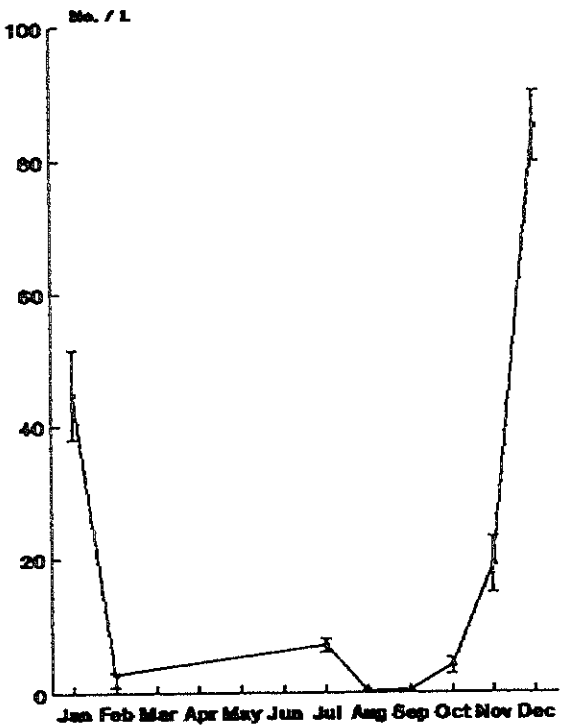

Fig.12A. Relative abundance of Brachionus. in Lake Arenguade.

Values are means ± S.D.

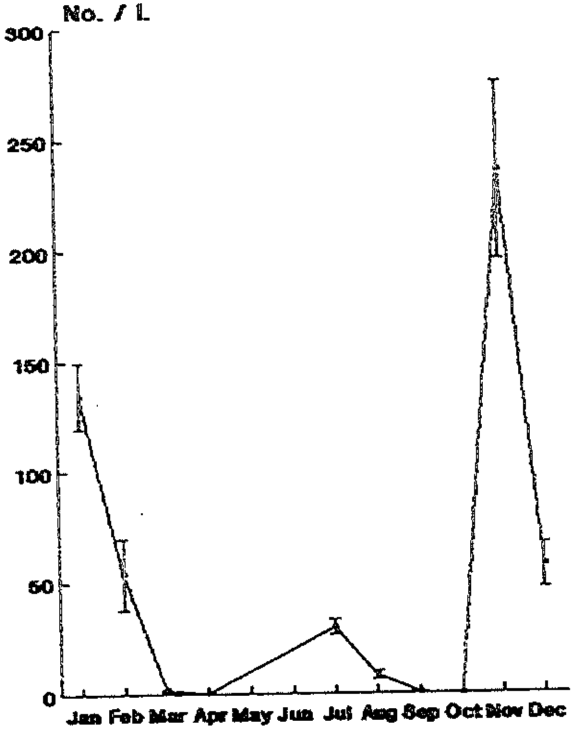

Fig. 12B. Relative abundance of Brachionus in Lake Bishoftu.

Values are means ± S.D.

Zooplankton population seasonality in the nearby lake, Lake Bishoftu, is similar to that of Lake Arenguade (Fig. 13 & 14). There were a two fold increase in the adults of L. africana in August as from March minima (Fig. 14) and four fold increase of copepodites in September from the minima of March (Fig.13 B) whereas there were eleven fold increase in the nauplii from February to August (Fig. 13A).

The crustacean zooplankton of Lake Bishoftu is composed of a cyclopoid copepod, Mesocylops aequtorialis, and calanoid copepod, Lovenula africana. The calanoid copepod population in Lake Bishoftu collapse a month earlier than Lake Arenguade's population in November. All stages of calanoid copepod of Lake Bishoftu were absent in January and February except few nauplii, and recovered in March. The adults steadily increase with slower rate as compared to the juveniles and to the population of Lake Arenguade. Peak adult densities were attained during the rainy season in August and were followed by a collapse in November. Copepodites were recovered in March and attained their maxima late in September and sharply declined in October and collapsed in November. The nauplii remain low from January to July and a sharply increased and attained maxima in August. The nauplii density remained high up to October and collapsed in November. (Fig 13A).

The proportion of male to female was inclined (X2 = 79.9, P < 0.001) infavour of females (1 : 1.1 male to female) (Fig.15A & B).

