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Dissertation

**Zooplankton community structure, population dynamics and production
and its relation to abiotic and biotic factors in Lake Ziway, Ethiopia**

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Abstract

Long term quantitative studies on zooplankton of Ethiopian water bodies on the basis of short sampling intervals are still scarce. Information on secondary production is even much more limited. For this reason zooplankton community structure, population dynamics and production was studied in relation to abiotic and biotic factors in Lake Ziway, a shallow turbid Rift Valley lake. Between October 2008 and September 2009 field sampling was performed on a biweekly basis with Schindler sampler (10l) and plankton nets of 40 and 100 μm mesh sizes; data on dry weights and development times of crustaceans were determined in the laboratory and were applied to the field data to describe population dynamics and to estimate secondary production.

Abiotic parameters (e.g. water temperature, dissolved oxygen, and pH) did not show marked temporal variation except the dissolved oxygen in the inshore station with dense macrophyte stands. Frequent and well mixing of the water column resulted in very low difference in those abiotic parameters between the upper and lower water stratum. Water transparency (secchi depth) showed significant variation between dry and rainy season. The increase in turbidity following rainfall is clearly a basic limnological feature of the lake that led to a decline in the physical, chemical and biological parameters.

The phytoplankton community of Lake Ziway was dominated by large colonial forms like *Microcystis* species and filamentous, *Anabaena* and *Oscillatoria* species. Maximum Chlorophyll a concentration was recorded during the short wet period before the main rains. Species composition of zooplankton in Lake Ziway reflects typical tropical aspects, with rotifers being the dominant taxa (49 species) and 10 crustaceans (3 cyclopoids and 7 cladocerans) contribute the rest. *Brachionus* and *Keratella* species were the dominant and major contributors to the total rotifer abundance. Rotifers comprised 43% of the total zooplankton abundance. Crustaceans were dominated by one species *Thermocyclops decipiens*. *Moina micrura*, *Diaphanosoma excisum*, *Ceriodaphnia cornuta* and *Daphnia barbata* represent the cladocerans. Larger *Daphnia* and calanoid species are absent. Change in species composition of zooplankton was evident. *Ceriodaphnia cornuta* and *Daphnia barbata* were absent from the plankton following the decline in the water transparency. *Pseudosida szalayii* and *Chaoborus* sp. which were not reported from the lake earlier could be identified. Rotifer and copepod species reported in earlier investigations were confirmed by this study.

The importance of sampling strategy which considers the development times of the various plankton organisms becomes apparent. Comparison between the temporal distribution patterns of total zooplankton in Lake Ziway from two different sampling intervals (biweekly and monthly) indicates that in the monthly sampling short-term fluctuations in the population were masked, but becomes obvious from the biweekly taken samples. Variations in the horizontal distribution pattern of zooplankton species became obvious, two to five fold abundances of zooplankton could be revealed inshore compared to the offshore station of Lake Ziway. Among the species, the littoral species *Alona* reported to be dominant in the open water of lakes Ziway and Awassa was not confirmed in the present study. *Alona* occurred in higher (as high as fivefold) density inshore. On the contrary size variation in the distribution of copepod species was evident, larger adults and egg carrying *Mesocyclops aequatorialis* females were almost absent from day samples and rare in the inshore station. A clear vertical distribution gradient mainly by the larger and egg carrying copepods was also observed. Numbers of egg carrying females and their clutch size were larger from night samples and increased with depth in the day samples. Predation by fish (catfish) and the invertebrate predator *Chaoborus* seemed to be the major cause for variation in the distribution. High predation pressure on large sized adults and egg carrying *Mesocyclops* females were evident in the present study; the stomach contents of catfish consisted mainly of the larger copepods and the biomass of adult *Mesocyclops*, the largest sized among the crustaceans in Lake Ziway, was lower than the biomass of the nauplii.

Rotifers and copepods comprised about 96% of the total zooplankton abundance. Zooplankton biomass was dominated by copepods, rotifers and cladocerans comprising only 14% of the annual mean zooplankton biomass (91 mg dwt m⁻³). Temporal variation of cladocerans biomass was associated with the water transparency with a general decline towards the rainy season, copepods however showed an increase at the same time. Correlation analysis also revealed that standing stocks of cladocerans were highly correlated with water transparency and weakly and negatively with Chlorophyll a concentration. Copepods however correlated best with Chlorophyll a. Predation pressure on the larger zooplankton organisms (e.g. *Daphnia barbata* and *Mesocyclops*) shifted zooplankton community structure in Lake Ziway towards the dominance of the smaller sized *Thermocyclops*, pre-adult copepods and rotifers.

Embryonic and post-embryonic development times of *Ceriodaphnia cornuta*, *Monia micrura* and two cyclopoid copepods *Mesocyclops aequatorialis* and *Thermocyclops decipiens* were determined in the laboratory at mean temperature range of 21,3-25,1 °C. Cultures of *Diaphanosoma excisum* and *Daphnia barbata* were not completed successfully. The relationship between temperature and development time of crustaceans was best fitted by quadratic equations. The results on embryonic and post-embryonic development times were comparable with the results from other tropical lakes.

Productions of the dominant Cladocera (*Moina micrura*) and cyclopoid copepods (*Mesocyclops aequatorialis* and *Thermocyclops decipiens*) were estimated by growth increment (Winberg) method. Copepods contributed 84% of the total crustacean production in Lake Ziway. Lake Ziway showed well expressed seasonal variation in crustacean production. The production of *M. micrura* was usually greater during the dry season (2,3 times) than during the wet season. Cyclopoid copepods however showed about 2 fold greater production during the wet season. The total annual crustacean production in Lake Ziway was 3,2 g dw m⁻³. The mean annual P/B ratio for the dominant crustaceans was 38,7. The dominance of small sized zooplankton as well as high contribution of post-embryonic stages to the total copepod production and relatively uniform high temperature throughout the year and correspondingly short development times result in low production but high turnover rate. Bottom up (quality of food) and top-down (predation by fish and *Chaobours*) control, turbidity and dense macrophyte in the littoral could be the major factors to govern the zooplankton community structure and productivity of Lake Ziway.

Zusammenfassung

Quantitative Langzeituntersuchungen über das Zooplankton äthiopischer Gewässer, deren Probenentnahmen in kurzen Zeitintervallen erfolgten, sind eher selten, Angaben über die Sekundärproduktion sind eine Rarität. Aus diesem Grunde wurde das Zooplankton im See Ziway, einem trüben Flachsee des ethiopischen Grabenbruches, untersucht, die saisonale Entwicklung und die steuernden abiotischen und biotischen Faktoren beschrieben und die planktische Sekundärproduktion der wichtigsten Vertreter der Zooplanktongemeinschaft berechnet. Die Untersuchungen wurden von Oktober 2008 bis September 2009, basierend auf 14-tägigem Probenintervall, durchgeführt; die Probenentnahmen erfolgten mit einem 10-Liter Schindler-Schöpfer und Planktonnetzen einer Maschenweite von 40 und 100 μm . Trockengewichte und Entwicklungszeiten der einzelnen Arten und Entwicklungsstadien wurden im Labor ermittelt. Die Verbindung der Feld- mit den Labordaten ermöglichte die Beschreibung der Populationsdynamik und die Berechnung der Sekundärproduktion.

Abiotische Parameter wie die Wassertemperatur, Sauerstoff (ausgenommen die Bereiche mit dichtem Makrophytenbewuchs) und pH ließen keine ausgeprägten Unterschiede im Verlaufe der Untersuchung erkennen; dafür zeichnet die fast ständige windbedingte Durchmischung des Wasserkörpers verantwortlich. Die Sichttiefe hingegen ließ klare Unterschiede zwischen Trocken- und Regenzeit erkennen. Der mit den Niederschlägen einhergehende Anstieg der im Wasser suspendierten Partikel ist für den See charakteristisch und führt zu Auswirkungen im physikalisch-chemischen Bereich und in den Lebensgemeinschaften.

Das Phytoplankton des Ziway bestand vor allem aus koloniebildenden (*Microcystis* spp.) und fädigen Arten (*Anabaena* sp., *Oscillatoria* sp.). Die Chlorophyll a-Werte schwankten zwischen 6,8 $\mu\text{g.l}^{-1}$ und 59,4 $\mu\text{g.l}^{-1}$, die Maxima wurden kurz vor der Regenzeit gemessen. Das Zooplankton des Ziway entsprach den Erwartungen von tropischen Seen, Rotatorien dominierten (49 Arten), 10 Crustaceenarten (3 Cyclops spp., 7 Cladocera) ergänzten die Artenzahl. Die Rotatorien bildeten 43% der Individuendichte, *Brachionus* spp. und *Keratella* spp. waren vorherrschend. *Thermocyclops decipiens* war die wichtigste Crustaceenart, dazu traten die Cladoceren *Moina micrura*, *Diaphanosoma excisum*, *Ceriodaphnia cornuta* und *Daphnia barbata* in Erscheinung. Große Daphnien und calanoide Copepoden fehlten. *C. cornuta* und *D. barbata* verschwanden aus dem Plankton mit abnehmender Sichttiefe. Neu für den Ziway waren die Funde von *Pseudosida szalayi* und *Chaoborus* sp.

Die Bedeutung der Sammelstrategie und vor allem der zeitlichen Abfolge der Probenentnahmen konnte durch einen Vergleich von einmonatiger mit 14-tägiger Beprobung aufgezeigt werden. Auch die horizontalen Unterschiede (Uferbereich – offener See) im Vorkommen der einzelnen Arten konnten klar dargestellt werden. So wurde *Alona* nicht wie in früheren Untersuchungen im Freiwasser vorherrschend gefunden sondern im Uferbereich. Die großen und eiträgenden Weibchen von *Mesocyclops aequatorialis* waren in den Uferbereichen seltener als im Freiwasser. Klare Vertikalverteilungen waren gleichfalls feststellbar. Eitragende Copepoden waren im Freiwasser tagsüber in den tieferen Wasserschichten zu finden, in der Nacht wanderten diese Tiere in die oberflächlichen Wasserschichten. Räuberdruck von *Chaoborus* und Fischen (*Tilapia*, catfish) scheint der Auslöser für dieses Verhalten zu sein.

Rotatorien und Copepoden bildeten 96% der Zooplanktonabundanz. Die Zooplanktonbiomasse (Jahresdurchschnitt: 91 mg dw.m⁻³) prägten die Copepoden, der Beitrag der Rotatorien und Cladoceren lag bei 14%. Die Cladocerenbiomasse nahm gegen die Regenzeit hin deutlich ab, jene der Copepoden stieg hingegen in der Zeit an. Eine Korrelationsanalyse bestätigt die stark positive Beziehung zwischen zunehmender Sichttiefe (in der Trockenzeit) und Cladocerenbestand und zwischen Chlorophyll a (Maxima knapp vor der Regenzeit) und Copepodenbestand. Für die Dominanz kleiner Arten und junger Entwicklungsstadien scheint der Räuberdruck verantwortlich zu sein.

Embryonale und postembryonale Entwicklungszeiten von *Ceriodaphnia cornuta*, *Moina micrura*, *Mesocyclops aequatorialis* und *Thermocyclops decipiens* wurden experimentell für einen Temperaturbereich von 21,3°C – 25,1°C ermittelt. Kulturen von *Diaphanosoma excisum* und *Daphnia barbata* waren nicht erfolgreich. Die Beziehung zwischen Temperatur und den jeweiligen Entwicklungszeiten konnten mit einer quadratischen Regression sehr gut beschrieben werden. Die Ergebnisse stimmten größtenteils sehr gut mit den Ergebnissen von Populationen aus anderen tropischen Gewässern überein.

Die Produktion von *Moina micrura*, *Mesocyclops aequatorialis* und *Thermocyclops decipiens* wurde mittels der „growth increment“ (Winberg)-Methode berechnet. Die beiden Copepoden des Ziway bildeten 84% der Crustaceenproduktion. Die Produktion von *M. micrura* war während der Trockenzeit 2,3 mal höher als während der Regenzeit, die 2 Copepoden hingegen waren in der Regenzeit doppelt so produktiv wie in der Trockenzeit. Die Jahresproduktion der drei Crustaceen betrug 3,2 g dw.m⁻³, die Jahres-P/B-Rate 38,7. Die relativ geringe Produktion

und die doch hohe P/B-Rate erklären sich aus der Dominanz von kleinen Zooplanktern und deren postembryonalen Entwicklungsstadien (geringe Biomasse) und den, der kontinuierlich hohen Temperatur entsprechenden, kurzen Entwicklungszeiten. „Bottom up“ (Qualität der Nahrung) und „top down“ (Räuberdruck durch Chaoborus und Fische) Kontrolle, hoher Gehalt an suspendierten Partikeln und ein dichter Makrophyten-bestand im Uferbereich sind jene Faktoren, die die Entwicklung des Zooplanktons im Ziway (Populationsstruktur, Vorkommen, Produktion) steuern.

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Chapter 1

General introduction

The base line for our knowledge about tropical freshwater science stems from pioneering scientists coming from temperate regions. The earlier limnological expeditions to the tropics such as the Ruttner and Thienemann Expedition to Sunda-Indonesia in 1928-1929, the Hugh Scott Expedition (Omer-Cooper) to the Ethiopian lakes in 1927 and the Cambridge Expedition to the East African lakes by Worthington between 1930-1931 are some of the early works (for details see also Talling, 1996, Talling & Lemoalle, 1998). Despite such long time the progress in the development of tropical limnology is slow, limited number of trained scientists and lack of field and laboratory equipment being the major problems up-to-date (Hart, 1996). However, several efforts are made and are going on by local and international scientists.

Earlier studies on tropical water bodies are more qualitative than quantitative. Concrete studies on zooplankton of tropical lakes come from the early works of Grass and Saint-Jean (1969) in Lake Chad, Burgis (1971) in Lake George and a general account on an introduction to tropical limnology by Beadle (1981). The absence of marked seasonal variation in the water temperature of tropical lakes a potential for continuous growth and reproduction (Hart, 1981) give the impression that zooplankton population fluctuation in tropical lakes is generally muted. However, recent studies indicated the presence of seasonal variations in the composition and abundance of tropical zooplankton (Lewis, 1978; Infante, 1982; Twombly, 1983; Hart, 1986; Saunders and Lewis, 1988; Mengestou and Fernando, 1991a; Irvine and Waya, 1999; Dejen *et al.*, 2004; Isumbisho *et al.*, 2006).

Community compositions of tropical zooplankton have been addressed in various publications. The taxa in the composition are characteristically tropical and composed of smaller planktonic organisms, particularly rotifers and protists (Lewis, 1979; Fernando, 1980 b; Arcifa, 1984; Gillooly and Dodson, 2000). Large zooplankton taxa such as *Daphnia*, which accounts for much of the biomass of zooplankton in temperate lakes is seldom present in tropical lakes and even the species that are present are of small size (Arcifa *et al.*, 1992; Fernando, 1994). According to Lewis (1979) and Fernando (1980b), calanoid copepods are absent or rare in many tropical lakes. Fernando (1980a) assumed that a general decrease in daphnid species numbers and body size in tropical lakes may be the result of physiological

responses to high and uniform temperatures, food availability and predation by fish and invertebrates.

Spatial heterogeneity, resulting from interacting physical, chemical and biological processes is a common feature of ecosystems. In temperate lakes temperature and light are important environmental factors which influence the seasonal variation of the zooplankton. However, in tropical lakes hydrological events, wind and associated consequences and predation loss are mechanisms responsible for zooplankton population seasonality (Kalk, 1979; Lewis, 1979; Mavuti and Litterick, 1981; Infante, 1982; Gras and Saint Jean, 1983; Twombly, 1983; Hart, 1986, 1996; Mengestou and Fernando, 1991a; Masundire, 1997; Irvine and Waya, 1999; Kâ *et al.*, 2006; Isumbisho *et al.*, 2006). It is well known that planktonic organisms are important components of food webs and are basic food resources for fish communities. It is indicated in the literature that post-larval and juvenile fish of *Oreochromis niloticus* (Tudorancea *et al.*, 1988), different groups of young fishes (Robotham, 1990), *Tilapia* and omnivorous common carp (Chapman and Fernando, 1994) have zooplankton as an important component of their diet. The extraordinary success of tilapias to give high fish yields is their ability to utilize zooplankton more efficiently than other fish in their early stages (Fernando, 1983). Their presence in most tropical water bodies and worldwide economic importance in aquaculture (Pullin, 1991) will double the importance of understanding tropical aquatic ecosystems. However, in most developing countries less attention is given to limnological investigations which are overshadowed due to overemphasis on fisheries. The increasing introduction of alien fish species are examples of how rarely ecological implications have been taken into account, e.g. introduction of *Lates niloticus* and *Tilapia* species in Lake Victoria and Kyoga, *Limnothrissa miodon* and *Stolothrissa tanganyicae* in lakes Kariba and Kivu (for the details see Ogutu-Ohwaya, 1992 and references therein). Pitcher (1995) clearly showed how the African lakes are endangered through introduction of fish species, impoundment and heavy exploitation.

Introduction of exotic fish species in the Ethiopian water bodies was conducted in the 1950s when two temperate trout species were introduced into Bale highland rivers. Other introduction for aquaculture purpose, currently happening in most water bodies is stocking cyprinid species (*Cyprinus carpio* and *Carassius carassius*). Moreover, the communication between engineers and ecologists when damming or diverting rivers is rather loose. Most hydropower plant constructions and damming of rivers lack considerations of ecological consequences.

Ethiopia is endowed with a variety of water bodies (lakes, rivers and reservoirs) which are of great scientific interest and economic importance. According to Greboval *et al* (1994) the total surface area of inland waters in Ethiopia is 8,800 km². The area of the water bodies range from a few square meters up to 3200 square kilometers (i.e. Lake Tana, the largest lake in the country). These water bodies are situated in a wide range of altitude, from below 300 m (e.g. Lake Abhe) to above 4000 m (highland mountain lakes which include freshwater as well as saline soda lakes). Despite such a wide range of water resources, the biological communities of those water bodies are yet to be explored although the high numbers of lakes are situated in the Rift Valley in which most studies conducted so far are concentrated compared to the highland water bodies.

Studying on how the interactions of the various components of a water body and community change at different temporal scales has high significance for a better understanding of the functioning of the ecosystem. However, we still know little about the species composition of planktonic populations and their population dynamics from the Ethiopian water bodies. Information about long-term fluctuation in zooplankton composition, abundance and population dynamics is limited in most water bodies. Zooplankton production studies are very rare except that of Mengestou and Fernando (1991b) and a recent attempt by Wondie and Mengestou (2006). Information about the rivers and streams is still not available. Short time sampling has been performed by the expeditions since the earlier times of the beginning of tropical limnology (e.g. Lowndes, 1930; Bryce, 1931; Van de Velde, 1984; Dumon, 1983; Green, 1986); most studies dealt with taxonomic descriptions and faunistic/floristic lists. The only quantitative data on zooplankton of the Rift Valley lakes comes from Wodajo and Belay (1984) and Belay (1988). Recently some efforts are emerging including studies on the high land lakes (Mengestou and Fernando, 1991 a,b; Dejen *et al.*, 2004; Wondie and Mengestou, 2006; Dagne *et al.* 2008; Dejenie *et al.*, 2008; Tadesse, 2010; Fetahi, 2010).

Zooplankton studies from Lake Ziway are either taxonomic (Van de Velde, 1984; Defay, 1988; Green and Mengestou, 1991) or a short term quantitative study (Dagne *et al.* 2008). Fernando *et al.* (1990) reported about the abundance of *Alona diaphana* in the plankton of lakes Awassa and Ziway. Belay (1988) generated some quantitative data on the abundance of zooplankton in Lake Ziway based on monthly sampling. Recent studies showed well expressed variations in the species composition and numbers of zooplankton population in temporal and spatial scales (Dagne *et al.*, 2008; this study). In the present study, zooplankton

community structure and its relation to abiotic and biotic factors was investigated based on biweekly samplings from three stations for a period of one year.

The present study is structured as follows: in chapter 1, general introduction about limnological studies in tropical lakes, some physical, chemical and biological aspects of Lake Ziway and a description of the sampling site are presented.

In chapter 2, I review the literature on zooplankton species composition and distribution in tropical waters in general and shallow lakes in particular and present zooplankton community structure, composition and distribution (inshore and offshore) during the study period and discuss the relation of the observed changes with abiotic and biotic factors. Sampling stations, sampling materials and procedures used are presented in this chapter. Biomass estimates (μg dry weight per individual) of crustaceans determined from dry weight measurements of individuals and linear regressions from length-weight relationships are presented for *Ceriodaphnia cornuta*, *Moina micrura*, *Mesocyclops aequatorialis*, *Thermocyclops decipiens*, cyclopoid copepodid and nauplii. Dry weight of *Daphnia barbata* and *Diaphanosoma excisum* were determined using length-weight relationship from literature (Dumont *et al.*, 1975 and Gras and Saint-Jean, 1983, respectively). The results are compared with other studies from tropical water bodies.

In chapter 3, I present laboratory culture results on the duration of development times of crustaceans under field conditions using filtered lake water. Culturing methods used are described and production of dominant crustaceans calculated. Seasonal crustacean population dynamics was discussed based on field and laboratory determined data.

In the chapter 4, I discussed general aspects of plankton community dynamics in shallow lakes based on the results and literature.

Study site

The Ethiopian Rift Valley floor, along which many of the lakes aligned are of tectonic origin created by volcanic and faulting activity that formed various volcano-tectonic depressions in the floor of the rift (Di Paola, 1972). The Ethiopian Rift is part of the Great East African Rift Valley, which extends from Jordan in the Middle East, through Eastern Africa to Mozambique in Southern Africa dividing the highlands of central Ethiopia. According to

Alemayehu *et al.* (2006) the floor of the Rift valley consists of three major water basins from North East to South West: Awash basin with Koka, Beseka, Gemari, and Abhe; Central Ethiopian Rift Valley with Ziway, Langano, Abijata and Shala and Southern basin with Awassa, Abaya, Chamo and Chew-Bahir as the most important lakes under each category.

The study lake, Lake Ziway, belongs to the Central Ethiopian Rift and is the third largest lake in the Ethiopian part of the Rift Valley and fourth in the country. It lies in a shallow down-felted basin (Gasse & Street, 1978) flanked in the east by a large basalt field with sandy or rocky shores (Schröder, 1984). During the pluvial period lakes Langano, Abijata and Shala were united with Lake Ziway to form a large lake, which had a northern outflow into Awash River (Gasse & Street, 1978), later they got isolated by faulting and other crystal movements (Di Paola, 1972). The maximum limit of this large pluvial lake is indicted to be at 1670 m altitude at its outflow to River Awash (Fig. 2 of Wood and Talling, 1988). Lake Ziway and Langano drain into Lake Abijata which is a terminal lake whereas Lake Shala is no longer connected to the other lakes. During the pluvial periods Lake Abijata and Shala were connected through Digo River (see Fig. 2, Wood and Talling, 1988).

Lake Ziway (7°55'N and 38°43'E) is a turbid freshwater lake situated in the most northern section of the Central Ethiopian Rift Valley. It lies at an altitude of 1636 m above sea level within a broad down-faulted basin formed through local subsidence of the Rift Valley floor to the north, the land rises gently and to the south the landscape is dominated by mount Altu (Makin *et al.*, 1975) that separates Lake Ziway from Lake Langano. There are five main islands in the lake: Gelila, Debre Sina, Tulu Gudo, Tsedecha and Fundro (Fig. 1.1). The lake has a surface area of 442 km², a maximum depth of 7m, an average depth of 2.5 m and a volume of 1,1 km³. According to Schröder (1984) Lake Ziway has a maximum length and width of 32 and 20 km, respectively. The lake is mainly fed by the two rivers from the highlands Meki North West and Katar North East and drains into Lake Abijata through Bulbula River in the south (Fig. 1.1). The latter usually falls dry during the dry season.

The lake region is characterized by a semiarid to sub-humid climate with mean annual precipitation and mean annual temperature varying between 650 mm and 25°C close to the lake and 1200 mm and 15°C on the humid plateau escarpment, respectively (Legesse *et al.*, 2004). The rainfall pattern is largely influenced by the annual oscillation of the inter-tropical convergence zone, which results in warm, wet summers (with most of the rainfall occurring from June to September) and dry, cold and windy winters. There is also a short wet period

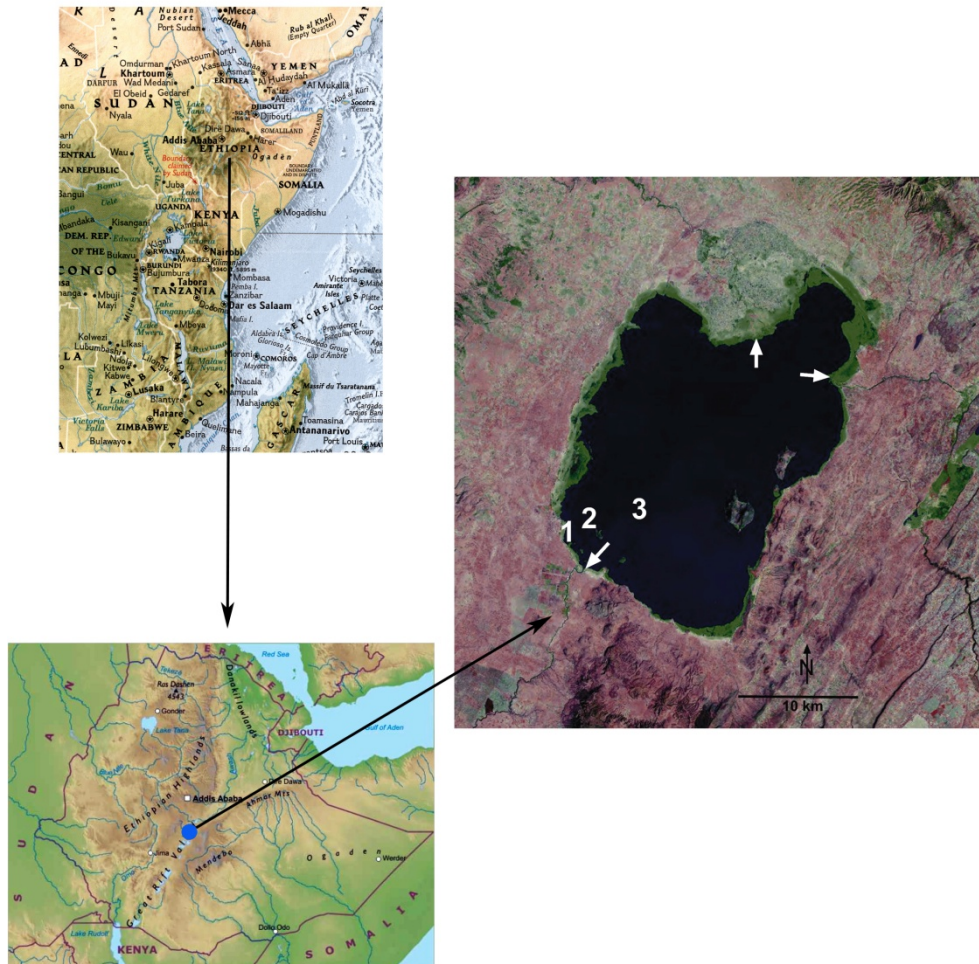


Fig.1.1. Location of Ethiopia in Africa, study lake (blue circle) in the Rift Valley and Lake Ziway; numbers showing sampling stations and white arrows indicate positions of inflowing rivers in the north (Meki, Katar), and outflowing River Bulbula in the south.

originating from moist south-easterly winds between March and May. However, the Lake region in general is arid and even during the wet seasons dry periods of several weeks are common. Since 2002 meteorological data from National Meteorological Agency- Awassa branch from Lake Ziway station show most rainfall between June and September with a monthly mean total of 105,2 mm and a maximum of 160 mm in July. During the study period (October 2008 to September 2009) a maximum total rainfall of 187,4 mm in July and 82 mm in August were recorded (Fig. 1.2); in the dry period October- January precipitation was higher than the earlier years. The water temperature at 0,5 m depth in the open water zone ranged between 19,2 °C in December and 25,8 °C in March. The overall mean for the sampling period was 23 °C (Table 1.1).

The weather in the lake region is frequently windy to stormy (Schröder, 1984). Due to the large surface area relative to the shallow depth and highly exposed to wind, slight wind can cause complete mixing of the lake. Strong wind-induced water currents, especially in the afternoon is a common phenomenon in Lake Ziway, which is also indicated in Wood *et al.* (1978) who found no strong thermal stratification in the lake. The lake is highly turbid, with a secchi depth of less than 30 cm due to resuspended sediment particles and algae. The water budget of Lake Ziway is regulated by superficial inflows and outflow, evaporation and precipitation mainly from the distant uplands as the precipitation in the lake area is inadequate to maintain the lake level. The major inflowing rivers are Ketar and Meki and an outflowing Bulbula River in the south (Fig. 1.1). The Meki River discharges the runoff from the plateau west of Lake Ziway where as Ketar River discharges the water from the eastern and southeastern plateaus. According to Legesse *et al.* (2004) the catchments of these two rivers cover 5610 km². An earlier report indicates that Lake Ziway receives 0,42 and 0,44 km³ via Rivers Katar and Meki, respectively, and losses through Bulbula River are about 0,21 km³ and additional loss through evaporation of 0,2 km³yr⁻¹ in 100km² lake area (Wood and Talling, 1988). However, a more recent estimate indicated much reduced inflows from those rivers into Lake Ziway. According to Ayenew (2004) the annual inflows from Meki and Ketar rivers into Lake Ziway are 264,5 and 392 million m³, respectively. He also indicated that the inflow into the lake has an annual deficit of 74 million cubic meters over the overall water loss from the lake. An increasing water demand and uncontrolled water abstractions from the inflowing rivers as well as lake water for irrigation, outflow through River Bulbula, domestic use (drinking water supply to Ziway town, watering cattle) and loss through evaporation from the

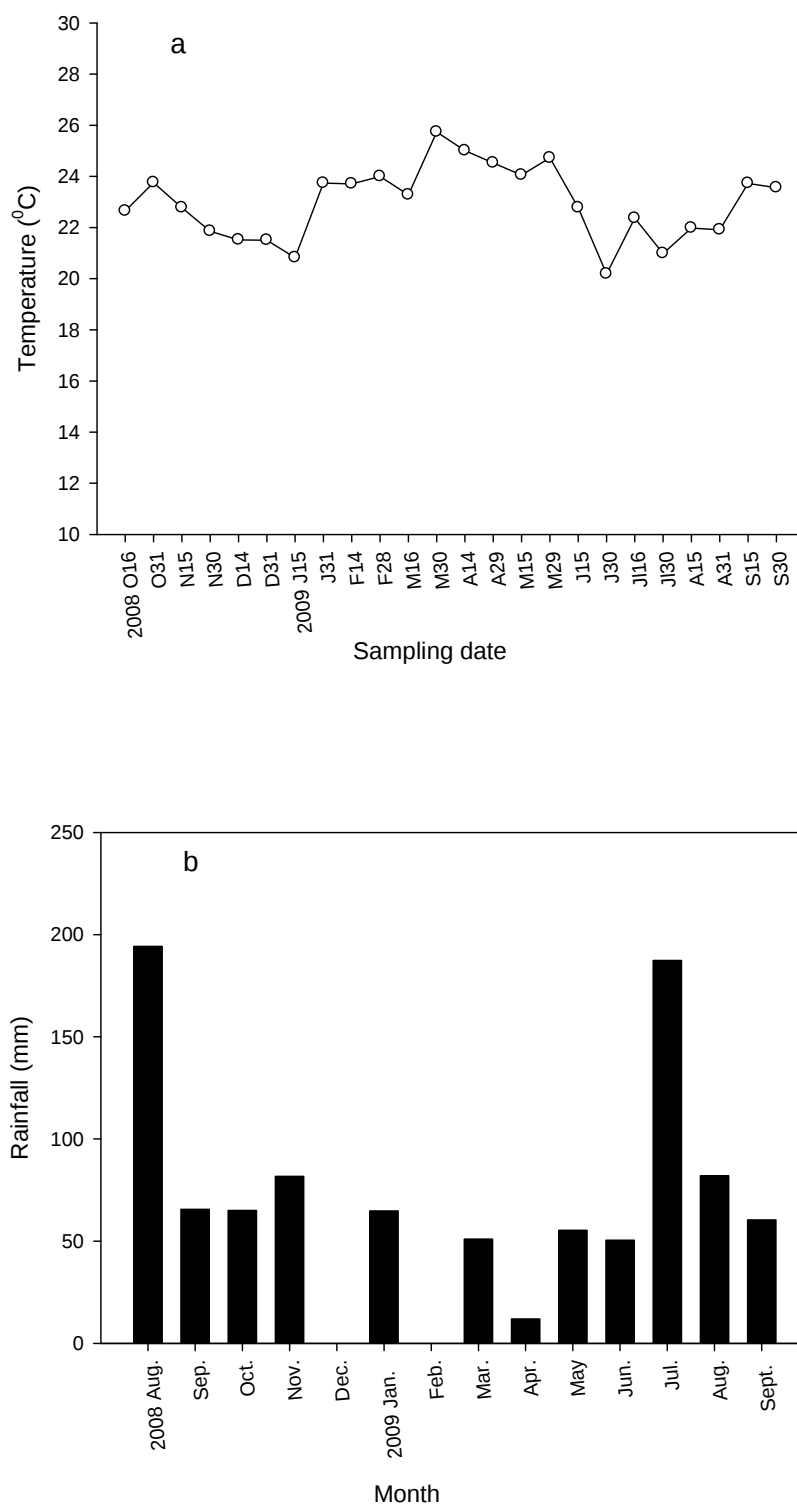


Fig.1.2. Mean water temperature (a) and total monthly rainfall (b) from Ziway station.

Table 1.1. Morphometric attributes, physical and chemical features of Lake Ziway during the study period (October 2008 to September 2009). Measurements from this study are indicated in bold. Other sources: * UNEP, 2006, ** Zinabu *et al.*, 2002, others reproduced from Kebede *et al.* (1994)

Latitude	7° 55'N	Na ⁺ (meq l ⁻¹)	2,87
Longitude	38° 43'E	Ca ²⁺ (meq l ⁻¹)	0,56
Altitude a.m.s.l (m)	1636	Mg ²⁺ (meq l ⁻¹)	0,64
Catchment area (km ²)	7025	HCO ₃ ⁻ + CO ₃ ²⁻ (meq l ⁻¹)	4,0
Area (km ²)	442	Cl ⁻ (meq l ⁻¹)	0,32
Max. depth (m)	7	SO ₄ ²⁻ (mg l ⁻¹)	0,32
Mean depth (m)	2,5	NO ₃ ⁺ + NO ₂ -N (µg l ⁻¹)	3,9
Volume (km ³)	1,1*	NH ₄ ⁺ -N (µg l ⁻¹)	36,3
Turbidity (FTU)	80,2	SiO ₂ (mg l ⁻¹)	37,0
Secchi depth (m)	0,3	TP (µg l ⁻¹)	219,0
pH	8,7	SRP (µg l ⁻¹)	34,4**
Conductivity (µS cm⁻¹)	425,4		
Water temperature (°C)	23,0		
Chlorophyll-a (µg l⁻¹)	23,4		
Salinity (g l ⁻¹)	0,4		
Dissolved oxygen (mg l⁻¹)	7,1		

lake and evapotranspiration from the extensive vegetation which are a greater portion of the littoral part are the major cause for the reduction.

During the study period the highest precipitation was recorded in July which lasted only for short period. Shore level fluctuations, receding in hundreds and even more meters in the fish landing sites were observed. The shore level of Lake Ziway receded 100 m from the level at the beginning of this study which had not recovered even after the main rainy season. It affected the water levels of most water bodies in the Rift Valley. The most pronounced evidence was from Lake Koka, a large reservoir built by damming River Awash for hydropower plant that receded hundreds of meters from the level it experienced before. It was in September at the end of the main rainy season that the lakes gained part of their water levels from surface run-off and rivers inflows which had high precipitation in the headwaters.

Increasing population pressure and economic developments put an increasing pressure on the precious freshwater resources in the semi-arid Rift Valley area. Although the lake's presence in such water stressed area has immense role in ameliorating the effects of drought and protein shortage and its macrophytes to the lake's life serving as a breeding and a refuge site for the commercially important fish species, sink for the increasing pollutants from agricultural fertilizers, pesticides and domestic wastes of the growing Ziway town, fodder for livestock around the lake where the lake shore is the only green area for the majority of the year, management of the lake is still far off being effective. Efforts are going on both by the government and non-governmental organizations, but its implementation is not as forthcoming as desired.

Irrigated agriculture is a common practice around Lake Ziway, by pumping water from the lake and from the rivers that flow into the lake. Previously water abstraction from Lake Ziway was mainly by state farms, cooperatives and/or individuals. The intermittent rainfall in the lake region and the increasing population with increasing demand for water use undoubtedly increase the pressure on the lake. Recently there are different agricultural activities in the vicinity of the lake shore going on which solely depend on irrigation by lake water abstraction with higher efficiencies than before. The blooming floriculture in Ethiopia mainly in the Rift Valley area is also a major concern to the lakes in the area. The previous irrigated state farm near the shore of Lake Ziway is currently running a large scale horticulture and floriculture greenhouse complex (currently 35 greenhouses with an area of 315-420 ha) by a private firm.

About 15000 active workers from the region and around are involved in the farm and will be additional feature treat to the lake together with the growing population of Ziway town where the waste treatment is not growing likewise. However, this rapid expansion which will increase the stress on the water resources as it abstracts lake water directly and with high risk of polluting the lake waters with nutrients, pesticides and biocides from the effluents released back directly into the lake is still unknown.

The physico-chemical and biological features of the lake are documented by various papers. The salinity of the lake shows little variation over a long time period compared to other nearby Rift Valley lakes (Zinabu *et al.*, 2002). Mean conductivity and pH of the lake during the study period were $425 \mu\text{Scm}^{-1}$ and 8,7 respectively; these values are in the order of magnitude of the values recorded about four decades ago in Talling & Talling (1965). An increase in the conductivity in the present study might be explained by the concentration of ions accumulated from the river inflows and surface runoff from the agricultural areas around

the lake. However, the macrophyte belt around the lake shore might either utilize or retain much of the nutrients. An increase in the concentration of solutes in the nearby lakes (e.g. Langano 6 times and Abijata 60 times over Lake Ziway) is reported by Wood and Talling (1988).

Lake Ziway is quite unique in its macrophyte coverage compared to the nearby Rift Valley lakes. It has an extensive area of littoral vegetation including emergent, sub-merged and floating plants. The shoreline of Lake Ziway (nearly 100%) has a ring of emergent vegetation which is dominated by reeds. A pronounced reed belt is found in the northern part of the lake where the two rivers join the lake. Both the shallowness and the freshwater of the lake might favour the vegetation which is not the case in the other nearby lakes which are saline and/or deeper. According to Martens and Tudorancea (1991) the most common emergent macrophytes in Lake Ziway are *Phragmites* sp., *Typha angustifolia*, *Scirpus* sp., *Cyperus papyrus* and *Paspalidium geminatum*. The common submerged and floating plants are *Potamogeton* sp. and the water lily *Nymphaea coerulea*. Nevertheless, this extended macrophyte cover is endangered around the lake. Agricultural activities are common up to the shore and even when the shore level recedes during the dry season the macrophytes are burnt. Lake Ziway has a reasonable number of *Hippopotamus* commonly seen in and/or near the macrophytes which graze in the littoral in the evening and could be additional nutrient source as they defecate in the lake. Different bird species are also inhabitants of the lake.

Benthic ostracod species of Lake Ziway are described by Martens and Tudorancea (1991). Six ostracod species of which *Limnocythere thomasi thomasi* Martens (subspecies endemic to Lake Ziway) and *Gomphocythere angulata* Lowndes (common within the East African range) were reported. The authors indicate that the species densities were significantly reduced during the short and main rains, a fact they could not explain. In the present study most species reached their lowest density during the main rain when the turbidity was generally high. The benthic community of Lake Ziway in general is reported by Tudorancea and Taylor (Tudorancea and Taylor, 2002 Table 6.1).

No typical zooplanktivorous fish is present in Lake Ziway. According to Golubistov *et al.* (2002) Lake Ziway has eleven fish species of which *Oreochromis niloticus*, *Tilapia zilli*, *Clarias gariepinus* and *Barbus intermidus* are commercially important. Two endemic fish species, *Barbus ethiopicus* and *Garra makinsis* are also reported from the lake (Golubtsov *et al.*, 2002). Lake Ziway had a high fish yield of 3000 to 6680 tons per year (FAO, 1982). A sign of overexploitation with the reduction in the average size of catch was reported after the introduction of improved fishing technologies by EU funded Lake Fisheries Development Project (LFDP, 1998). According to Yared (2003) there is a continuous decline in the annual catches of *Tilapia* from Lake Ziway since 1997, but on the other hand an increase of the *Clarias gariepinus* population which was also observed from the fishermen catches during the study period.

Chapter 2

Zooplankton community structure, abundance and biomass and their relation to abiotic and biotic factors

Introduction

Long term quantitative plankton studies from tropical water bodies on the basis of short sampling intervals are still scarce. Studies so far indicated that in deep, stratified lakes high abundance of zooplankton coincided with the mixing cycle and hence redistribution of nutrients and subsequent phytoplankton growth (Mengestou and Fernando, 1991a; Irvine and Waya, 1999; Isumbisho *et al.*, 2006). However, in shallow turbid lakes lacking stratification fluctuations in zooplankton population are related to complex processes mediated by interactions between abiotic and biotic factors. In most shallow tropical lakes turbidity and water level fluctuations associated with seasonal rainfall affect composition and distribution of zooplankton (Kalk, 1979; Saint-Jean, 1983; Hart, 1986, 1996; Dejen *et al.*, 2004). It has been indicated that sediment carried in suspension influences complex biotic food web interactions and affect the community structure (Threlked, 1986). In turbid waters, the fluctuation in zooplankton standing stock is due to subsequent depression of the phytoplankton by light limitation (e.g. Allanson *et al.*, 1990). An increase in turbidity has been seen to influence zooplankton species composition and abundance (Hart, 1988) and is related to the variation in the response of species to the resource depression which is also evident in this study. Cladocerans correlate best with water transparency and rotifers do weakly. Copepods however are not correlated. In cladocerans, experimental studies also showed the decline in *Daphnia* filtering rates with rising suspended sediment concentrations (Arruda *et al.*, 1983; Hart, 1988; Levine *et al.*, 2005) and Kirk (1991) even indicated the detrimental effects of suspended particles in *Daphnia* filtering.

Fluctuations in the species composition are the result of the changes and/or variations in their environment. In temperate lakes, temperature and light are important abiotic factors with marked seasonal variation being reflected in the chemical and biological components of the water bodies. Presence of higher stability in tropical plankton population has been indicated in earlier studies due to the presence of high temperature and light throughout the year which allow primary production to occur on a high level all year round (Talling, 1965; Lewis, 1974). The absence of marked variation in the water temperature of tropical lakes favours

zooplankton to continuously grow and reproduce (Hart, 1981) and hence little variation in production, biomass and species composition is found in tropical zooplankton (Burgis, 1971). However, many studies from tropical lakes documented the presence of variations in tropical zooplankton (e.g. Lakes: Chilwa, Kalk, 1979; Naivasha, Mavuti and Littrick, 1981; Valencia, Infante, 1982; Abijata and Langano, Wodajo and Belay, 1984; Valencia, Saunders and Lewis, 1988a,b; Awassa, Mengestou and Fernando, 1991a; Tana, Dejen *et al.*, 2004; Guiers, Kâ *et al.*, 2006; Ziway, Dagne *et al.*, 2008; this study and in larger great African lakes as well in Lakes Tanganyika, Kurki *et al.*, 1999; Malawi, Twombly, 1983; Irvine and Waya, 1999; Kivu, Isumbisho *et al.*, 2006).

In stratified lakes zooplankton vertical distribution could be caused by different interacting factors such as the vertical gradients in the abiotic factors, food availability and predation. Lampert (1993) also indicated the advantages of diel vertical migration by zooplankton in such lakes as the dark hypolimnion is considered as a refuge from visual predators (fish). However, in shallow turbid lakes where water transparency is generally low diel vertical migration is muted. On the other hand the presence of vertical migration of zooplankton in turbid water is also reported (Dodson, 1990). Abiotic factors which have a potential to structure the vertical distribution of zooplankton in deep lakes were not so in the horizontal gradients in shallow lakes (e.g. Burks *et al.*, 2002). Instead structural complexity in the littoral (dense macrophytes) common in most shallow lakes has strong influence on zooplankton distribution along horizontal gradients. Although macrophytes are used as a refuge for zooplankton and juvenile fish from their predators (Timmes and Moss, 1984; Lauridsen and Buenk, 1996), there is also a possibility of predation within the macrophytes (see the review by Burks *et al.*, 2002). According to Schriver *et al.*, (1995) at high fish densities even dense macrophyte stands cannot prevent *Daphnia* population from a predation driven collapse.