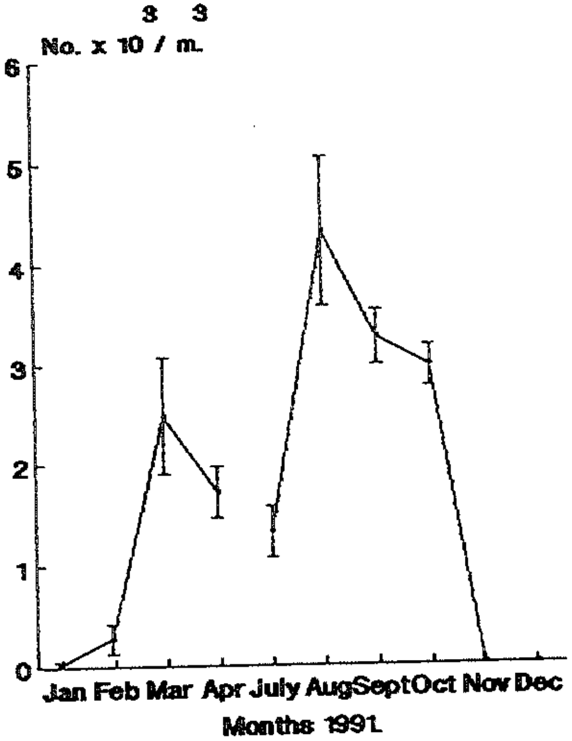

Fig.13A. Relative abundance of Nauplii of L. africana in Lake Bishoftu.
Values are means ± S.D.

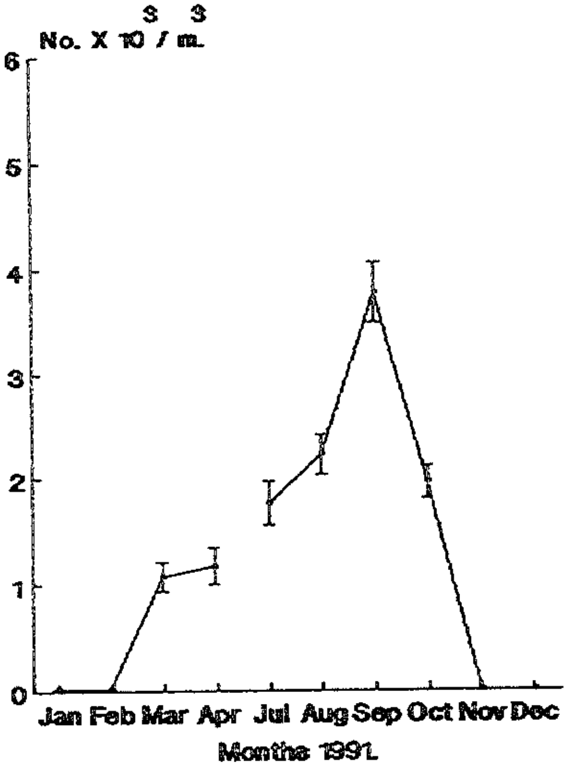

Fig.13B. Relative abundance of Copepodites of L. africana in Lake Bishoftu.
Values are means ± S.D.

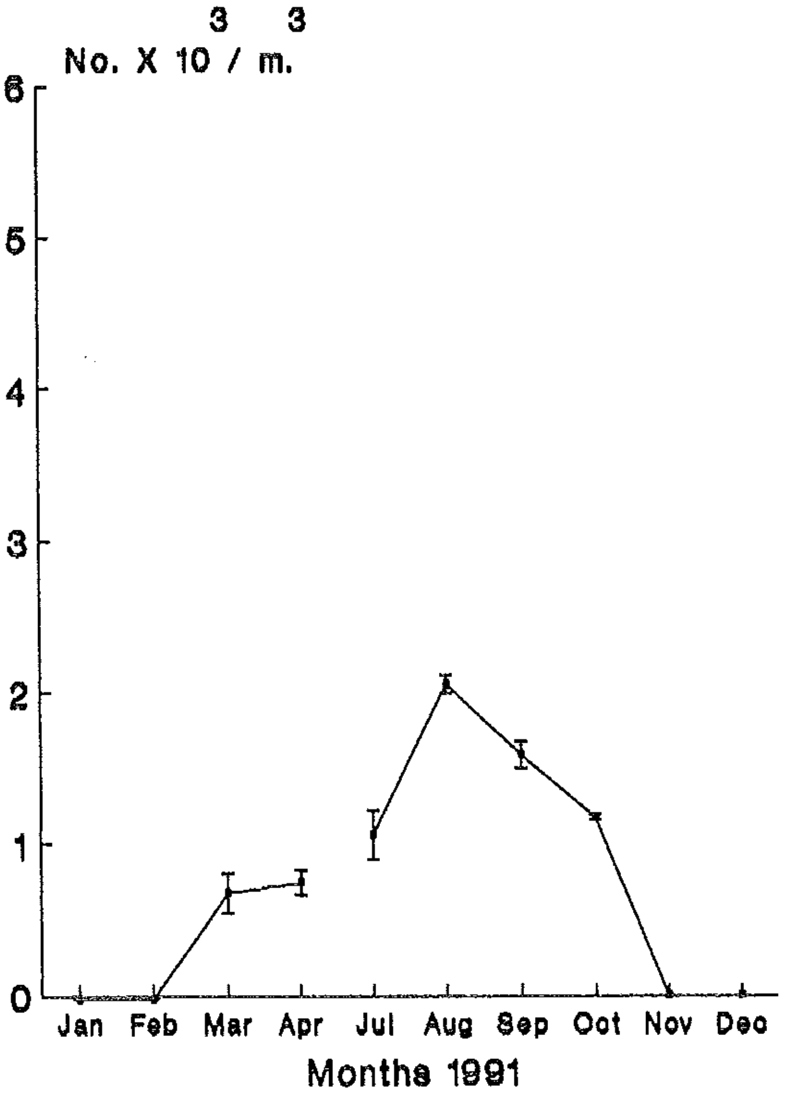

Fig.14. Relative abundance of adult *L. africana* in Lake Bishoftu.
Values are means ± S.D.

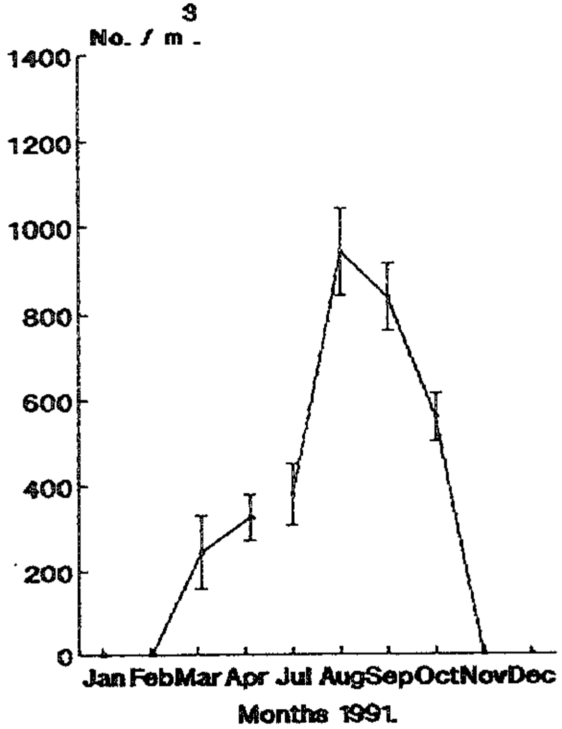

Fig. 15A. Relative abundance of male *L. africana* in Lake Bishoftu.

Values are means ± S.D.

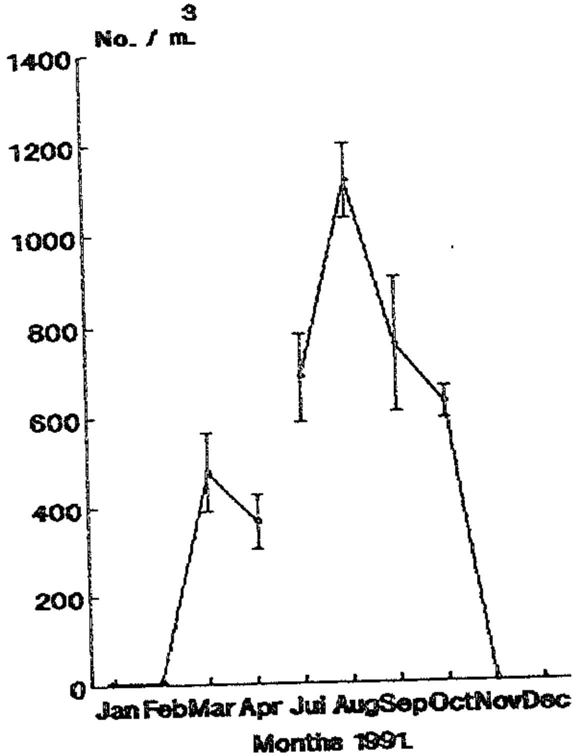

Fig. 15B. Relative abundance of female *L. africana* in Lake Bishoftu.