Besides the abiotic factors, biological factors such as quantity and quality of food (Lewis, 1979) and predation by fish and invertebrates are also shown to affect zooplankton populations. Blooms of blue green algae such as *Microcystis aeruginosa* are a wide phenomenon in eutrophic lakes and reservoirs (Oh *et al.*, 2000; Haande *et al.*, 2007). As there is a scarcity of large cladocerans (*Daphnia*) and calanoids in shallow tropical freshwater ecosystems (Lewis, 1979; Fernando, 1980) the main zooplankton grazers are small cladocerans and rotifers (Aka *et al.*, 2000; Fernando, 2002; this study). In such water bodies, the small size of the dominant zooplankton and their grazing inefficiency on large particles may explain the dominance of blue greens (Lazzaro, 1997). In addition to the quantity, the

phytoplankton composition in the lake has also a considerable impact on the annual variations of zooplankton species composition and abundance. The presence of filamentous blue-greens has been reported to exert greater negative influence on zooplankton (Infante and Riehl, 1984; Gliwicz, 1980). Many species disappeared as a result of algal toxins or the clogging of filter feeding apparatus during algal blooms (e.g. Infante, 1982).

Long ago predation by fish (Brooks and Dodson, 1965) and invertebrate predators (Lewis 1977; Zaret, 1980; Hare and Carter, 1987) has been recognized to structure zooplankton communities. There are planktivorous fishes in tropical lakes (e.g. *Limnothrissa miodon* and *Stolothrissa tanganyikae* in Lake Tanganyika (Coulter, 1981), *Alestes baremoze* in Lake Chad (Gras and Saint-Jean, 1983) and also introduced into other water bodies like in Lake Kivu which have an impact on composition and biomass of zooplankton (Isumbisho *et al.*, 2006). Post-larval and juvenile fishes (Tudorancea *et al.*, 1988), different groups of young fishes (Robotham, 1990), *Tilapia* and omnivorous common carp (Chapman and Fernando, 1994) have zooplankton as an important component of their diet. Due to continuous breeding nature of *Tilapia* species in the tropics (Admassu, 1996), juveniles will have an impact on the population of zooplankton. Zooplanktivory by the larvae of dipteran genus *Chaoborus* is the other important factor to structure zooplankton communities in tropical lakes (Lewis, 1977; Irvin, 1997). *Chaoborus* can coexist with fish because it undergoes diel vertical migration (Dawidowicz *et al.*, 1990). According to Irvine (1997) *Chaoborus* instars can prey on different zooplankton body sizes in Lake Malawi where higher selectivity was shown for the cyclopoid *Mesocyclops aequatorialis*. In an experimental study of *Chaoborus* predation on zooplankton communities in a shallow tropical reservoir, large zooplankton such as cladocerans or copepods and adults of *Mesocyclops* species were significantly reduced in enclosures with *Chaoborus*, nauplii and rotifers on the other hand were not (Pagano *et al.*, 2003).

According to Fernando and Holcik (1988) the higher efficiency in the use of animal food by the newly hatched fish may be the critical factor linking fish yields to zooplankton in tropical freshwaters. Understanding the dynamics of zooplankton and possible regulating mechanisms is hence crucial in managing the water bodies and the resources (e.g. enhancing fishery production and mitigating water quality problems through stocking and/or harvesting zooplanktivorous fish). The seasonal and spatial dynamics of zooplankton in shallow tropical lakes are not well studied when compared with the vast literature in the temperate regions. Several studies on zooplankton dynamics in tropical water bodies are either from monthly

samplings or point sampling of several replications. However, sampling intervals should consider the rapid zooplankton development times and short term environmental changes as well. As indicated by Twombly (1983) monthly sampling is not sufficient to obtain a realistic picture of population dynamics of zooplankton as well as their role in the ecosystem. Annual and seasonal trends may be hidden by short-term irregular changes. Herzig (1983) suggested that two or three samplings a week will be required for most entomostracan crustaceans inhabiting water bodies above 20°C. In the present study, it was not achievable to sample twice a week for one year, rather biweekly sampling was employed. To back up field data and get insights on the population dynamics in the natural habitat, laboratory experiments were conducted and the duration of development times of common crustaceans determined.

In this part of my study the standing stock of zooplankton (numbers as well as biomass) are quantified and the spatial and temporal patterns and compositional changes in zooplankton species in relation to abiotic and biotic parameters discussed.

Material and Methods

Sampling stations

Sampling was done fortnightly from three stations, one inshore and two in the offshore open part of the lake from October 2008 to September 2009. The location at the offshore stations was taken from a GPS navigational unit. The three stations (hereafter referred to as S1, S2 and S3) are in the order from the southwestern shore of the lake to the east, respectively (Fig. 1.1). S1 is for the inshore station one kilometer off the shore within the macrophytes and at a water depth of 1,2 m. S2 and S3 are the offshore stations approximately 5 km off the shore at a depth of 3 m and 10 km off the shore at a depth of 3,5 m, respectively. Sampling depth profiles of the three stations were assigned to be 0,5 m at S1, from 0,5 down to 2,5 m for S2 and S3.

Field sampling and measurement of environmental variables

Quantitative samples were collected using a 10L Schindler sampler from each depth (S1, 0,5 m, S2 & S3 from 0,5 m down to 2,5 m at 0,5 m interval) and plankton nets of 40 and 100 µm mesh size for qualitative samples. Water samples from each depth were filtered through 40

µm plankton gauze and with thorough rinsing the contents retrieved by the mesh gauze were transferred into separate plastic sampling bottles. Water samples for Chlorophyll a determination were taken by the Schindler sampler from the two offshore stations S2 from 0,5, 1 & 2 m water depth and S3 from 0,5 m to 2,5 m every 0,5 m interval. Sampling times at each sampling date were maintained between 09:30 -10:30 am at S3, 10:45- 11:30 am at S2 and between noon and 01:00 pm at S1. In addition to the day samples, vertical distribution of zooplankton was investigated at the open water station from overnight samplings on 4 to 5 July, 2009. Repeated vertical samples (n=10) were taken at hourly intervals and two samples at four hours interval with Schindler sampler (10L) and horizontal tows with 100 µm mesh size plankton net. Sampling started at 17:00 pm and ended at 8:00 am in the next day. Sampling was done at a 0,5 m interval down to 2 m depth. The last sampling depth 2,5 m (which we have in the day sampling) was excluded because of the high turbulence at night which will have a chance to include sediment samples as this would represent bias from the resuspension of particles and dead zooplankton. Repeated night sampling was not performed because of lack of manpower due to the difficulty to sample at night with the facilities at hand.

Physico-chemical variables such as water temperature, water transparency (Secchi depth), turbidity, dissolved oxygen (DO), conductivity and pH were measured at every sampling date and depth with a combined sensor probe (model HQ 40 D Multi HAC Instrument) for 12 months on biweekly basis. At times of high turbulence measurements were done from water samples collected by the Schindler sampler from each depth to avoid biased measurements. Water transparency was measured with a 30 cm diameter black and white secchi disc. Water sample collected from each depth with Schindler sampler was emptied into big plastic container, poured into one liter plastic bottle and transported with ice box to the laboratory for Chlorophyll a and turbidity determination. Turbidity of the lake water was directly determined after every sampling in the laboratory with turbidity meter LP 2000 HANNA instrument calibrated at 0,0 FTU. Integrated plankton samples were collected by towing horizontally and hauling vertically with conical plankton nets of 40 and 100 µm mesh size and 30 cm opening diameter for phytoplankton and zooplankton samples, respectively. After rinsing the sides of the nets, filtered plankton sample plus lake water were transferred into 100 and 250 ml plastic bottles. Zooplankton samples were immediately preserved with formalin (5% final concentration) for subsequent microscopic analysis but phytoplankton samples were investigated live and then preserved with Lugol's solution for further checkup.

Fish diet samples were collected from fish species caught by the commercial fishermen (usually gillnets and long lines seated for overnight) and from live fish caught by beach seining and hooks. Total lengths of the fish were measured to the nearest 0,1 cm before dissecting. Fish stomach contents were collected from the guts of most fish species in the lake such as *Tilapia* (*Oreochromis niloticus* and *Tilapia zillii*), catfish (*Clarias gariepinus*) which are dominant and commercially important, *Carassius carassius* and two abundant but not commercially important small size species *Barbus* and *Gara*. Gut contents were preserved with formalin. Stomach contents of fish species caught live were not preserved since they were identified immediately. Despite repeated effort, attempts to catch juveniles of catfish were not successful.

Routine laboratory activities

Immediately after each sampling usually 300 ml of lake water were filtered through glass micro fiber filters using suction pressure in the laboratory. Because of the high clogging of suspended particles on the filter paper, I divided the 300 ml into two portions. Filtrates on filter papers were kept in a deep freeze for further photo-spectrometric determination of the algal pigment. Filter papers with filtrates were cut in to pieces, added into grinding vessel containing 90% acetone and harmonized using glass road. The glass road and grinding vessel were rinsed with 90% acetone and samples were carefully poured into a 14 ml centrifuge tubes and centrifuged for 10 minutes at 3000 pm. Spectrophotometer absorbance was calibrated at 665 nm wavelength against a blank and centrifuge tubes were gently taken out and poured into the cuvet and absorbance readings of the pigment noted. No corrections were made for the degradation products. Chlorophyll a expressed as $\mu\text{g l}^{-1}$ was estimated according to Talling and Driver (1963).

Plankton species and fish stomachs contents were identified live and from preserved samples under compound and dissecting microscopes at magnifications of x100 and x 4,5 the latter for larger organisms in the fish stomachs. Rotifers from littoral macrophytes (benthic species) were not identified in this study as it was done in Dagne *et al.* (2008). Zooplankters were identified to the species level except nauplii and copepodides which were identified as groups. Most phytoplankton species were identified to the generic level and fish gut contents to groups. Routine zooplankton enumeration spanning for twelve months period was carried out for planktonic crustaceans and rotifers. Concentrated zooplankton samples were rinsed with

distilled water, placed in a small gridded circular petridish which could be rotated under the microscope and counted under dissecting microscope. Total count was performed for the inshore S1 and open water station S3 while 40 to 100% for the second station S2. Although the samples were very turbid and counting was tedious, total count was preferred because of the lower abundance of most cladoceran and larger sized adult copepod species in the samples. Subsampling in such conditions would lead to a tremendous increase in the standard error variation in the final estimate. Thirty three categories of zooplankton were counted routinely. Nauplii and copepodid stages were not counted separately to their respective developmental stages and species but as a combined group. Fish stomach contents which were possible to identify as genus or group levels were counted as an individual irrespective of its preservation state. Those difficult to identify in to any of the groups were grouped with detritus. Counts were expressed as the number of individuals per liter and or per cubic meter. Identifications of the plankton were done using various identification keys, journals and books some of which are: Jose De Paggi (2002); Fernando (2002); Dahms and Fernando (1992); Jeje (1988); Korovchinsky (1992); Koste (1978); Nogrady *et al.* (1995); Segers (1995); Sanoamuang (2002); Defay (1988); Van de Velde (1984); Linnen Von Berg *et al.* (2004).

Dry weight determination and estimation of biomass

Zooplankton samples collected from inshore, offshore and different depth of Lake Ziway both during day and night were used for dry weight determination. Samples were collected by both Schindler trap (10L) and 100 µm mesh size plankton net and were preserved in 5% formalin. To get a representative sample size of each species for the determination of the dry weight, samples from all stations and sampling dates were mixed and rinsed using distilled water to remove preservative. Specimens selected for dry weight measurements were sorted with pipette from the mixed plankton in to homogenous groups as to species, stages, sexes and reproductive stages (ovigerous females) under dissecting microscope and inverted microscope when necessary for smaller stages. Each species and stage group of zooplankton was further sorted into size classes as small, medium and large.

Body lengths of as much as 1130 individuals from *Ceriodaphnia cornuta*, *Moina micrura*, *Mesocyclops aequatorialis*, *Thermocyclops decipiens*, cyclopoid copepodides and nauplii were measured with a calibrated ocular micrometer from the tip of the head to the base of tail spines for cladocerans and from tip of the head to both the base of the furcal rami and base of

caudal spines for copepods. Measurements of copepod body length from the tip of the head to the base of the furcal rami and base of caudal spine were to compare the results with literature data because of the difference in length measurement approach by different researchers (e.g., Burgis, 1974; Culver *et al.*, 1985). Length measurements of all crustaceans and some rotifer species were also done with a stereomicroscope fitted with a calibrated ocular micrometer during the routine counting from each sampling date which was used to calculate the dry weight of the species for the sampling date using length-weight relationship. After length measurement group of individuals, usually 20 for adult stages of *Moina micrura*, *Thermocyclops decipiens*, *Mesocyclops aequatorialis*, 50 individuals for larger *Ceriodaphnia cornuta*, small *Moina micrura*, small *Thermocyclops decipiens* and copepodides and 100 individuals for smaller *C. cornuta* and naupii were grouped per size and transferred into small glass vials and further washed with distilled water for a minimum of half an hour before transferred into a pre-dried hand-made aluminum pans. Weighing pans containing zooplankton were placed in a crucible and then into a drying oven at 100 °C for overnight. In the subsequent day the crucible containing samples were cooled in desiccators and then pans containing dried samples were weighed on a Mettler Toledo XS 205 Dual Range electronic microbalance. Since the balance has an accuracy of 10µg, animals were weighed in batches to get more accurate biomass estimates than weighing of individuals. Dried group weights were then computed by subtracting the dried weights of each aluminum pans from the weight of dried aluminum pans plus specimens on it and then divided by the number of individuals within the group to get dry weight (µg) per individual. Length-weight relationships were then obtained for those species and stages.

Species specific least squares regression were calculated from

$$\ln W = \ln a + b \ln L \quad (2.1)$$

where W is biomass (µg dry wt.) and L is total body length (µm), a is intercept and b is slope of the regression line.

Dry weight estimates of *Daphnia barbata* and *Diaphanosoma excisum* were taken from literature (Dumont *et al.*, 1975 and Gras and Saint-Jean, 1983) because the specimens did not occur in high enough numbers for appropriate weight determination. For fresh weight estimates of rotifer species, I used data from Dagne *et al.* (2008) which were calculated from length measurements and individual volume approximations through the use of geometric formula (Ruttner-Kolisko, 1977). Comparisons of regression results were done with literature

from tropical lakes. Zooplankton species standing biomasses were estimated from mean sizes of species at each sampling date converted into size specific dry weight and multiplied by mean abundance of species for the sampling date. The mean of each sampling date and station were expressed as total biomass of zooplankton per liter or cubic meter. The average biomass estimates in milligram per cubic meter was multiplied by the average depth of the lake to convert in to areal estimates for comparisons.

Data analysis

Zooplankton counts showed large variances, therefore, zooplankton count data were log transferred to satisfy the premises of homogeneity of variances and normality of the analysis. Descriptive statistics like standard deviation and coefficient of variation were used to describe the variance around means of zooplankton counts. One-way ANOVA was applied to check the variation in zooplankton counts among the stations and sampling dates. There was no significant difference in the zooplankton counts in the two open water stations (S2 and S3). Therefore, I combined the two and used the average. All comparisons and discussions are based on the results of inshore and offshore stations. To check the presence of variation in zooplankton density between dry and wet season an analysis of variance (ANOVA) was applied. Linear regression was used to estimate the weight of crustaceans using length measurement which were then used to compute species specific biomass for each sampling date. To assess which abiotic and biotic variables were the most important determinants of zooplankton community structure, correlation coefficients for non-zero estimates of zooplankton abundance with selected variables were checked. In all cases Stat View and Sigma Plot version 10 computer software were used for the analysis.

Results

Physico-chemical conditions

The spatio-temporal variation in water temperature is presented in Fig. 2.1. Water temperature varied between 19,3 °C to 24, 2 °C in the offshore station and raised up to 27,3 °C at the inshore station. The lowest temperature occurred during the cold dry period end of November to January. The variation in water temperature along the water column was generally low, the difference between the upper 0,5 m and bottom 2,5 m was only less than 1 °C during daytime. According to the rainfall data from the National Meteorological Agency- Awassa branch, monthly mean total rainfall around Lake Ziway varied between 62 to 65 mm with a progressive decline since 2006. The record during the study period was about 59 mm. Despite with such low rainfall even during the rainy season together with high water output through evaporation, outflow and water abstractions for different purposes, the lake level is maintained by the inflows through two rivers which received their water from the distant highlands. The rainfall during the study period was different than the year before which started late in the rainy season and ended shortly with a recorded rainfall of 82 mm in August which is usually the peak rainy season and is about 2,5 time less than the previous year record.

Lake Ziway was very turbid throughout the study period with a single peak during the rainy season. Turbidity measurements varied between 49,4 and 299 FTU (mean 80,2; n = 81, Fig. 2.2a). The turbidity during the dry period was nearly uniform and started to progressively increase from March till it sharply increased to its maximum end of July which was about 8 times greater than the minimum turbidity measured in mid April and was the result of high rainfall which brought sediment- laden waters from the surface runoff and rivers. Two phases of water transparency (secchi depth) were observed during the study period. An increase in the water transparency from around 23 cm secchi depth in the beginning of the study until it doubles to its peak in mid April and then continuously declined to as low as less than 15 cm in July following the rainfall (Fig. 2.2b). The mean for the study period was 29,3 cm.

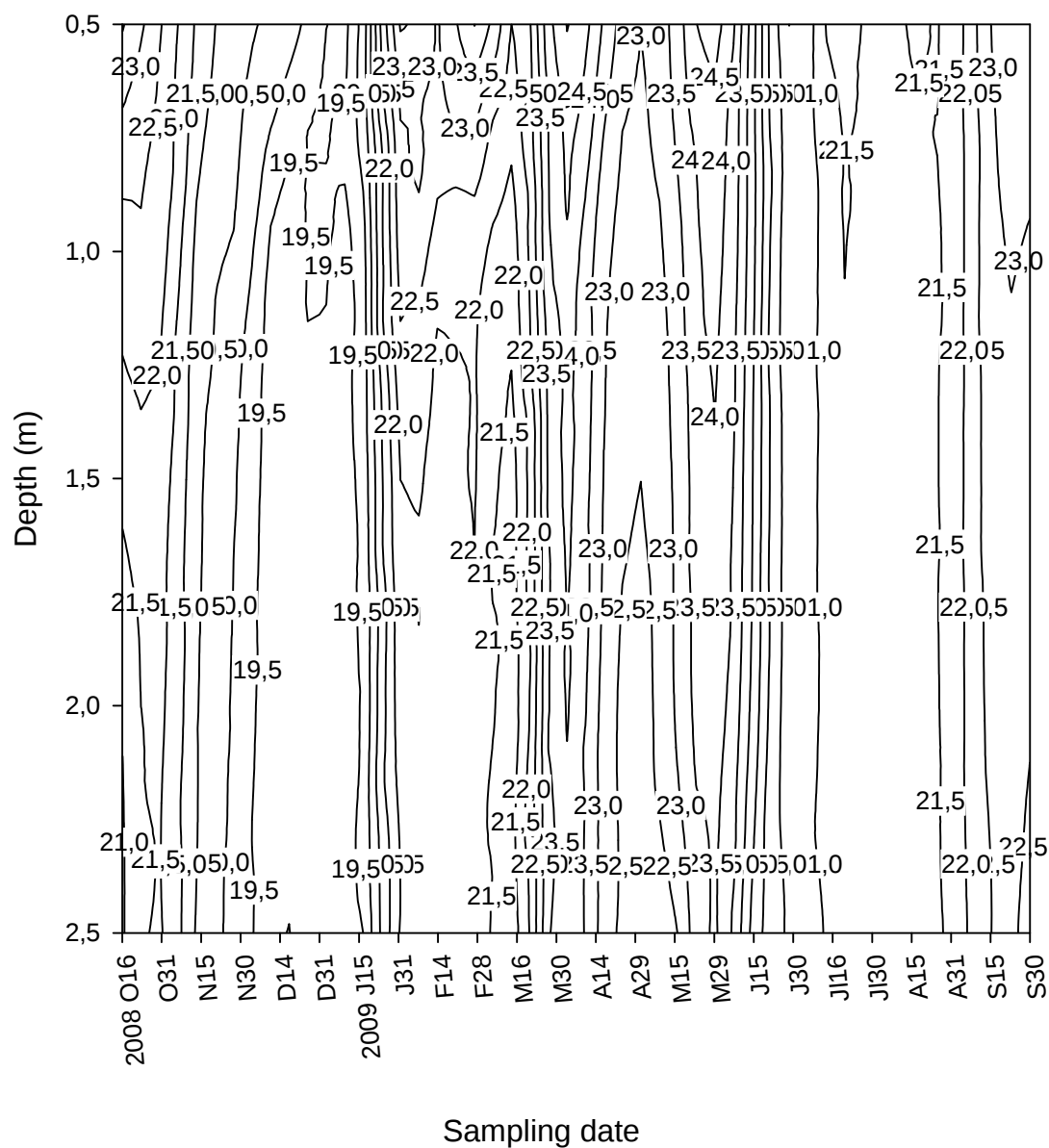


Fig. 2.1. Depth-time diagram with contours of water temperature ($^{\circ}\text{C}$) at offshore station of Lake Ziway.

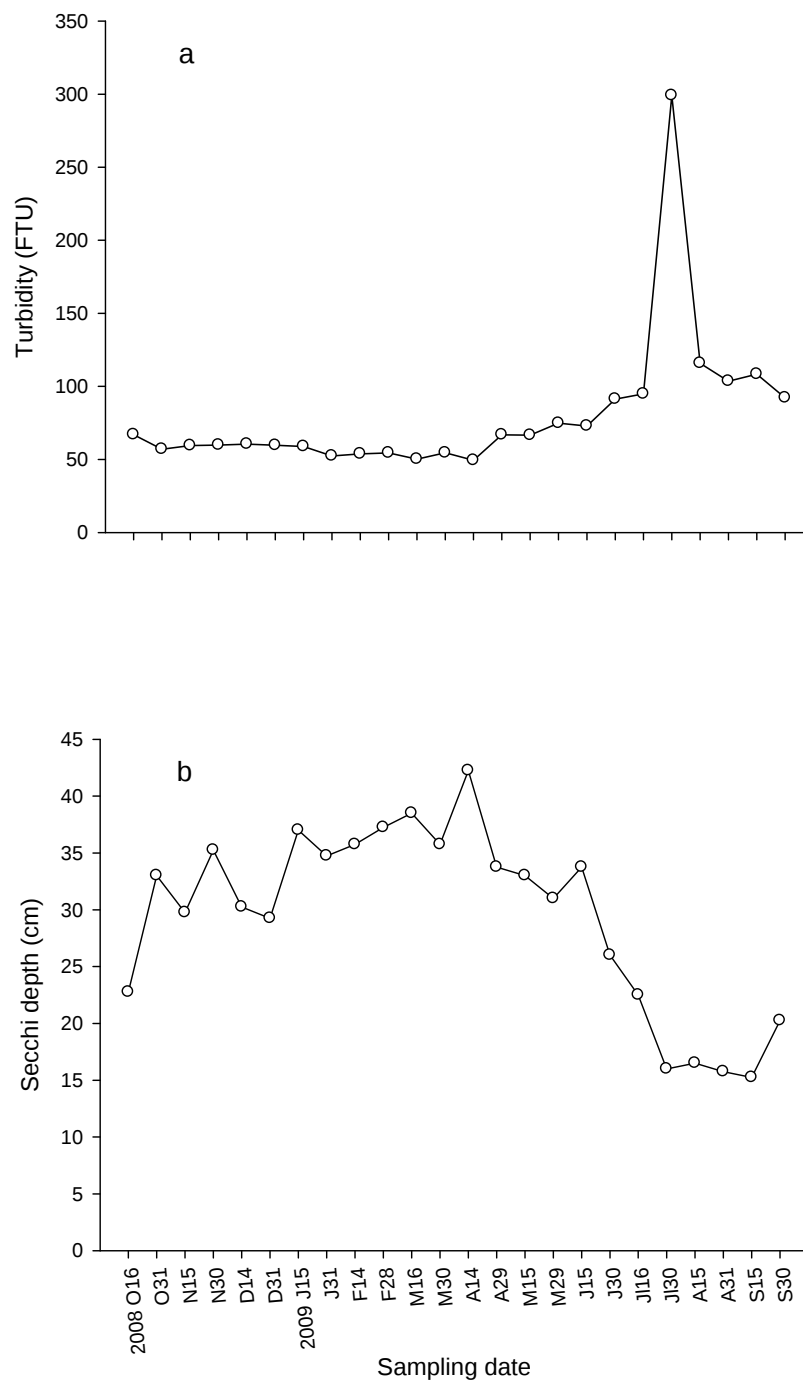


Fig. 2.2. Turbidity (a) and secchi depth (b) (Oct. 2008 – Sept. 2009).

The pH was rather constant throughout the sampling period with an overall lake mean of 8, 7 (Fig. 2.3a). Conductivity varied between 389-458 μScm^{-1} with an average for the study period of 425 μScm^{-1} . Conductivity increased progressively between December to March, fluctuated till June and declined during the rainy season (Fig. 2.3b).

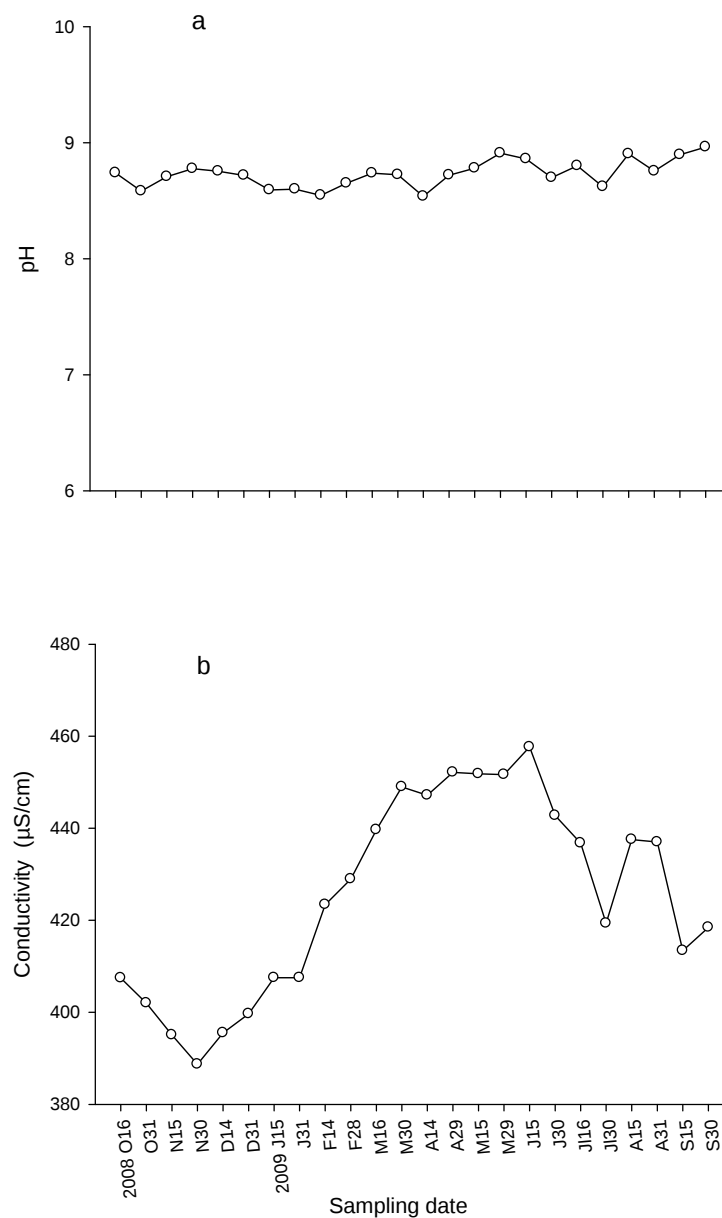


Fig. 2.3. pH (a) and conductivity (b) (Oct. 2008 – Sept. 2009).

Dissolved oxygen (DO) was in the range of 6,9 to 8,2 mg l^{-1} at the offshore station and 3,2 to 8,4 mg l^{-1} in the inshore station. The overall lake mean was 7,1 mg l^{-1} (Table 2.1). The lowest values from both stations were recorded during the rainy season in July. The spatial variation in the dissolved oxygen was higher between the inshore and offshore stations than within the vertical depth profile of the open water station (Figs 2.4; 2.5). Depth profile in the offshore station showed nearly uniform concentrations of dissolved oxygen in the water column (Fig. 2.5). The dissolved oxygen concentrations in the water column at the offshore station during the night varied between 8 to 9 mg l^{-1} .

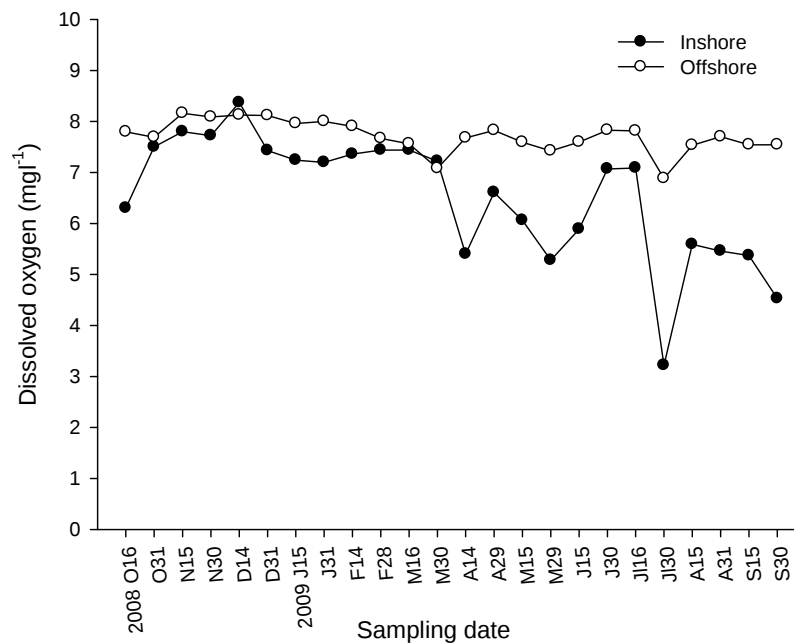


Fig. 2.4. Dissolved oxygen concentration inshore and offshore (Oct. 2008 – Sept. 2009).

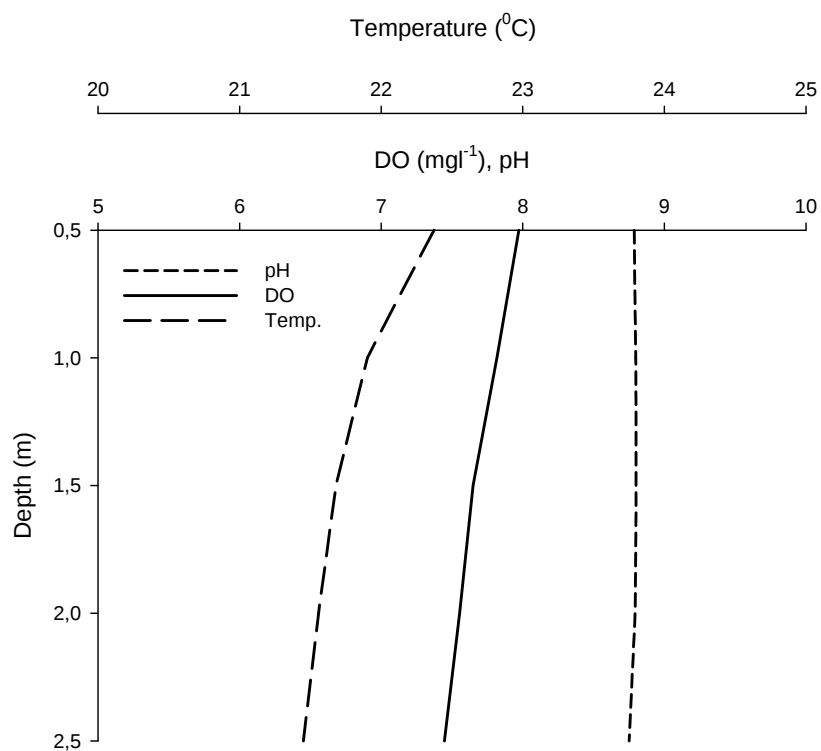


Fig. 2.5. Depth profile of average, temperature, dissolved oxygen and pH.

Table 2.1. Mean $\pm$ SD., range and sample size (n) of physico-chemical variables and Chlorophyll a in Lake Ziway (October 2008 to September 2009)

Variables	Units	Mean $\pm$ SD.	Range	n
Water temperature:				
Inshore 0,5m depth	$^{\circ}\text{C}$	24,1 $\pm$ 1,8	19,8-27,3	24
Offshore 0,5m depth	$^{\circ}\text{C}$	22,4 $\pm$ 1,6	19,2-25,8	48
2,5m depth	$^{\circ}\text{C}$	21,5 $\pm$ 1,3	18,9-24,1	48
Over all lake water	$^{\circ}\text{C}$	23 $\pm$ 1,4	20,2-25,7	256
Rainfall:				
Dry period	mm	30,5 $\pm$ 30	0-65	6
Wet period	mm	85 $\pm$ 51	51-187,4	6
Turbidity (offshore)	FTU	80,2 $\pm$ 50,6	49,4-299	81
Secchi depth	cm	29,4 $\pm$ 0,1	15,3- 42,3	72
pH		8,7 $\pm$ 0,1	8,5-9	245
Conductivity:	μScm^{-1}	425 $\pm$ 22	389-458	245
Dissolved oxygen (DO):				
Inshore -0,5m depth	mg l^{-1}	6,5 $\pm$ 1,2	3,2-8,4	23
Offshore -0,5m depth	mg l^{-1}	8 $\pm$ 0,4	6,8-8,8	46
-2,5m depth	mg l^{-1}	7,5 $\pm$ 0,4	6,4-8,2	46
Over all lake water	mg l^{-1}	7,1 $\pm$ 0,7	5,1-8,2	245
Chlorophyll a (offshore)	$\mu\text{g l}^{-1}$	23,4 $\pm$ 13,1	6,8-58,4	190

Phytoplankton

Phytoplankton of Lake Ziway consists of diatoms, green algae and blue-green algae. A total of 42 phytoplankton genera were identified during the study period, of which 16 were diatoms, 13 green algae and 9 blue green algae and four other genera (*Peridinium* sp., *Euglena* sp., *Lepocinclis* sp. and *Phacus* sp.) were also identified (Table 2.2). Most phytoplankton species were present in all stations except some diatoms occurred mainly inshore. More phytoplankton genera were more frequent in the inshore station than offshore, i.e. especially diatoms with 10 genera inshore and 6 in offshore. The frequency of occurrence among genera varied from zero (absence) to 100% (presence during the entire 24 sampling cruises) the latter being the dominant *Microsystis* and commonly occurring *Pediastrum*. The numbers of phytoplankton genera present (in 25-100% of sampling periods), their absence and dominance when present during sampling is presented in Table 2.3. *Microsystis* species were dominant throughout the sampling periods in all stations. *Synedra* and *Fragilaria* were co-dominant with *Microcystis* during the dry periods. Most phytoplankton genera were common in the short wet periods which also contributed for the peak Chlorophyll a concentration. *Anabaena* and *Oscillatoria* were co-dominant with *Microcystis* throughout the rainy season.

Table 2.2. Phytoplankton taxa identified from Lake Ziway

Green algae	Blue-greens	Diatoms	Others
<i>Botryococcus</i> sp.	<i>Anabaena</i> sp.*	<i>Asterionella</i> sp.	<i>Peridinium</i> sp.
<i>Closterium</i> sp .	<i>Chroococcus</i> sp.	<i>Aulacoseira</i> sp.	<i>Euglena</i> sp.
<i>Coelastrum</i> sp.	<i>Gloeocapsa</i> sp.	<i>Cyclotella</i> sp.	<i>Lepocinclis</i> sp.
<i>Cosmarium</i> sp.	<i>Lyngbya</i> sp.	<i>Cymatopleura</i> sp.	<i>Phacus</i> sp.
<i>Dictyosphaerium</i> sp.	<i>Merismopedia</i> sp.	<i>Cymbella</i> sp.	
<i>Kirchneriella</i> sp.	<i>Microcystis</i> sp.*	<i>Diatoma</i> sp.	
<i>Micractinium</i> sp.	<i>Oscillatoria</i> sp.*	<i>Epithemia</i> sp.	
<i>Mougeotia</i> sp.	<i>Pseudoanabaena</i> sp.	<i>Fragilaria</i> sp.*	
<i>Pediastrum boryanum</i>	<i>Spirulina</i> sp.	<i>Gyrosigma</i> sp.	
<i>Pediastrum duplex</i>		<i>Melosira</i> sp.	
<i>Pediastrum simple</i>		<i>Navicula</i> sp.	
<i>Pediastrum</i> sp.		<i>Nitzschia</i> sp.	
<i>Scenedesmus</i> sp.		<i>Pinnularia</i> sp.	
<i>Spirogyra</i> sp.		<i>Stauroneis</i> sp.	
<i>Staurastrum</i> sp.		<i>Surirella</i> sp.	
<i>Zygnema</i> sp.		<i>Synedra</i> sp.*	

*Dominant species

Table 2.3. Percentage occurrence of phytoplankton taxa in each station; months of dominance are indicated (D); genera that occurred in $\geq 25\%$ of the sampling dates (n=24)

Taxa	Stations					
	S1		S2		S3	
	%	D	%	D	%	D
<i>Synedra</i> sp.	87,5	J-M	79,2	F-J	100	Jun-May
<i>Fragilaria</i> sp.	75	N-J	75	N-M	79,2	D-J
<i>Cymbella</i> sp.	66,7					
<i>Navicula</i> sp.	58,3					
<i>Nitzschia</i> sp.	54,2		54,2		62,5	
<i>Melosira</i> sp.	54,2		95,8		91,7	
<i>Surirella</i> sp.	45,8				37,5	
<i>Gyrosigma</i> sp.	29,2					
<i>Stauroneis</i> sp.	29,2					
<i>Pinnularia</i> sp.	25		41,7		45,8	
<i>Pediastrum</i> sp.	95,8		87,5		100,0	
<i>Scenedesmus</i> sp.	70,8		41,7		87,5	
<i>Closterium</i> sp.	62,5		91,7		91,7	
<i>Cosmarium</i> sp.	50					
<i>Spirogyra</i> sp.	29,2		41,7		50,0	
<i>Staurostrum</i> sp.	29,2		29,2		37,5	
<i>Botryococcus</i> sp.			33,3		41,7	
<i>Kirchneriella</i> sp.						
<i>Microcystis</i> sp.	87,5	except O & May	100	throughout	100	throughout
<i>Anabaena</i> sp.	50	since Jun	83	since Jun	75	since Jun
<i>Oscillatoria</i> sp.	25	since Jun				
<i>Spirulina</i> sp.					50	
<i>Euglena</i> sp.	54,2				75	
<i>Phacus</i> sp.	41,7					

Letters: O-October, N-November, D-December, J-January, M-March, since Jun- from June to end of the study

Chlorophyll a (Chl-a) concentration reached its maximum during the short wet period in June, but during the main rainy period a sharp decline was observed (Fig. 2.6). Temporal variation in Chl-a concentration was high and ranged between 6,8-58,4 $\mu\text{g l}^{-1}$. The lowest Chl-a record coincided with the relatively lower water temperature during the cold dry period of December-January and with the highest turbidity and hence lowest water transparency in July. No trend was found in Chl-a concentration along the water column, it was common to measure maximum concentrations, even in the dark, at the lower part of the water column.

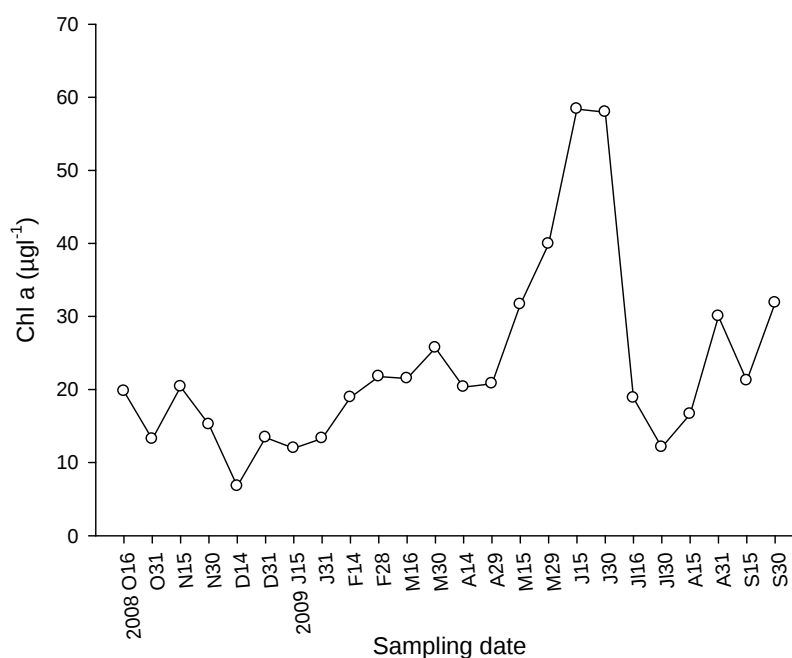


Fig. 2.6. Seasonal variation of Chlorophyll a concentration.

Zooplankton

59 species comprised the zooplankton in Lake Ziway: 49 rotifers, 7 cladocerans and 3 cyclopoid copepods (Table 2.4). The highest species richness occurred in rotifers and they also contributed 43 % of the total zooplankton abundance (Fig. 2.7). *Brachionus* and *Keratella* species were the dominant and major contributor of the total rotifers abundance. Of the 21 rotifer species routinely counted, *Brachionus angularis*, *Brachionus caudatus*, *Keratella tropica* and *Filinia novaezealandiae* comprised 70% of the total rotifer abundance (Fig. 2.8). Cladocerans comprised only less than 5% and cyclopoid copepods 53% of the total zooplankton (Fig. 2.7).

Seven species of cladocerans were identified: *Moina micrura*, *Diaphanosoma excisum*, *Alona* sp., *Ceriodaphnia cornuta*, *Daphnia barbata*, *Diaphanosoma mongolianum* and *Pseudosida szalayii*. *Pseudosida szalayii* is the first record from the lake. *Moina micrura* was the dominant species representing 49% of the Cladocera. *Diaphanosoma excisum* and *Alona* species commonly occurred. *Ceriodaphnia cornuta* which was observed during more than half of the sampling period contributed 19% to the total cladocerans abundance; it was absent from June onwards. *Daphnia barbata* was very rare, lower than an individual per liter and progressively declined till it finally disappeared after February. *Diaphanosoma mongolianum* and *Pseudosida szalayii* were very rare and were not counted. Copepods were represented by three cyclopoid species: *Thermocyclops decipiens*, *Mesocyclops aequatorialis* and *Afroscyclops gibsoni*. *Afroscyclops gibsoni* was very rare, *T. decipiens* dominated among the adult copepods at all stations throughout the sampling period and *Mesocyclops aequatorialis* commonly occurred (Fig. 2.9). Species identified from the open water were also present in the inshore station and vice versa. Because of frequent and high turbulences, a common feature in Lake Ziway, even the littoral species were observed in the open water samples. However, detailed observation on both spatial and temporal scales on their presence and absence in the samples revealed the presence of variations. Percentage occurrence of zooplankton species (n = 24 sampling cruises) in the inshore and offshore samples ranged from 100% (mostly the dominant species) in samples from both stations to as low as 17% and 29% inshore and offshore stations, respectively. For example among the 21 rotifer species counted 13 showed 92-100% presence in the offshore samples, 8 of which and one other species in the inshore.