The cyclopoid copepod, Mesocyclops aequtorialis, was absent in January but recovered soon in February and show irregular fluctuations throughout the sampling season (Fig.16).

Rotifer density was high in January in both lakes and declined in February and March (Fig. 12A & B) with the emergence of the cyclopoid copepods and nauplii in Lake Bishoftu and all stages of calanoid copepod in Lake Arenguade. Rotifers remained low in density until the collapse of crustacean zooplankton. Following the collapse of the crustacean population, rotifers increased once again (Fig.12A &B).

Biomass of the net phytoplankton population fluctuation were less pronounced at most with three fold increase in the peak season from 1040 - 3120 colonies per litre of Microcystis in Lake Bishoftu and from 35000 - 72300 coils / litre Spirulina in Lake Arenguade. Essential nutrient were also relatively stable with time though there is exceedingly high amount of phosphate in Lake Arenguade ranging from 2600 - 3800 ug /l, and very low amount of oxidized nitrogen (NO_2 + NO_3) ranging from 44 - 66 ug / l in Lake Arenguade and 52 - 86 ug / l in Lake Bishoftu (Fig. 17A & B). The seasonal variation in P^H and conductivity was also more or less constant for both lakes (Table 5).

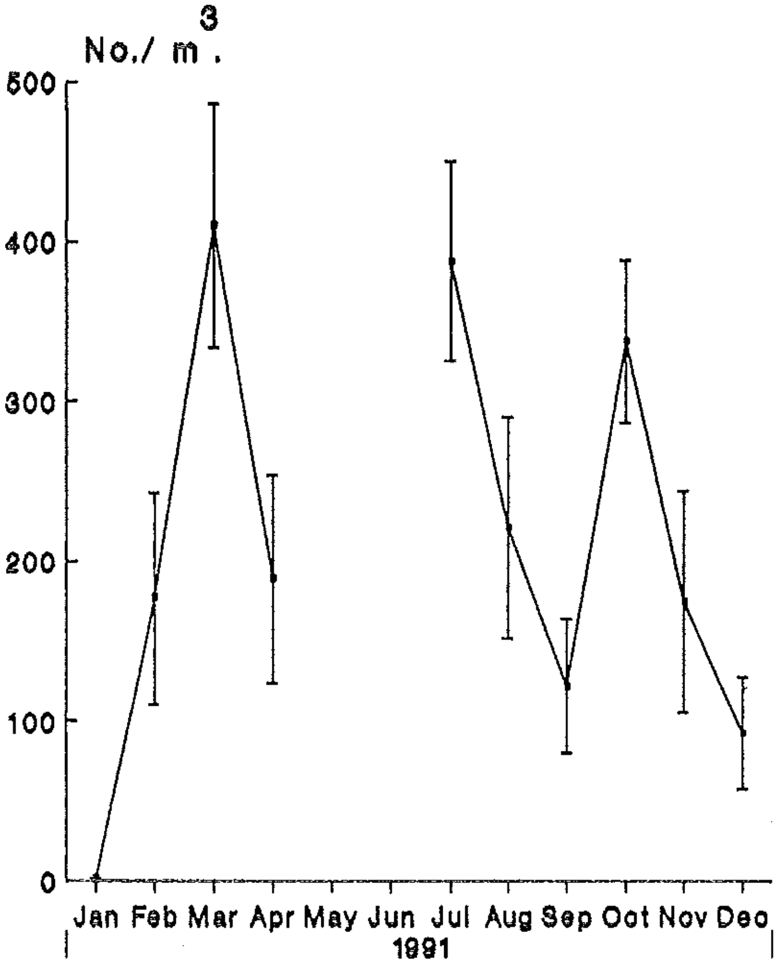

Fig. 16 Relative abundance of Mesocyclops aequatorialis in Lake Bishoftu.

Values are means + S.D.

Table 5. PH and conductivity measurement in Lake Arenguade and Lake Bishoftu in 1991.