Table 2.4. Zooplankton: species list

Rotifera

<i>Anuraeopsis coelata</i>	<i>Euchlanis oropha</i>
<i>A. fissa</i>	<i>Filinia longiseta</i>
<i>Ascomorpha</i> sp.	<i>Filinia novaezealandiae</i>
<i>Asplanchna brightwelli</i>	<i>Filinia opoliensis</i>
<i>Brachionus angularis</i>	<i>Hexarthra intermedia</i>
<i>B. bennin</i>	<i>Keratella tropica</i>
<i>B. bidentatus</i>	<i>Lecane aculeata</i>
<i>B. calyciflorus</i>	<i>L. bulla</i>
<i>B. caudatus</i>	<i>L. closterocerca</i>
<i>B. falcatus</i>	<i>L. furcata</i>
<i>B. quadridentatus</i>	<i>L. hamata</i>
<i>Cephalodella catellina</i>	<i>L. leontina</i>
<i>C. forficata</i>	<i>L. luna</i>
<i>C. gibba</i>	<i>L. papuana</i>
<i>Collotheca ornata</i>	<i>L. pyriformis</i>
<i>C. pelagica</i>	<i>L. Undulata</i>
<i>Colurella obtusa</i>	<i>Lepadella apsicora</i>
<i>C. uncinata</i>	<i>L. ehrenbergii</i>
<i>Eosphora najas</i>	<i>L. patella</i>
<i>Epiphanes brachionus</i> var. <i>Spinosus</i>	<i>L. triptera</i>

Rotifera cont. ...*Plationus patulus**Polyarthra indica**P. vulgaris**Pompholyx complanata**Proalides cf. wulferti**Trichocerca gracilis**T. pusilla**T. ruttneri**Walga sp.***Cladocera***Alona sp.**Ceriodaphnia cornuta**Daphnia barbata**Diaphanosoma excisum**Diaphanosoma mongolianum**Moina micrura**Pseudosida szalayii***Copepoda***Afrocylops gibsoni**Mesocyclops aequatorialis**Thermocyclops decipiens*

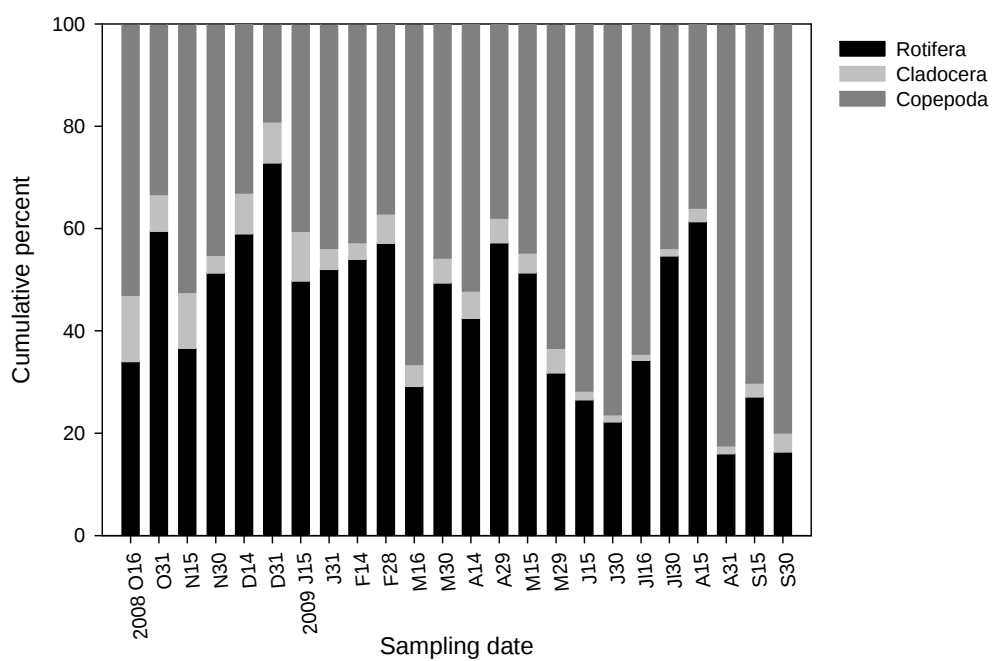


Fig. 2.7. Relative contribution of Rotifera, Cladocera and Copepoda to the total zooplankton (mean of three stations).

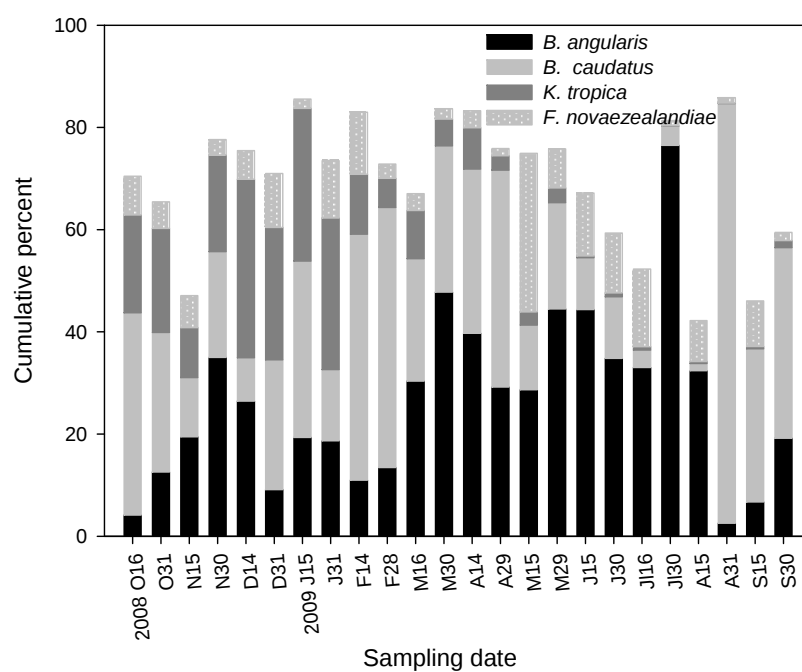


Fig. 2.8. Percent contribution of dominant rotifer species to the total rotifers abundance.

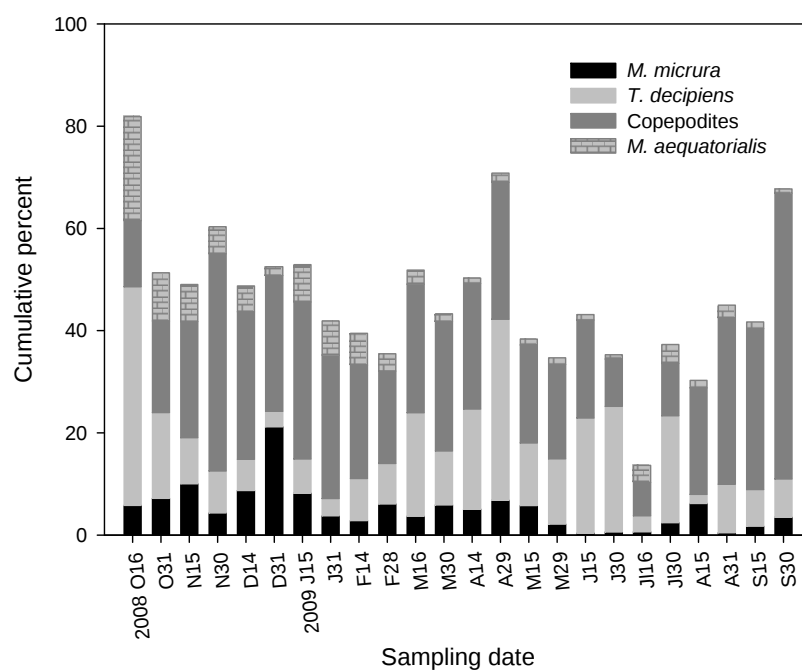


Fig. 2.9. Percent contribution of dominant and common species to the total crustacean zooplankton abundance (nauplii not included).

A common feature observed in the species composition of zooplankton in Lake Ziway was the temporal variation. Several rotifer species, the cladocerans *Daphnia barbata* and *Ceriodaphnia cornuta* and the copepod *Afrocylops gibsoni* were absent from most samplings. *Psudosida szalayi* and the invertebrate predator *Chaoborus* sp. which were not reported in previous studies (Fernando *et al.*, 1990; Dagne, 2004) could be identified during this study. *Diaphanosoma mongolianum* reported from Lake Ziway by Korovchinsky (1987) but not in Dagne (2004) was also identified in the present study but rarely found.

Length-weight relationship

Length and dry weights were determined for four crustacean species and two pre-adult stages (*Ceriodaphnia cornuta*, *Moina micrura*, *Mesocyclops aequatorialis*, *Thermocyclops decipiens* and cyclopoid copepodides and nauplii). The length-weight relationships and the numbers of individuals measured are presented in Table 2.5. The regressions of post naupliar copepods were combined and one representative regression equation computed. This regression was used to estimate the biomass of the two cyclopoid species and the copepodid stage for each sampling date. Since crustaceans used to determine the length-weight regressions are sub sampled from mixed samples collected over one year from inshore, offshore and also a night samples, I feel confident that the regressions are representative for Lake Ziway species. The regression for each species was compared to literature (*Moina micrura* from Lake Chad; *Ceriodaphnia reticulata* from Lake Kinneret; *Mesocyclops* from Lake Awassa and Lake Malawi; *Thermocyclops hyalinus* from Lake George).

Table 2.5. Length-weight regressions (mean values), $\ln W = \ln a + b \ln L$ (μm), W-dry weight μg , L-length μm , a intercept, b slope of the regression line, n is number of individuals measured

Species/stages	$\ln a$	b	n
<i>Ceriodaphnia cornuta</i>	-19,399	3,304	150
<i>Moina micrura</i>	-18,675	3, 05	160
<i>Mesocyclops aequatorialis</i>	-14,805	2,406	180
<i>Thermocyclops decipiens</i>	-13,732	2, 22	140
Cyclopoid copepodides	-15,725	2,563	150
Post naupliar copepods*	-14,081	2,258	470
Cyclopoid nauplii	-13,8244	2,3693	150

*used to calculate dry weights for each sampling date

Zooplankton abundance in time

Four rotifer species contributed 70% of the total rotifer abundance. More than half of the sampling period was dominated by *B. angularis*, *B. caudatus*, *K. tropica* and *F. novaezealandiae*. The occurrence of peak abundances of the various species revealed three patterns. Three rotifer species, *K. tropica*, *B. calyciflorus* and *Pompholyx complanata* showed an increase during the dry season and a decrease towards the rainy season. Others like *B. caudatus*, *F. novaezealandiae* and *Trichocerca ruttneri* showed maximum peaks during dry season with minor peaks during the rainy season. And, finally *A. fissa*, *B. angularis* and *F. opoliensis* reached peaks during pre and main rainy season, and smaller peaks during the dry season (Fig. 2.11). Some rotifer species (e.g. *K. tropica*, Fig. 2.11c) showed an increase during the dry season and a decrease towards the rainy season.

The Cladocera were mostly dominated by *Moina micrura* 67% of the sampling dates. *Moina* showed maximum peaks during dry season with minor peaks during the rainy season and *D. excisum* reached peaks during pre and main rainy season, and smaller peaks during the dry season (Fig. 2.12). Total cladoceran density was generally maximum during the dry season.

Among adult copepods, *Thermocyclops* dominated at sampling dates, *Mesocyclops* dominated only at one sampling occasion. Cyclopoid nauplii and copepodides composed the largest numerical proportion of the total crustacean and total zooplankton during the study period. The highest proportion of nauplii was observed in July (85%) and the lowest (less than 5%) at the beginning of the study period mid October (Fig. 2.13). Pronounced sharp decline in nauplii was observed in both stations at the end of April which was the result of continuous decline in egg numbers of cyclopoids between mid March to end of April. The maximum peak by *Mesocyclops* was during the dry season with minor ones during the rainy season. *Thermocyclops*, cyclopoid nauplii and copepodides reached peaks during pre and main rainy season and smaller peaks during the dry season (Fig. 2.13). Unlike cladocerans copepods showed an increase towards the rainy season (Figs 2.10; 2.13).

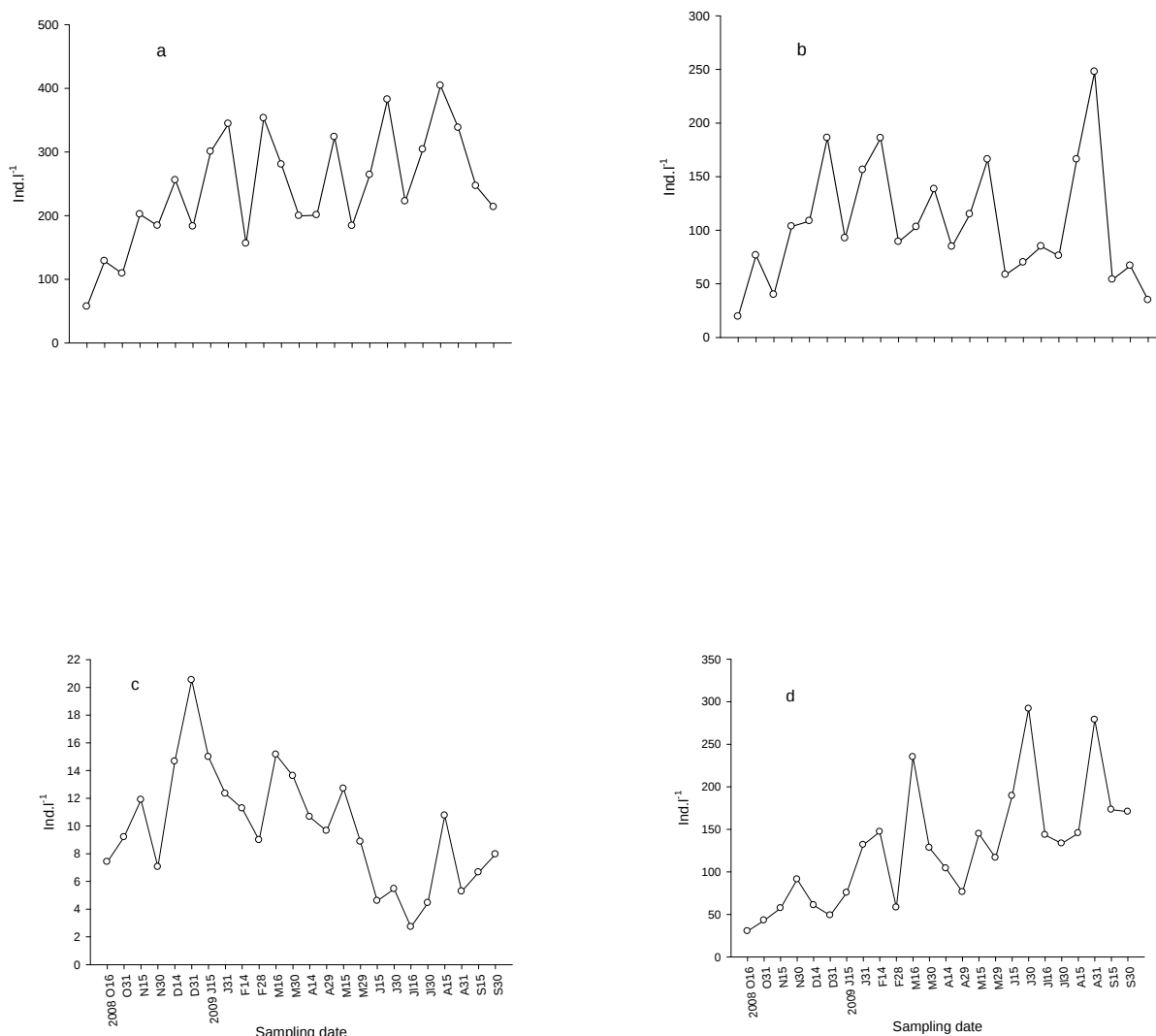


Fig. 2.10. Temporal patterns in the abundance of (a) total zooplankton, (b) rotifers, (c) cladocerans and (d) copepods (mean of three stations).

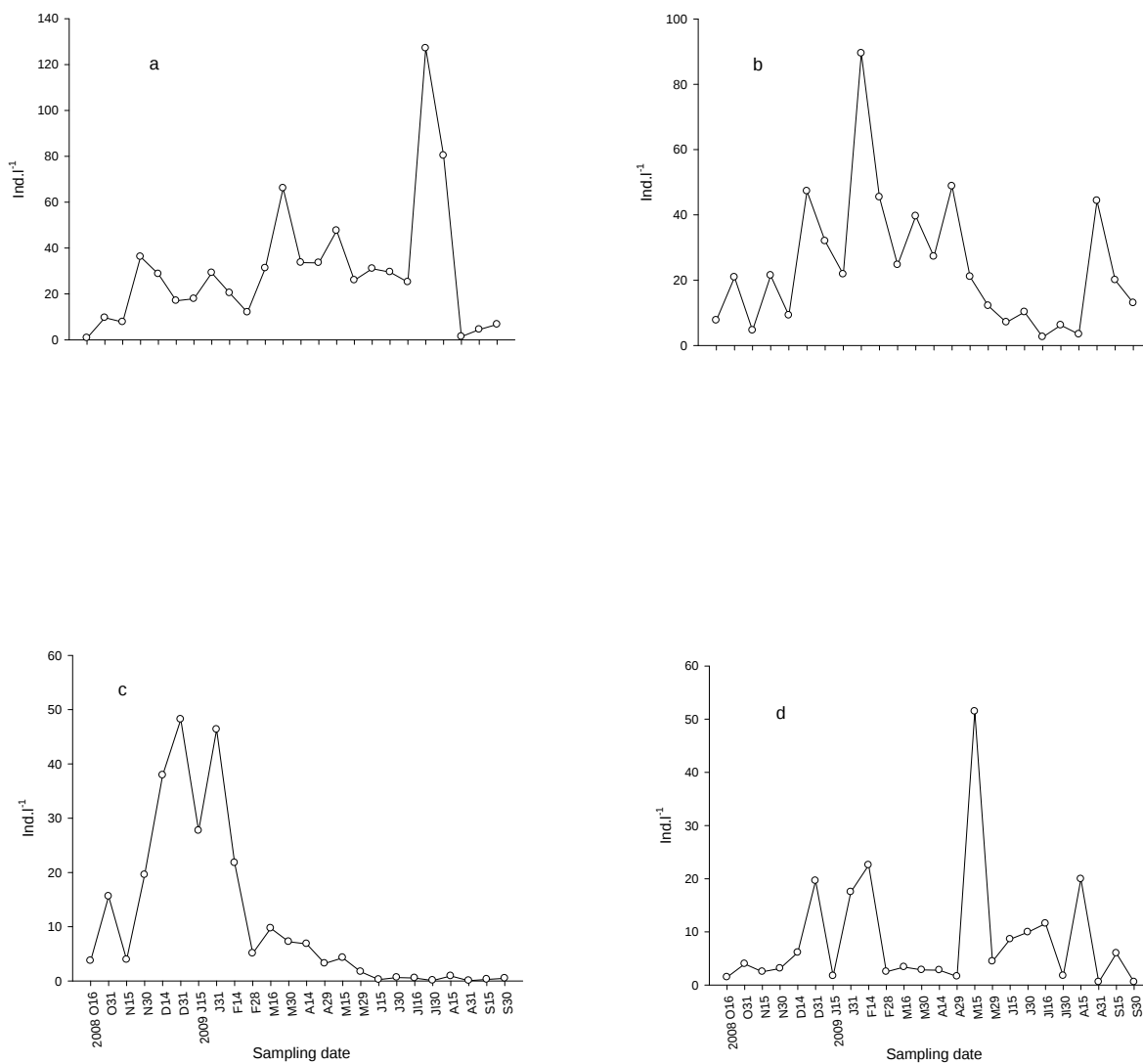


Fig. 2.11. Temporal abundance of rotifer species (a) *Brachionus angularis*, (b) *Brachionus caudatus*, (c) *Keratella tropica* and (d) *Filinia novaezealandiae*.

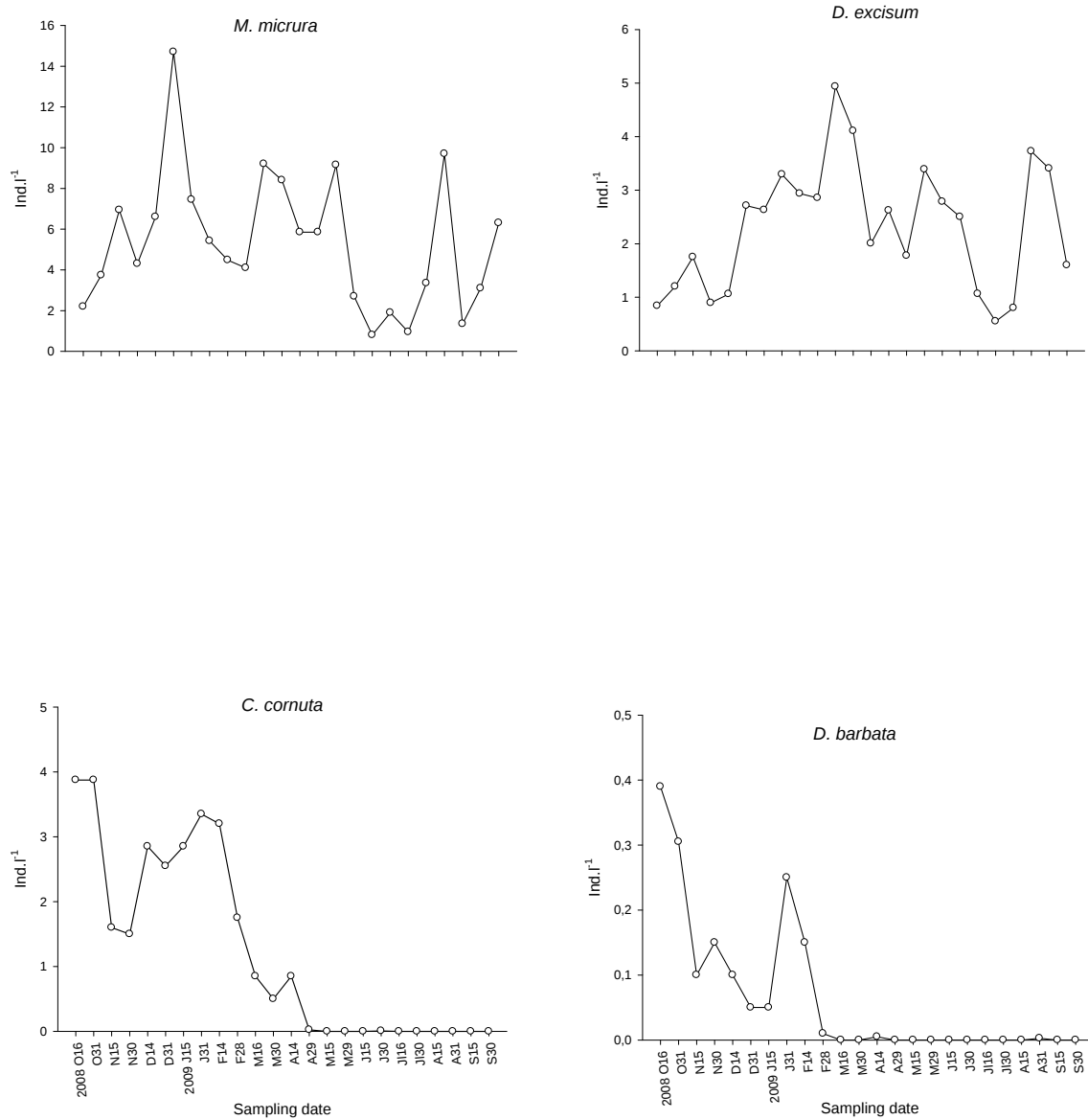


Fig. 2.12. Temporal abundance of cladoceran species.

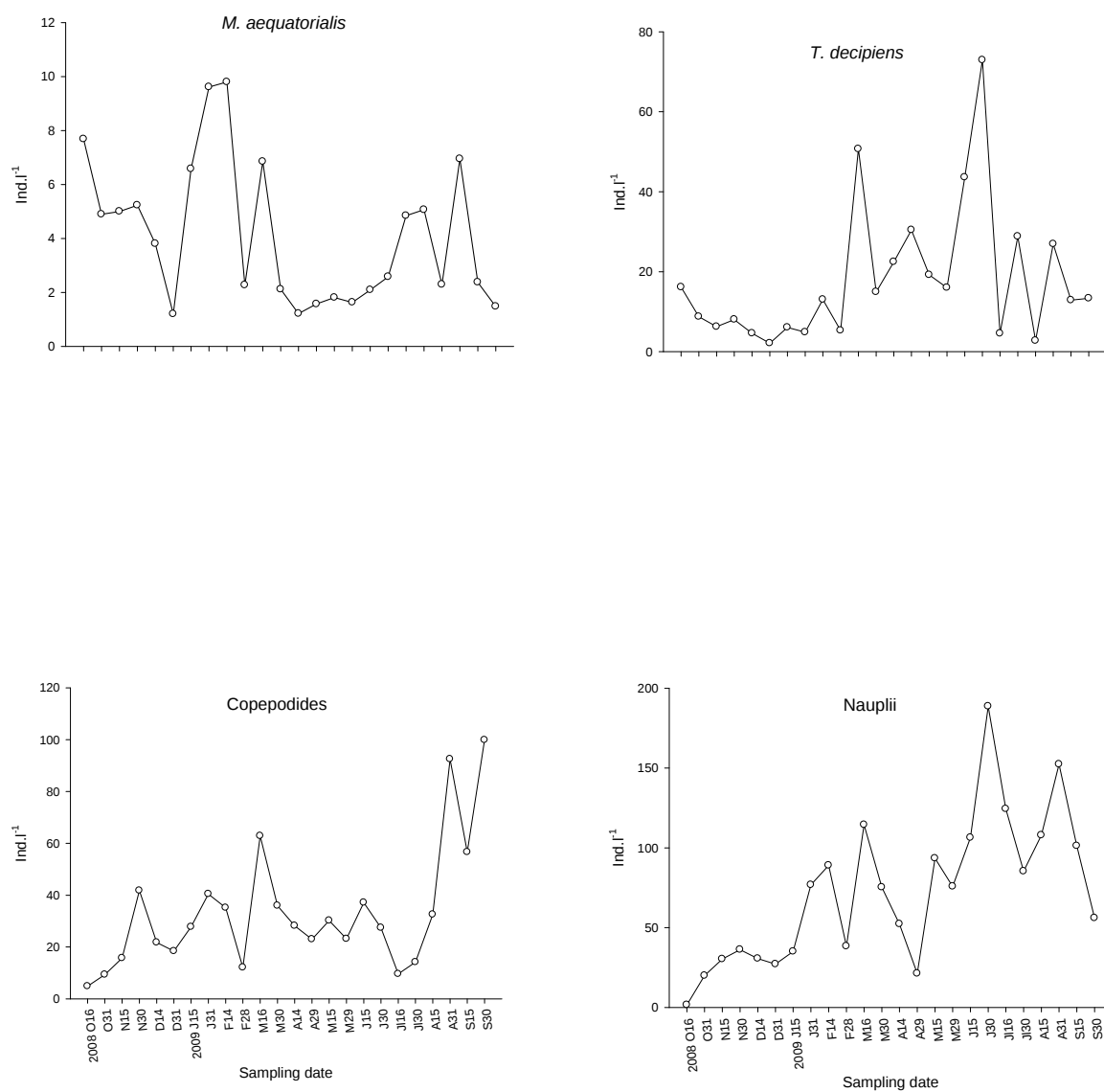


Fig. 2.13. Temporal abundance of naupliar and post naupliar cyclopoids.

Spatial gradients in zooplankton abundance

Most zooplankton species showed spatial gradients in their distribution. Generally there was a preference towards inshore with dense macrophytes (Fig. 2.14). Among the rotifers, *Brachionus caudatus*, *Keratella tropica*, *Filinia novaezealandiae*, *Trichocerca ruttneri* and *Anuraeopsis fissa* revealed highest densities in the inshore station (Figs 2.15b; 2.16). Two species, *Brachionus angularis* and *Brachionus calyciflorus* showed their peak occurrence in the offshore station (Figs 2.14b; 2.15a). Variations in spatial distribution patterns between inshore and offshore of the lake were common to all crustaceans (Fig. 2.14). From seven crustaceans counted, five species showed higher proportions as well as their maximum peaks inshore; only *Ceriodaphnia cornuta* and *Daphnia barbata* preferred the offshore region (Fig. 2.14c). However, the decline observed for the two species was similar in both stations. *Alona* occurred in high densities inshore (Fig. 2.17a). *Alona* contributed 12,1 % of the total crustaceans during its peak abundance at the inshore station but hardly reached 1% in the open water (Figs 2.13a; 2.14c). Higher abundances inshore than offshore following the increase in water transparency in April was observed for most species (e.g. *Diaphanosoma excisum*, *Moina micrura*, total cladocerans and *Thermocyclops decipiens* (Figs 2.17; 2.18)). Oviparous copepods avoided the inshore station located within the macrophytes and the upper water column. Only a few egg carrying *Thermocyclops decipiens* were found in the sample from the inshore but *Mesocyclops aequatorialis* were almost absent during the entire sampling period. The total abundance of Rotifera, Cladocera and Copepoda as well as total zooplankton remain in a comparable range (difference between inshore and offshore 1% in total rotifers, 17% in total copepods (Fig. 2.14a).

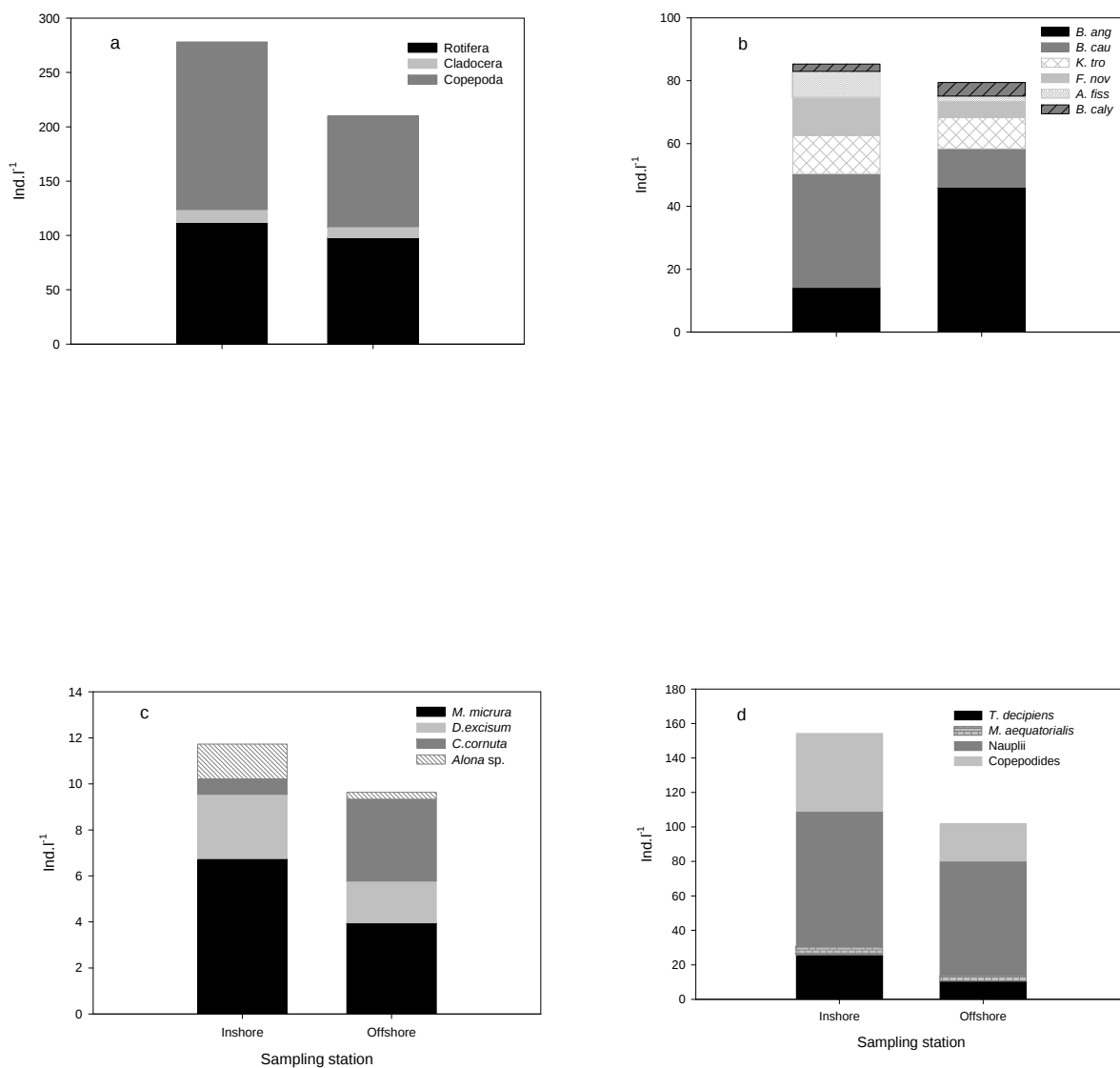


Fig. 2.14. Spatial distribution of (a) zooplankton groups, (b) rotifers (c) cladocerans, (d) cyclopoid copepods (mean of all sampling dates).

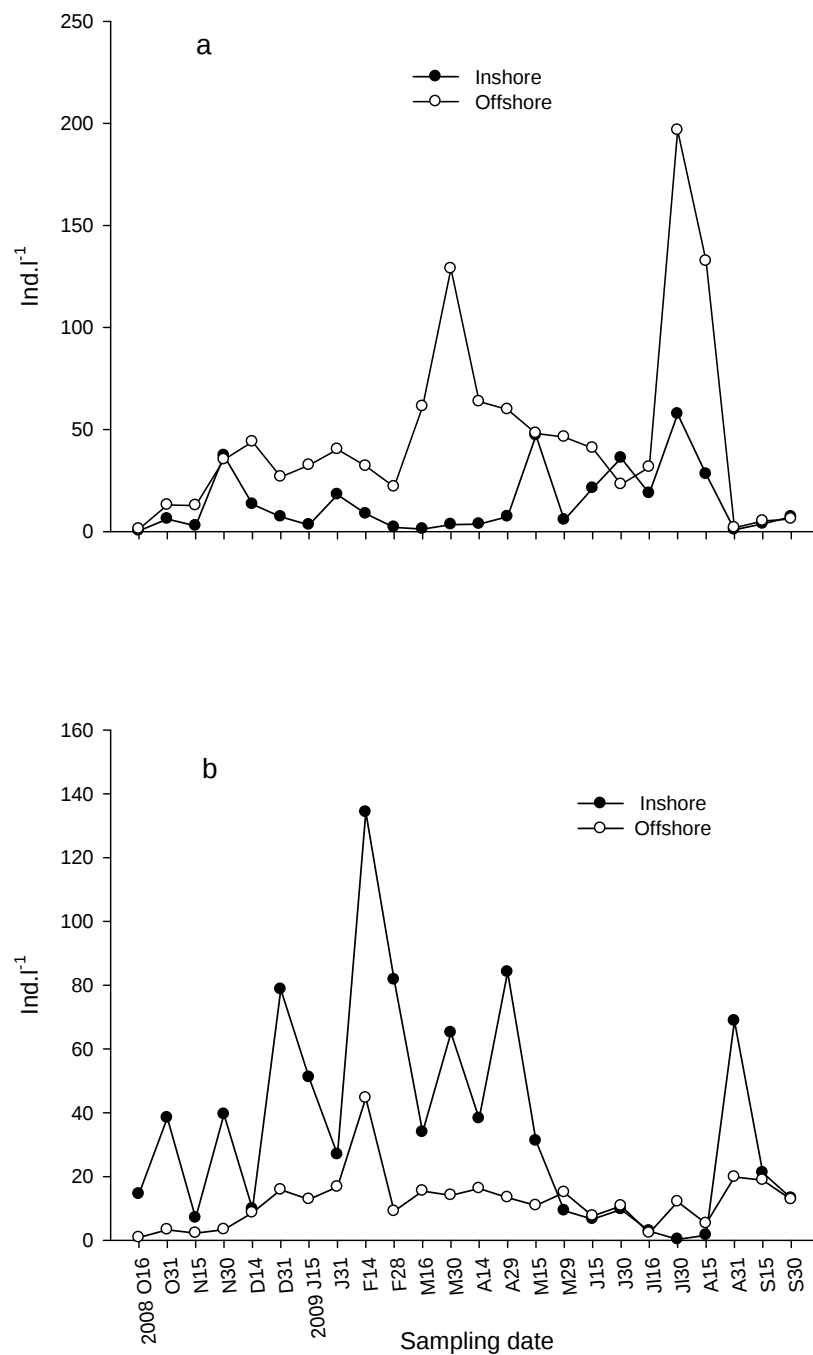


Fig. 2.15. Spatio-temporal distribution of *Brachionus angularis* (a) and *Brachionus caudatus* (b).

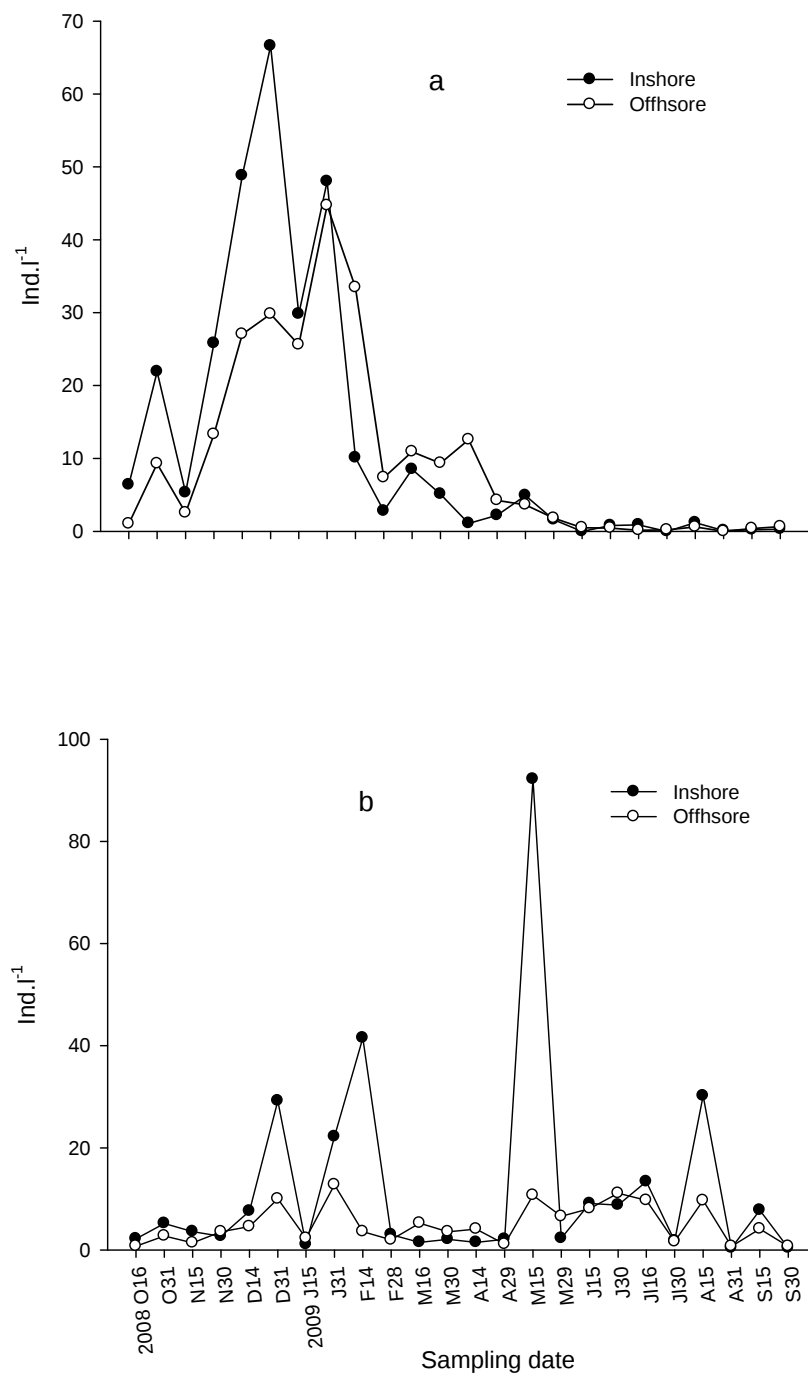


Fig. 2.16. Spatio-temporal distribution of *Keratella tropica* (a) and *Filinia novaezealandiae* (b).

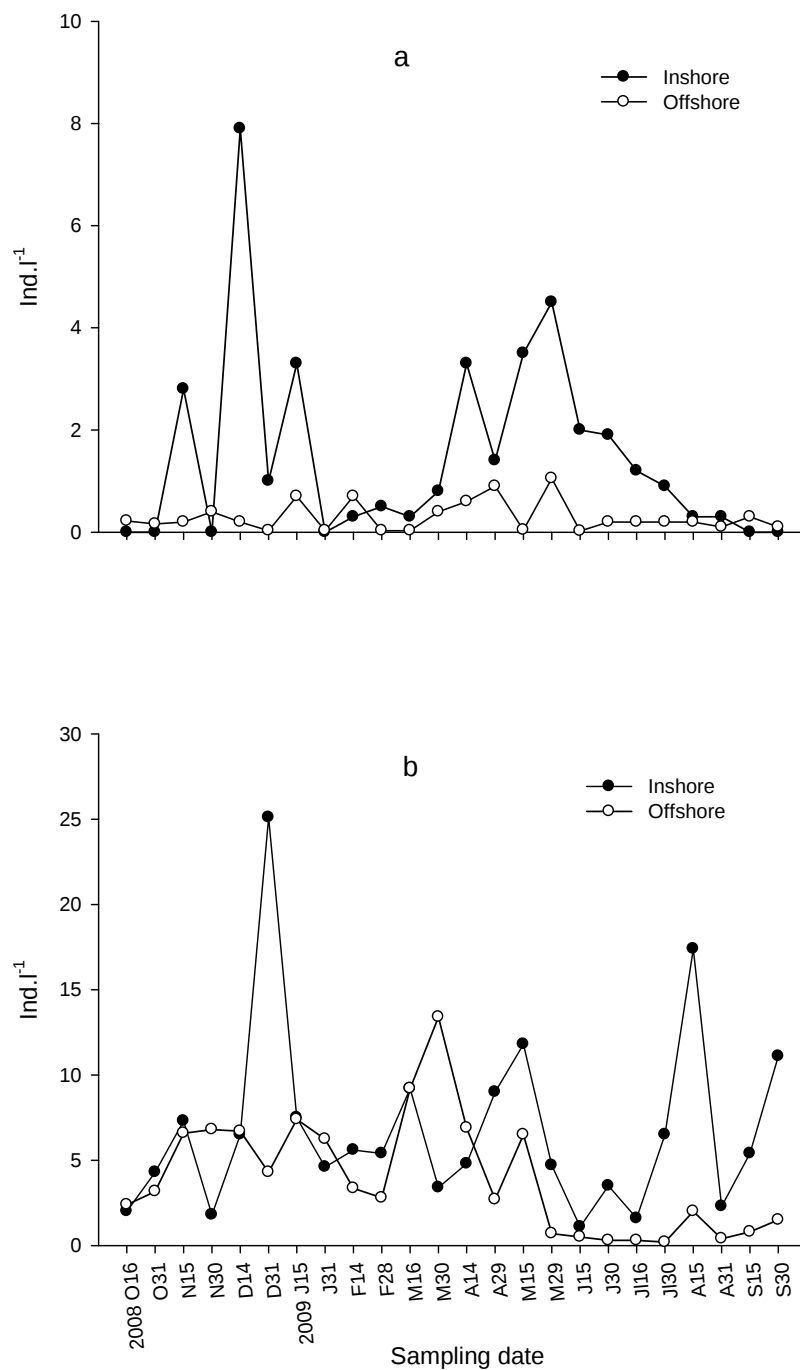


Fig. 2.17. Spatio-temporal distribution of *Alona* sp. (a) and *Moina micrura* (b).

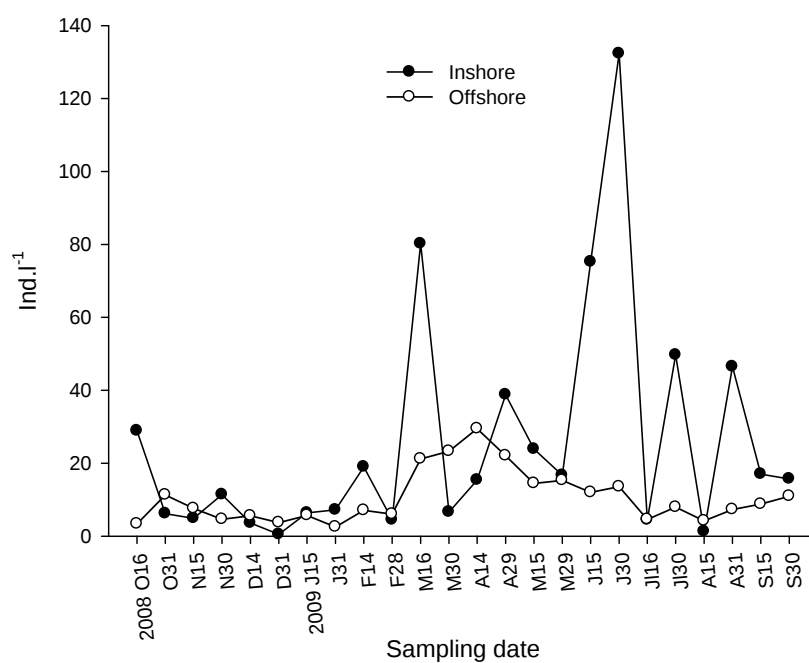


Fig. 2.18. Spatio-temporal distribution of *Thermocyclops decipiens*.