Month	Lake Arenguade		Lake Bishoftu	
	P^H	Conductivity(us/cm)	P^H	Conductivity(us/cm)
January	10.03	5300	8.76	1280
February	9.83	5500	8.84	1280
March	NM	NM	9.28	1280
April	NM	NM	9.07	1460
July	9.95	6200	8.92	1300
August	9.92	5800	8.78	1280
Septembe	9.91	6300	8.82	1280
October	10.17	6200	8.67	1280
November	10.08	6500	9.2	1280
December	10.00	6600	8.97	1450

* NM = No measurement

10. DISCUSSION II

The zooplankton composition of both Lake Arenguade and Lake Bishoftu is determined to be typical of tropical inland water population with very few crustacean zooplankton. Fernando (1980) has previously noted that the zooplankton of tropical lakes in Asia is generally less diverse than their temperate counterparts. Calanoid copepods are often restricted to very local distributions. These descriptions appear to apply to the African tropical lakes as well with possible modification that the herbivorous cyclopoid may be quantitatively replaced in old, deep lakes by a single calaniod (Hecky, 1984). Lake Arenguade and Lake Bishoftu also fits this modification though they are not relatively old (Mohr, 1961). As a result they are dominated by a single calanoid copepod, Lovenula africana, and are entirely devoid of cladocerans.

Typically two small cyclopoid species, one herbivorous and one carnivorous, usually Mesocylops leuckarti are common in tropical waters (Fernando, 1980). Similarly a cyclopoid copepod, Mesocyclops aequatorialis, was present in this region but only in Lake Bishoftu. Planktonic rotifer were also less diverse in these soda lakes. Brachionus was the only planktonic rotifer encountered in both lakes though other forms were also reported (Green, 1986; Green & Seyoum, 1991). Brachionus prefers alkaline waters and B. calyciflorus has been mentioned as an indicator of eutrophic conditions (Jarnefelt, 1952 cited in Infante, 1982) whereas B. dimidiatus was found to be dominant in lakes with salinities over 2°/₀₀ where there is a marked reduction in the number of rotifer species (Green & Seyoum, 1991).

Zooplankton abundance pattern clearly indicate seasonality for all planktonic copepods, their developmental stages, and rotifers in both Lake Arenguade and Lake Bishoftu.

Direct food limitation is a powerful mechanism of population control in copepods (Herbert, 1985). A decline in the population size during mixing season is common for some monomictic tropical lakes such as Lake Lanao which was attributed to reduction of algal biomass (Lewis, 1979; Hart, 1985). Changes in the algal biomass of Lake Bishoftu and Lake Arenguade are muted throughout the year (Fig. 17A & B). The concentration of reactive phosphate in the water remained excessively high as recorded during the sampling year and from similar study by Prosser _et al_., (1968) and Wood _et al_.,(1984), so that phosphorus does not seem to be limiting in these lakes but surprisingly enough the concentration of oxidized nitrogen in the water is very low and uniform throughout the year (Fig. 17). Past records also revealed the same fact so it seems that the extremely high crop of algae were presumably absorbing all available inorganic nitrogen (Wood _et al_., 1984); so food limitation is unlikely to explain the seasonal fluctuation in the zooplankton population of these lakes. The seasonal decline of this calanoid copepod, _L. africana_, was documented from Lake Abiata and attributed to the rise in conductivity (Kassahun & Amha, 1984). Conductivity measurements during the study period (Table 5) and previous records by Wood _et al_., (1984) revealed that changes in conductivity are low and remained much below the upper reported limit (15000uohms/cm) at which this species naturally survive (La Barbara & Kilham, 1974). The decline of L. africana in Lake Langano was associated with the rise of cyanophyte population but this herbivore was observed ingesting cyanophytes in Lake Arenguade (Personal observation) where a dense crop of entirely cyanophyte, Spirulina were recorded (Talling et al., 1973 cited in Green, 1986).

Predation frequently alters prevailing competitive balances, but this can only be expected in Lake Bishoftu's population where there is planktivorous fish but competition seems less fierce in these lakes because there is no other herbivore except rotifer to compete with. Besides the density of these calanoids were found to be by far low by one order of magnitude as compared to less productive tropical lakes such as Lake Lanao and Lake Mutanda (Green, 1986).

In Lake Edward seasonal zooplankton population decline during mixing was attributed to upwelling of anoxic water (see Hart, 1985 for review), and also in Lake Chilwa (Kalk, 1979). Upwelling of toxic chemicals during complete mixing also brought a decline of zooplankton populations in Lake Valencia (Infante, 1981). Similarly the present study revealed that the population of these soda lakes also declined during the mixing season (November-February) when there is anoxia and upwelling of high concentration of H_2S which could be detrimental to zooplankton.

Mass mortality of fish during the mixing season is not uncommon in tropical lakes due to asphyxiation and upwelling of toxic chemicals such as H_2S (Beadle, 1981). This phenomenon is also common in Bishoftu crater lakes every year during complete mixing producing detectable smell of H_2S to the surrounding area. One incidence was reported from Lake Pawlo, one of the Bishoftu crater lakes, by Baxter et al.,(1965 cited in Talling and Talling, 1969). But no investigation were done on the effect of anoxia and upwelling of toxic chemical on the suvivialship of zooplankton in these lakes.