Night samples conducted on 4-5 July 2009 revealed the presence of diel vertical migration by the egg carrying copepods. The number of egg carrying females, clutch size and body size of *Mesocyclops aequatorialis* varied markedly from day samples (Figs 2.19a, b). In most cases ovigerous females with higher clutch were in the lower water column (2m and below) during the day and rose up to the upper water columns and surfaces at night (Fig. 2.19b). Body lengths measured from the day samples revealed that smaller sized *Mesocyclops aequatorialis*, usually males and copepodid stages were common while adult females and egg carrying females being very rare. The mean adult *Mesocyclops aequatorialis* body size from night samples was larger (1212,4 μm , n=179) compared to the mean body size from day samples (890 μm).

Analysis of variance of monthly rainfall, secchi depth and zooplankton densities for the various seasons revealed the presence of variation (Tables 2.6 – 2.8). Low Rotifera density was recorded during post rainy season whereas densities during dry, pre-rain and rainy seasons were high and closely comparable. Cladocera showed progressive decline in density from dry season to pre-rain and rainy season and showed an increase during the post rainy season. Copepoda density was high in all seasons, pre-rainy and rainy season being significantly higher (Fig. 2.20).

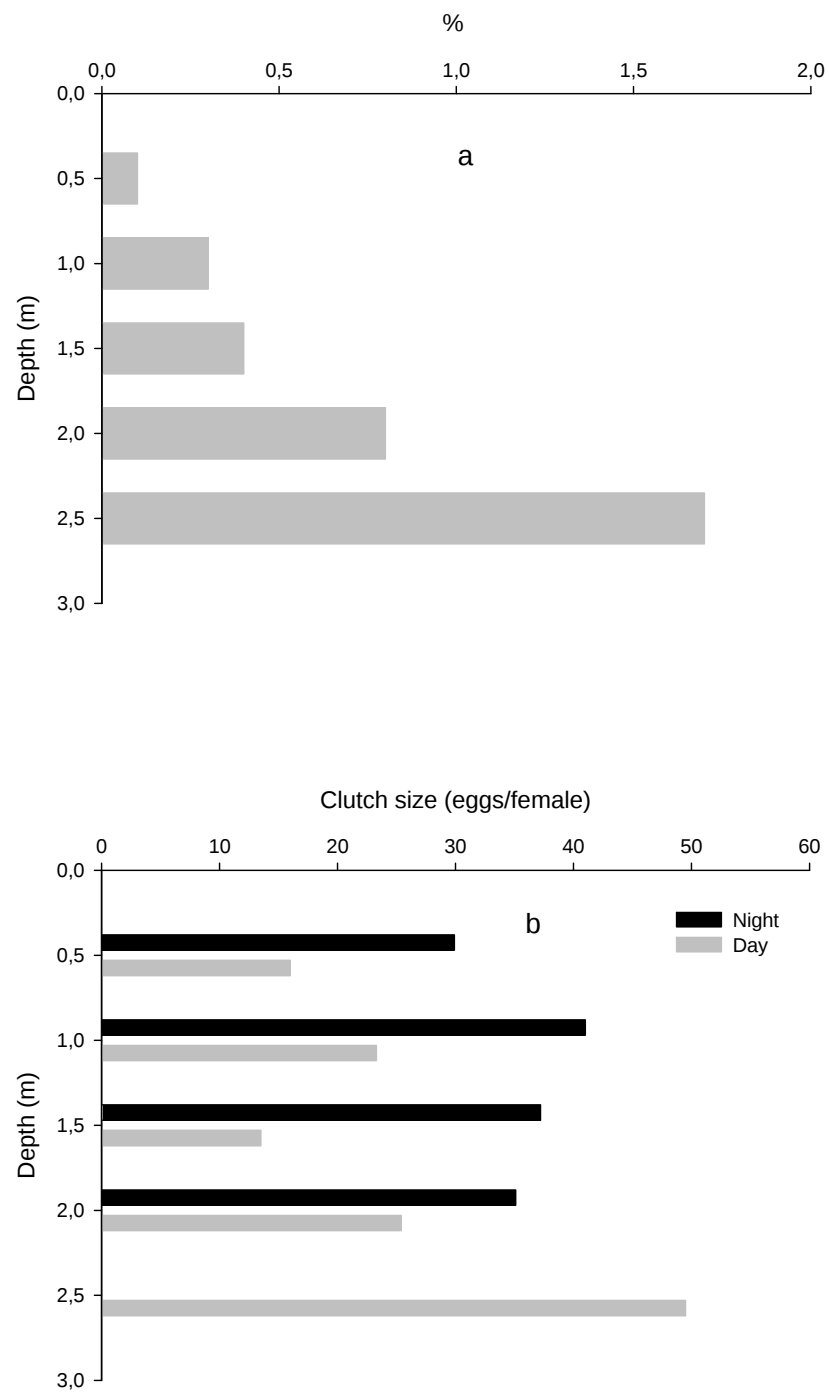


Fig. 2.19. Vertical distribution of (a) proportion of ovigerous females-day samples and (b) diel variation in clutch sizes of *Mesocyclops aequatorialis* at offshore station.

Table 2.6. ANOVA for monthly rain (mm) as a function of seasons. SS- Sum of Squares, MS- Mean Square, df- degrees of freedom, dry (December-April), pre-rain (May-June), rain (July-August), postrain (September-November)

	df	SS	MS	<i>F</i>	p-value
Seasons	3	34700	11567	12,201	<0,0001
Residuals	20	18959	948		

Fisher's PLSD (Protected Least Significance Difference) for rain (significance level: 5%) significant differences are listed

dry-rain: $p < 0,0001$

dry-postrain: $p = 0,0129$

pre-rain-rain: $p = 0,0013$

rain-postrain: $p = 0,0036$

Table 2.7. ANOVA for Secchi depth (cm) as a function of seasons

	df	SS	MS	<i>F</i>	p-value
Seasons	3	2005,6	668,5	25,265	<0,0001
Residuals	44	1164,3	26,5		

Fisher's PLSD (Protected Least Significance Difference) for rain (significance level: 5%) significant differences are listed

dry-pre-rain: $p = 0,0362$

dry-rain: $p < 0,0001$

dry-postrain: $p < 0,0001$

pre-rain-rain: $p < 0,0001$

pre-rain-postrain: $p = 0,0492$

rain-postrain: $p = 0,0008$

Table 2.8. ANOVA for zooplankton abundance ln (ind.l⁻¹) as a function of seasons

Zooplankton	df	SS	MS	<i>F</i>	p-value
Seasons	3	3,797	1,266	6,098	<0,0015
Residuals	44	9,132	0,208		

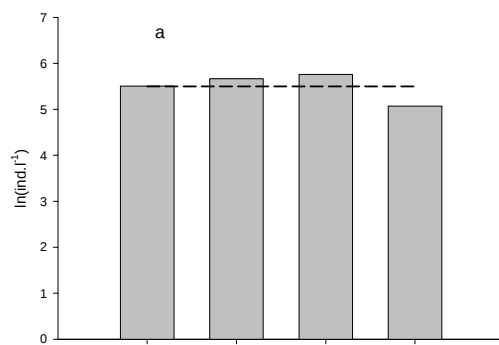
Rotifera	df	SS	MS	<i>F</i>	p-value
Seasons	3	7,108	2,369	6,798	<0,0007
Residuals	44	15,335	0,349		

Cladocera	df	SS	MS	<i>F</i>	p-value
Seasons	3	12,696	4,232	6,656	<0,0008
Residuals	44	27,975	0,636		

Copepoda	df	SS	MS	<i>F</i>	p-value
Seasons	3	5,134	1,711	4,597	<0,0070
Residuals	44	16,382	0,372		

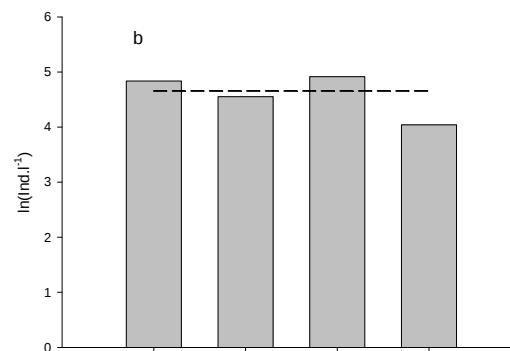
Fisher's PLSD

dry-postrain: $p=0,0024$
 pre-rain-postrain: $p=0,0026$
 rain-postrain: $p=0,0005$



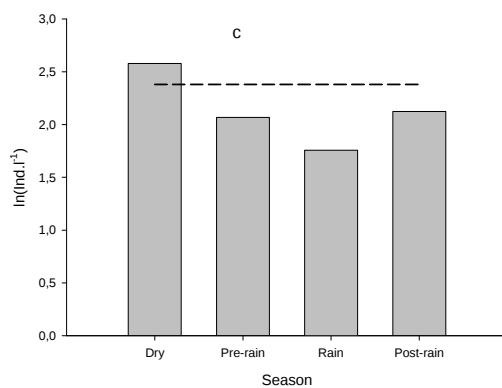
Fisher's PLSD

dry-postrain: $p<0,0001$
 pre-rain-postrain: $p=0,0360$
 rain-postrain: $p=0,0032$



Fisher's PLSD

dry-pre-rain: $p=0,0138$
 dry-rain: $p=0,0001$
 dry-postrain: $p=0,0336$
 rain-postrain: $p=0,0417$



Fisher's PLSD

dry-pre-rain: $p=0,0239$
 dry-rain: $p=0,0352$
 pre-rain-postrain: $p=0,0045$
 rain-postrain: $p=0,0068$

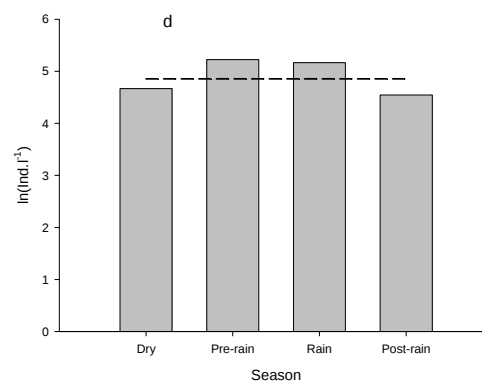


Fig. 2.20. Mean seasonal abundance of zooplankton groups (a- total zooplankton, b- Rotifera, c-Cladocera and d- Copepoda). Dotted lines are means for the study period. Seasons: dry (December-April), pre-rainy (May-June), rainy (July-August) and post-rainy (September-November).

Plankton in relation to abiotic and biotic conditions

To evaluate the relationship of zooplankton density with selected abiotic and biotic parameters, correlation analysis was applied. Water temperature, dissolved oxygen, pH and conductivity showed no significant correlation with density and were not included in Table 2.9. Rotifera, Cladocera and Copepoda were found to correlate either with water transparency or chlorophyll a and/or with both. Total zooplankton density was not significantly correlated with either of the two but was correlated best with the densities of Rotifera and Copepoda reflecting the contribution of both to total the zooplankton ($p < 0,0001$ in both cases). Density of Rotifera showed weak negative correlation with chlorophyll and with Cladocera ($p = 0,007$ and $p = 0,0067$), respectively and somehow with secchi depth (Table 2.9). The abundance of Cladocera correlated best with secchi depth ($p < 0,0001$) and weakly and negatively with chlorophyll ($p = 0,0067$). Copepoda respond to chlorophyll positively ($p = 0,0003$) but not to secchi depth.

Table 2.9. Spearman rank correlation coefficients for density of total zooplankton and zooplankton groups and selected environmental variables (the highest significant coefficients are shown in bold)

Independent variable	Dependent variable			
	Total zooplankton	Cladocera	Copepoda	Rotifera
Secchi depth	—	0,465***	—	0,237*
Chlorophyll	—	- 0,382*	0,531**	-0,392**
Cladocera	—	—	—	0,322**
Copepoda	0,776***	—	—	—
Rotifera	0,618***	0,322*	—	—

*p<0,01; **p<0,001; ***p<0,0001

Chaoborus was very rare in day samples (less than one individual per liter) but was found in the night samples in numbers like 19 individuals per net hauls from the upper most water column (Fig. 2.21).

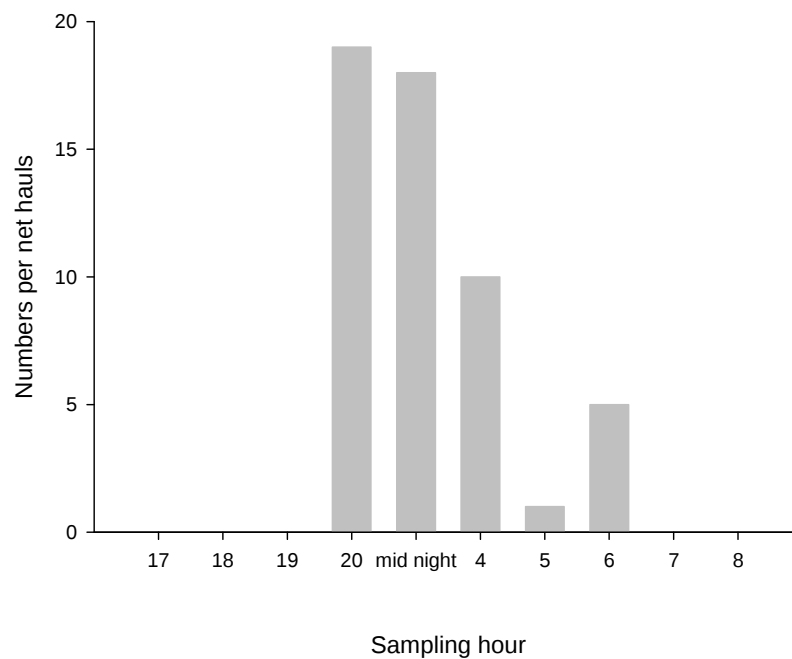


Fig. 2.21. Temporal distribution of *Chaoborus* from night net samples in upper 1m water column of Lake Ziway.

Fish gut analysis

The gut contents of six fish species, *Oreochromis niloticus*, *Tilapia zillii*, *Clarias gariepinus*, *Carassius carassius*, *Barbus* sp. and *Gara* sp. were examined. Total fish stomachs examined were: *O. niloticus* = 60, *T. zillii* = 35, *C. gariepinus* = 50, *C. carassius* = 29, *Barbus* sp. = 53 and *Gara* sp. 55. *Clarias gariepinus* fed mainly on copepods, *Carassius carassius* to a lesser extent, while the others not. From catfish stomachs examined (Fig. 2.22), 10% were found to contain more than 1000 copepods in a stomach, more than 2000 copepods were recorded as maximum. The high occurrence of copepods in the guts of *C. gariepinus* of different length classes revealed the importance of plankton in the diet of this benthic feeding catfish. Zooplanktivory by the juveniles of catfish, attempts to catch the juveniles were not successful, could be even higher than in the larger catfish. On the other hand, different phytoplankton species (blue greens mostly), detritus and mud were identified from the stomachs of various sized *Tilapia*. The gut contents of the other two small fish species *Barbus* and *Gara*, (also themselves a preferred prey to catfish) revealed solely chironomid larvae.

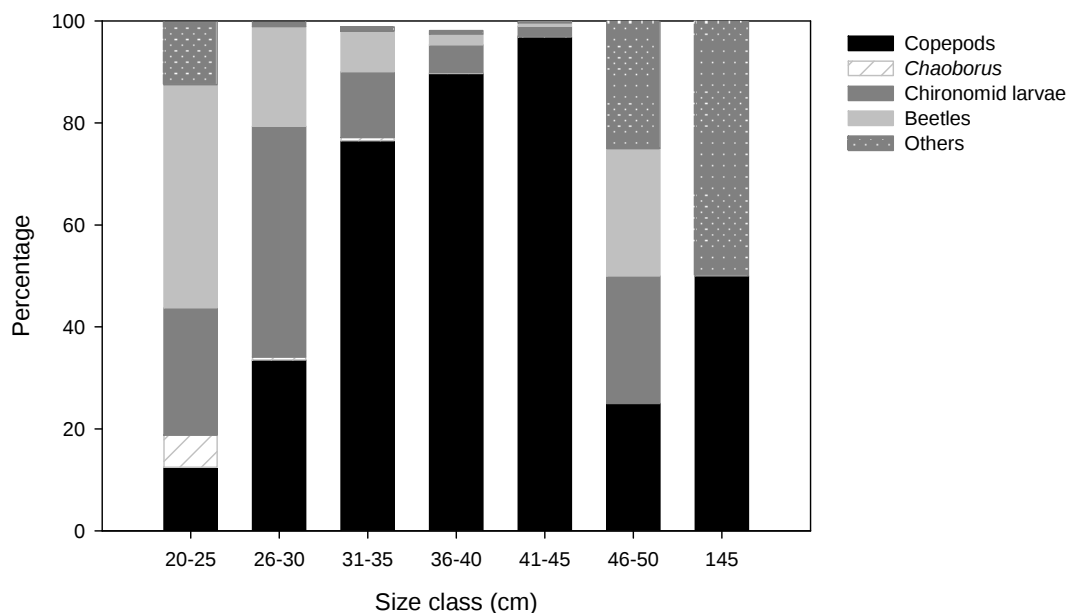


Fig. 2.22. Percentage occurrence of different food items in the stomachs of *Clarias gariepinus*.

Fecundity and age structure of cyclopoid copepods

Total numbers of cyclopoid eggs were very low for most of the sampling period. The mean for both *Mesocyclops* and *Thermocyclops* was 5,6 eggs l⁻¹ (0,05 to 28,7 eggs l⁻¹) (Fig. 2.23). The maximum egg stocks for the two species were 6660 and 22012 eggs m⁻³ for *Mesocyclops* and *Thermocyclops*, respectively. The lowest egg production was at the end of December and the highest in mid July. Most egg counts were from *Thermocyclops*, *Mesocyclops* females with eggs were not found for 8 sampling dates the maximum being only 6 eggs l⁻¹ during its peak in Mid July and <1 for the rest of the sampling. The maximum proportions of *Mesocyclops* and *Thermocyclops* ovigerous females in the adults were 3,1 and 20% in July, respectively. Declining pattern in egg production for two or more months was common (e.g. from March to April; mid July to August and an extended period of low egg production from end of October to mid January (Fig. 2.23). Mean clutch sizes of the two species were 12,9 and 24,1 eggs per female for *Thermocyclops* and *Mesocyclops*, respectively. Maximum clutch recorded for the two species were 26 and 64 eggs per female for *Thermocyclops* and *Mesocyclops*, respectively. Temporal variability in clutch size of *Mesocyclops* was very large compared with *Thermocyclops*. The mean clutch size from night sample (n = 40) was 35 eggs per female *Mesocyclops*. Increasing egg production and nauplii as well were observed from May to mid July.

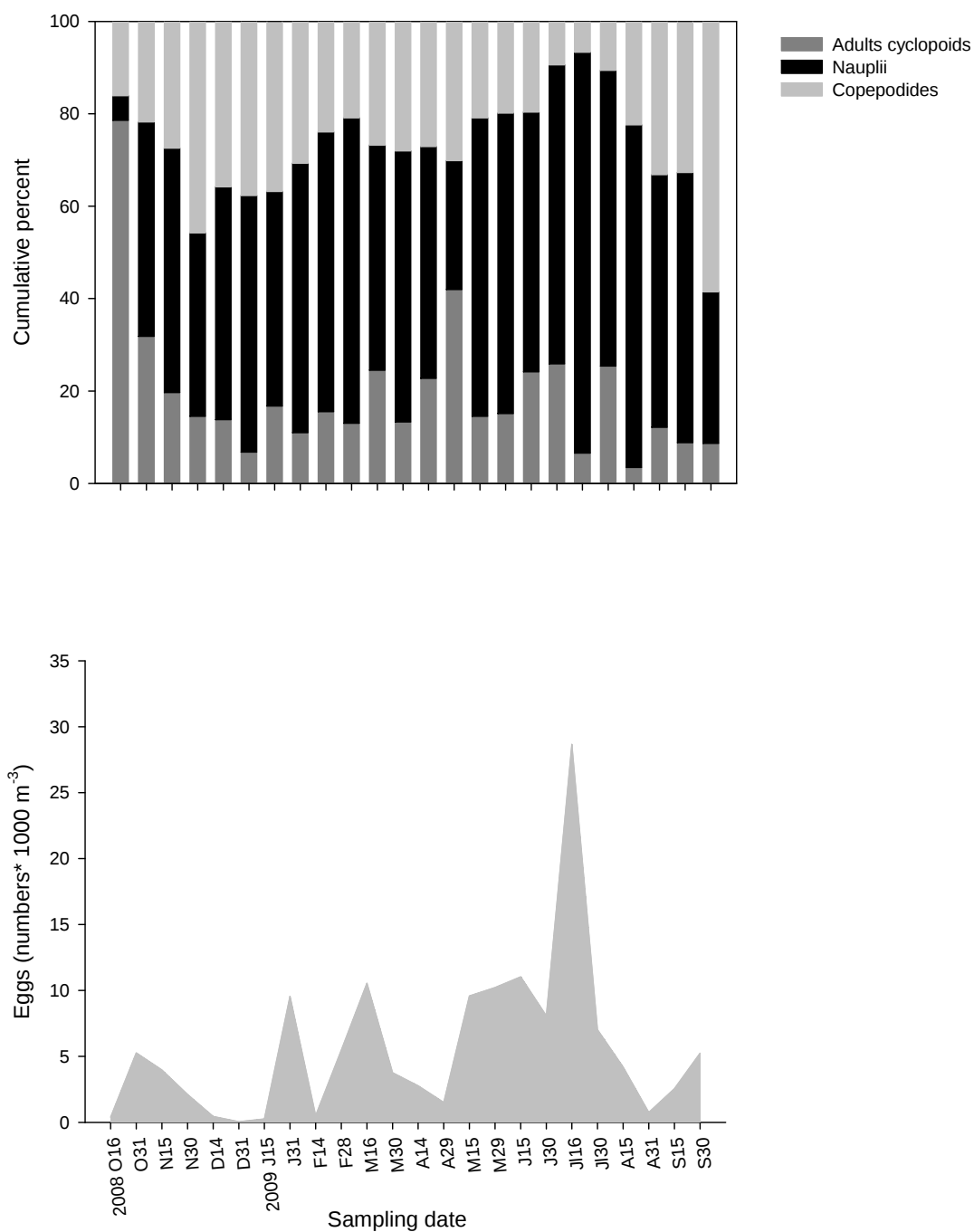


Fig. 2.23. Percentage of mean density of cyclopoid life stages (upper panel) and cyclopoids egg stocks (lower panel).