Seasonal predation pressure can also bring about seasonal decline in zooplankton population both by vertebrate predators mainly fish (Infante, 1982) and invertebrate predators mainly *Chaoborus* (Saunders & Lewis, 1988). In Lake Bishoftu the upwelling of anoxic water and H_2S could also affect the fish population, which is commonly reported from the local fishermen. As a result predation pressure would be minimum during mixing period and the steady increase in zooplankton population after recovery implies that predation is not seasonal but rather uniform resulting in the observed low rate of population growth in Lake Bishoftu as compared to Lake Arenguade.

Besides the proportion of adults to juveniles in both lakes vary in such a way that few individuals existed as adult in lake Bishoftu as compared to Lake Arenguade (Figs.10 & 14). The sex ratio is also more skewed in Lake Arenguade in favour of the females than Lake Bishoftu (Figs.11 & 15). This finding is in line with findings of Gophen (1988) whereby the adults of two cyclopoids and particularly the females became less abundant in Lake Kinneret (Israel) and was attributed to increased intensity of predation by planktivorous fish. So these differences and lower rate of population growth and lower biomass of zooplankton in Lake Bishoftu can be attributed to predation pressure.

According to Starkweather (1980) Brachionus calyciflorus and its congeners are common planktonic inhabitants of mesotrophic and eutrophic lakes and ponds. While truly a cosmopolitan species, its occurrence is often seasonally restricted. The species, however, reproduce rapidly and attain extremely high population numbers during those transient maxima.

The initial Pulse in the population of Brachionus in both lakes demonstrated the ability of the species to modify its reproductive physiology with changes in ecological conditions.(Figs.12 A & B). Coincident with the decline of the first pulse of Brachionus there was an increase of cyclopoid copepods, Mesocyclops aequatorialis (Fig.16) and nauplii of L. africana in Lake Bishoftu (Fig.13A) and all stages of L. africana in Lake Arenguade with high rate of the juveniles (Figs.9 & 10). This may have been the result of a direct competition for food between the nauplii and the rotifer. This event is in line with reports from another tropical Lake Valencia following the collapse of the zooplankton population caused by upwelling of toxic chemical during mixing (Infante, 1982). An interesting contrast as reported in the recovery of a tropical pond in Malaysia. The steady increase of crustacean population in both lakes signifies that continuous reproduction and population build up of crustacean community is less affected by other factors though in Lake Bishoftu the rate is reduced than in Lake Arenguade probably due to predation in the former.

The population of L. africana steadily increased during the rainy season (July-September). During the rainy season the surface oxygen concentration decreases and oxycline is lowered to nearly 2m in Lake Arenguade and 10m in Lake Bishoftu. In November these lakes start to mix or nearly mix following persistent cooling up to December. Heat flux and thermal stability depend on the delicate balance principally between solar inputs and evaporative heat loss, so that cooling and mixing are more likely to follow cloudless periods with low humidity, although associated with low solar influx, typify periods of warming leading to stratification (Baxter et al., 1976). During this mixing period the crustacean population declines whereas rotifer attained the second peak probably encouraged by the increase of nanoplankton populations and decreased competition and better tolerance of anoxia. During the mixing period, available phosphorous also increases (Fig. 17A & 17B), thereby initiating nonoplankton increases.

The nucleus population for recolonizing these lakes presumably are able to survive this catastrophe in microhabitat, or possibly produce resting stages as survival mechanisms. This requires further investigation.

11.CONCLUSIONS AND RECOMMENDATIONS.

The present study suggests that predation by planktivorous fish is size-dependent resulting in reduction of large-bodied zooplankton population. Other studies in line with these findings further implicate that size-selective predation of fish on zooplankton population leads to deterioration of water quality through eutrophication. Besides eutrophic lakes in the tropics often cause catastrophe in fish population during mixing (e.g. Lake Hayq). These findings call for further ecological studies to minimize such ecological backlashes.

The common practice of introducing fish in to water bodies and especially into reservoirs should be reconsidered in view of its purpose.

The factor that governs the species composition and seasonal dynamics of zooplankton in Lake Arenguade and Bishoftu is associated with mixing of the water bodies. The suggested factors are mainly the depletion of oxygen in the epilimnion and upwelling of H_2S.

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