Pre-adult stages of cyclopoids dominated the total zooplankton numbers. Pre-adult cyclopoides were about 83 and 43% of the mean total copepods and total zooplankton density, respectively. Nauplii represented more than 50% of the total copepods for 71% of the sampling period. The proportions of developmental stages in the total cyclopoid copepods were nauplii 56,5%, copepodides 26% and adults 17,5% for the sampling period. Within the adults, *Thermocyclops* dominated almost at all dates except at the end of January, when *Mesocyclops* occurred in numbers about twofold that of *Thermocyclops*.

The theoretical number of individuals passing through each developmental stage into the next stage is calculated using "Southwood method": The area under the curve of densities of a developmental stage against time divided by the development time of the developmental stage gives the theoretical number of individuals passing into the next stage (Southwood, 1978). Numbers passing through naupliar stage are the potential input into the copepodides stock and numbers passing through copepodid stage are the potential input into the adult stock. The number of *Moina* neonates passing into the adult stage in the periods between March and April were greater than the numbers in the samples (Fig. 2.24). In the cyclopoids, a much wider gap between the numbers of copepodides based on the theoretical input coming from nauplii was observed. At the end of the sampling period counts of adults were lower than the recruits coming from the copepodid stage (Fig. 2.25b).

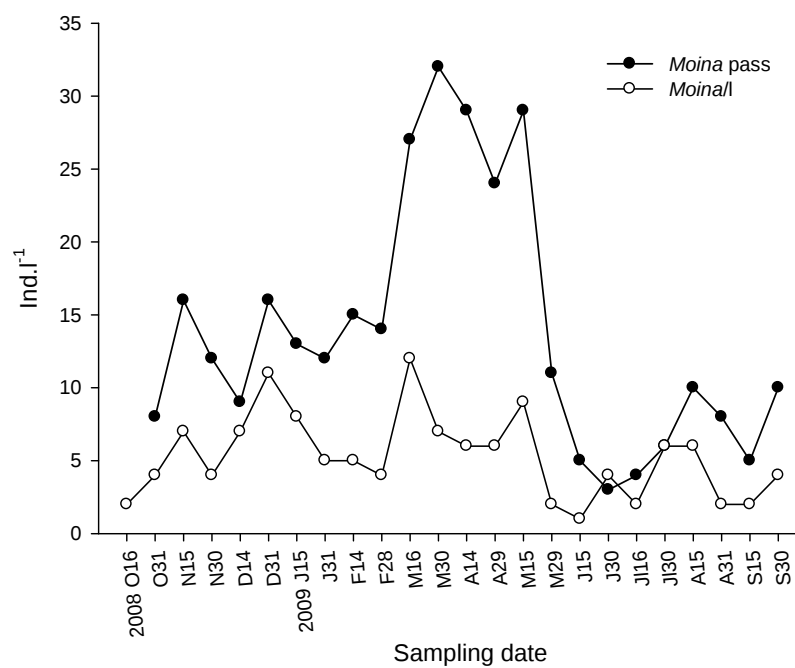


Fig. 2.24. Density recorded and predicted numbers of neonates passing into adult *Moina micrura*.

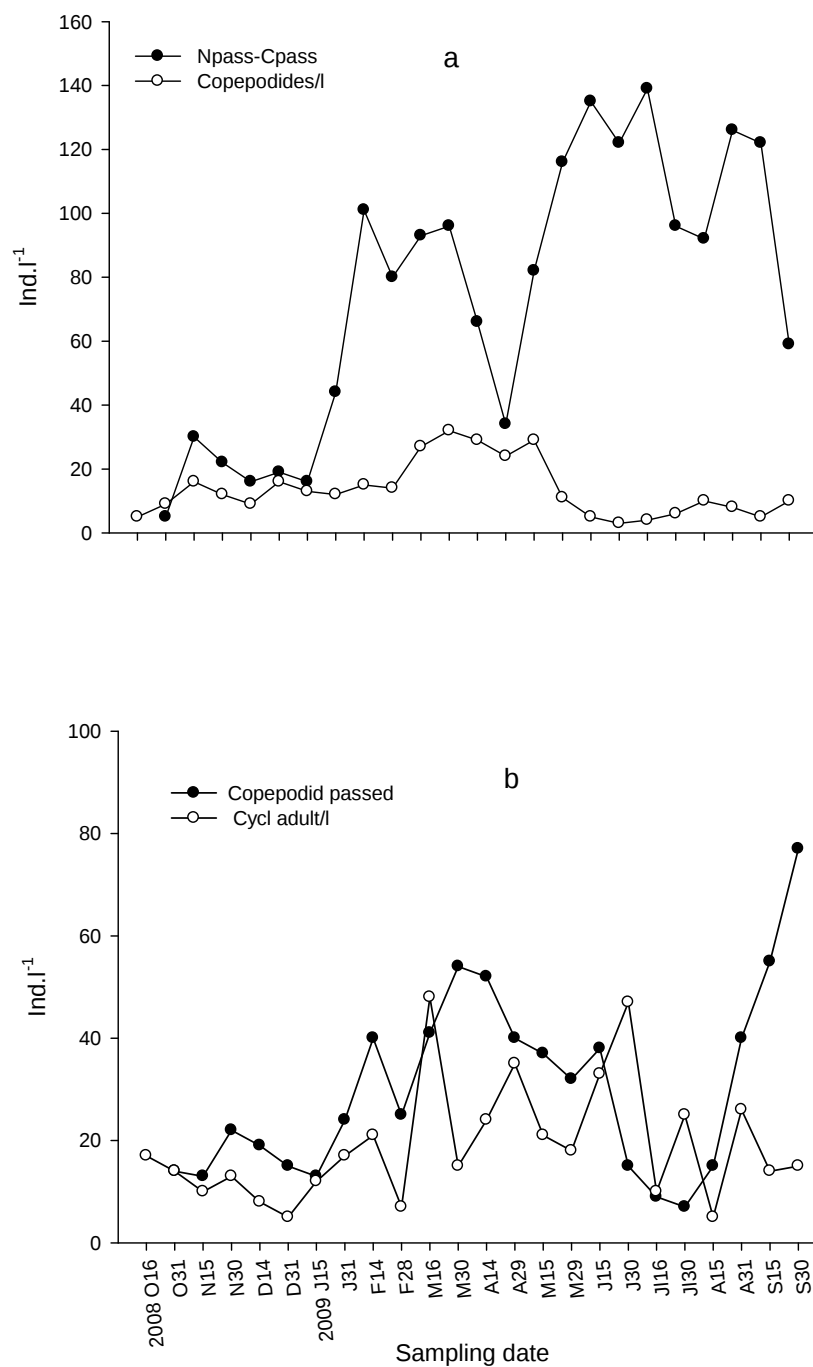


Fig. 2.25. Density of cyclopoid life stages (a) Copepodides recorded and nauplii passing into copepodid stage and (b) adult cyclopoids recorded and copepodides passing into adult stage.

Zooplankton biomass

Results of laboratory determined length and dry weights of crustacean species and pre-adult stages (*Ceriodaphnia cornuta*, *Moina micrura*, *Mesocyclops aequatorialis*, *Thermocyclops decipiens* and cyclopoid copepodides and nauplii) are presented in Table 2.10.

Table 2.10. Mean length (range), dry weight and sample sizes of crustaceans in Lake Ziway during the study period

Species/stages	Mean length (µm)	Mean dry wt. (µg)	n
<i>Ceriodaphnia cornuta</i>	295 (170-487)	0,5	569
<i>Moina micrura</i>	435 (212-742)	0,9	1256
* <i>Daphnia barbata</i>	716 (445-1377)	1,5	157
** <i>Diaphanosoma excisum</i>	644 (318-975)	1,5	119
<i>Mesocyclops aequatorialis</i>	890 (742-1504)	3,2	385
*** <i>Mesocyclops aequatorialis</i>	1212 (763-1526)	7,0	179
<i>Thermocyclops decipiens</i>	641 (424-890)	1,6	1047
Cyclopoid copepodides	432 (212-742)	0,7	1393
Cyclopoid nauplii	174 (106-297)	0,2	1197

Note: * and ** estimated using regressions from literature, Dumont *et al.* (1975) and Gras and Saint-Jean (1983), respectively and *** only from night samples.

Table 2.11. Mean $\pm$ SD. dry biomass ($\mu\text{g l}^{-1}$) of crustacean categories and their percentage in Lake Ziway (mean of all stations and sampling dates)

Species/stages	Mean $\pm$ SD.	% Within group total crust. total zoopl.		
<i>Ceriodaphnia cornuta</i>	1,3 $\pm$ 1	13,5	1,4	1,4
<i>Daphnia barbata</i> *	0,5 $\pm$ 0,4	5,2	0,6	0,5
<i>Diaphanosoma excisum</i> **	3,5 $\pm$ 1,7	36,8	4,0	3,8
<i>Moina micrura</i>	4,2 $\pm$ 2,7	44,5	4,8	4,6
Total cladocera	9,4 $\pm$ 3,8		10,7	10,4
<i>Mesocyclops aequatorialis</i>	13,3 $\pm$ 8,8	16,9	15,1	14,6
<i>Thermocyclops decipiens</i>	28,8 $\pm$ 26,3	36,8	32,8	31,7
Cyclopoid copepodids	21,8 $\pm$ 16	27,9	24,9	24,0
Cyclopoid nauplii	14,4 $\pm$ 9,9	18,4	16,4	15,9
Total copepods	78,3 $\pm$ 41,1		89,3	86,2
Total crustaceans	87,8 $\pm$ 40,3			96,6
Total rotifers	3,1 $\pm$ 1,3			3,4
Total zooplankton	90,87			

Dry mass calculated using regression from literature: * Dumont *et al.* (1975) and

**Gras and Saint Jean (1983)

Rotifers contributed nearly half of the total zooplankton numbers (43 %) but only 3,4% of the total zooplankton biomass (Fig. 2.26). Rotifer biomass values rarely reached $> 6 \mu\text{g dwt l}^{-1}$. Cladocerans contributed about 10%, a higher contribution ($\sim 38\%$) was found end of December when the dominant *M. micrura* reached peak abundance (Figs 2.26; 2.29). On average *Moina* contributed 4,6% to the total zooplankton biomass (Table 2.11). 86% of the zooplankton biomass was contributed by two cyclopoids and their larval stages. The two adult cyclopoids showed distinct biomass peaks, *T. decipiens* reached its maximum (>3 times the maximum of *M. aequatorialis*) end of June (Fig. 2.31) following the increase in phytoplankton (peak Chlorophyll a concentration) which itself was a response to an increase in nutrient availability following the rainfall. *M. aequatorialis* reached a maximum biomass during the dry period in mid February. Pre adult stages of cyclopoids showed their maximum peaks during the rainy season, end of August and September (Fig. 2.31). Despite their small size, pre adult cyclopoids had a significant contribution of about 40% to the total zooplankton biomass. Nauplii reached as high as 45% of the total zooplankton in July (Figs 2.26; 2.31).

Zooplankton biomass varied spatially and temporally. Three major peaks in total crustacean biomass were recorded inshore but a single maximum and less than half that of the inshore was recorded offshore. In 71% of the samples, inshore crustacean biomass was greater than offshore. Biomass was less than $100\mu\text{gl}^{-1}$ throughout the sampling period except one value end of March (Fig. 2.27). There were marked variations in the temporal peaks of zooplankton biomass inshore, with three conspicuous major peaks of 183,7; 182,5 and $162,8 \mu\text{gl}^{-1}$ ends of June, mid March and end of August, respectively. These major peaks were mainly due to *Thermocyclops decipiens* that contributed about 58, 45 and 26% in those periods. Cyclopoid copepodides were also the major contributor of the total biomass in the third peak 36 %. Temporal fluctuations in total zooplankton biomass were mainly a response to changes in copepods biomass (Fig. 2.28) because they contributed about 86% to the total zooplankton biomass (Fig. 2.26). At peak densities of one copepod species (*Thermocyclops decipiens*) highest biomass values could be recorded. During the main dry period between end of March to May and rainy period June to mid August a sharp decline in zooplankton biomass was observed. Another distinct temporal feature in this study was the decline in the cladocerans species (Fig. 2.29) and total cladocera standing biomass (Fig. 2.30) following the decline in the water transparency. Lowest biomass values of total zooplankton were recorded at the end of February ($40,5 \mu\text{gl}^{-1}$) and December ($47,8 \mu\text{gl}^{-1}$) due to the lower proportion of adult copepods in the samples and smallest body size as well. The overall mean total zooplankton biomass for Lake Ziway was $91 \mu\text{gl}^{-1}$.

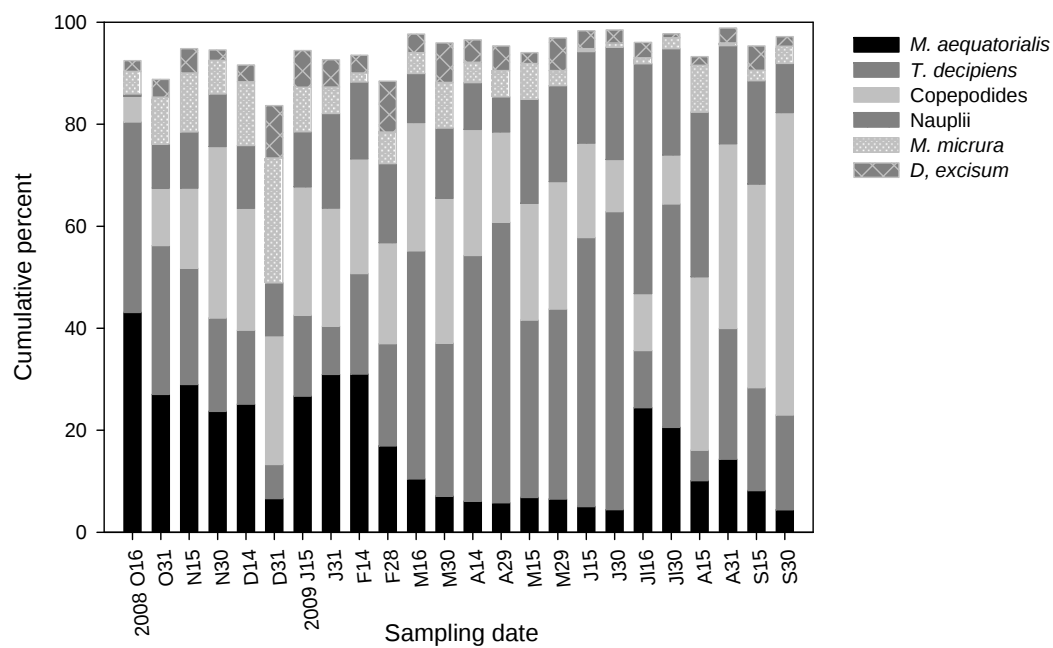


Fig. 2.26. Percent contribution of crustacean species to the total zooplankton biomass.

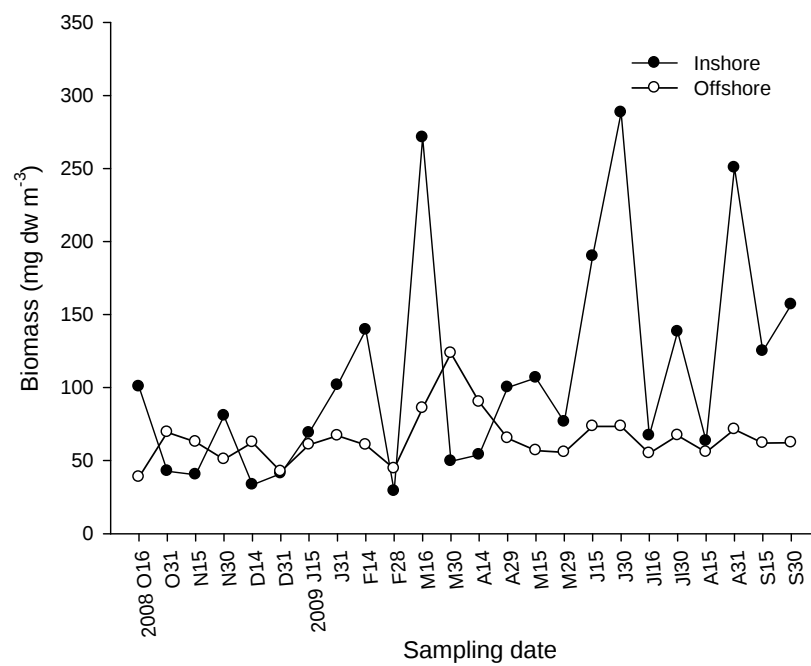


Fig. 2.27. Spatio-temporal variation of crustacean biomass.

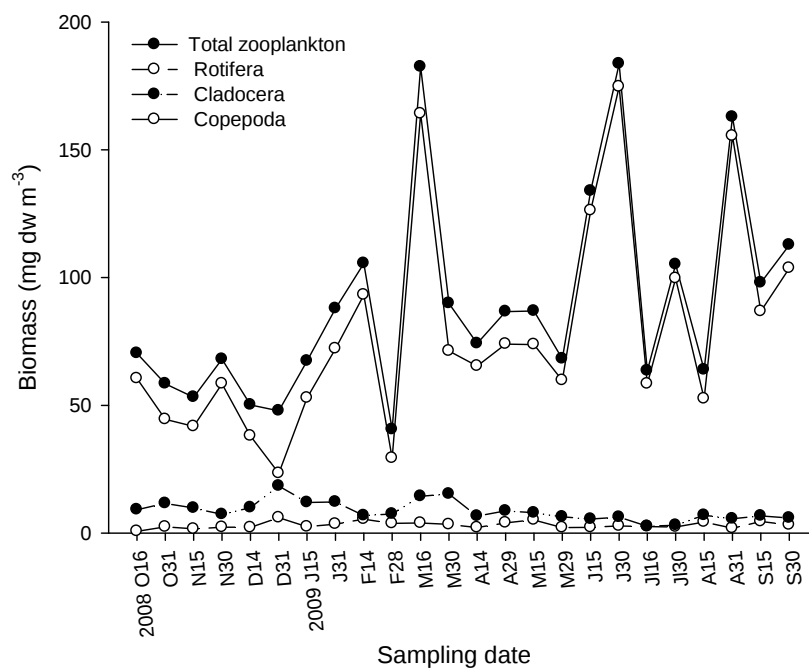


Fig. 2.28. Seasonal variation of zooplankton biomass, mean biomass of rotifers, cladocerans and copepods.

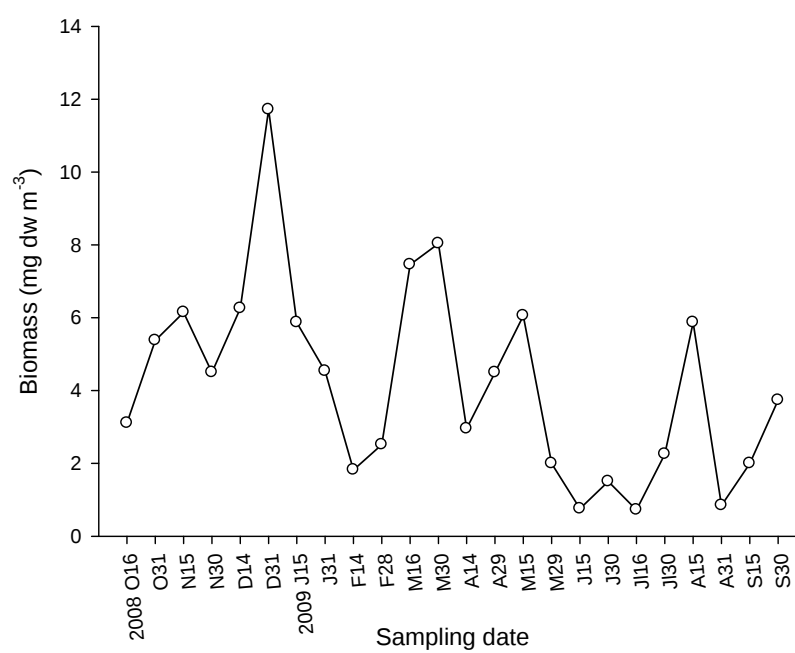


Fig. 2.29. Seasonal variation of *Moina micrura* biomass.

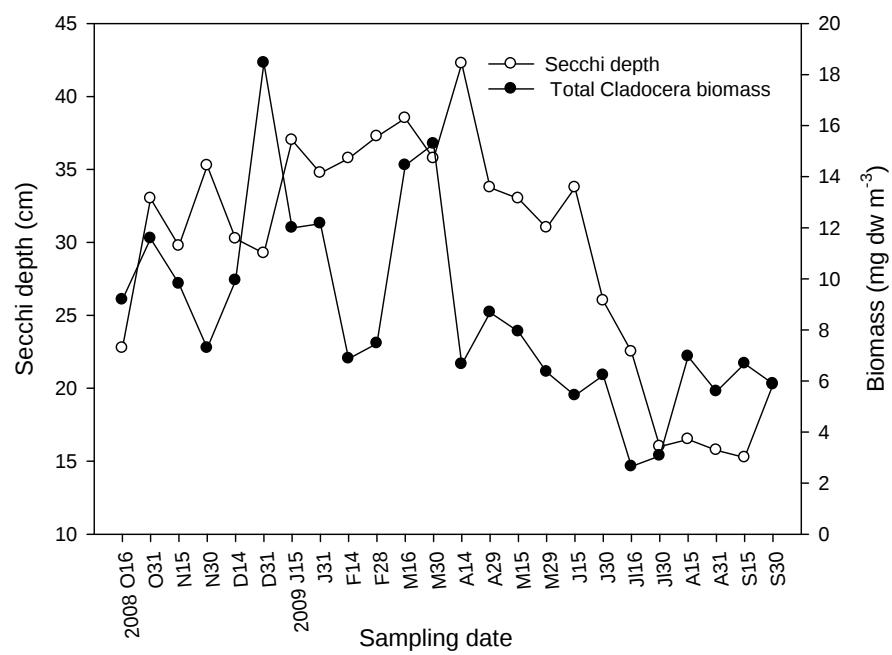


Fig. 2.30. Temporal variations in the total cladoceran biomass and lake water transparency.

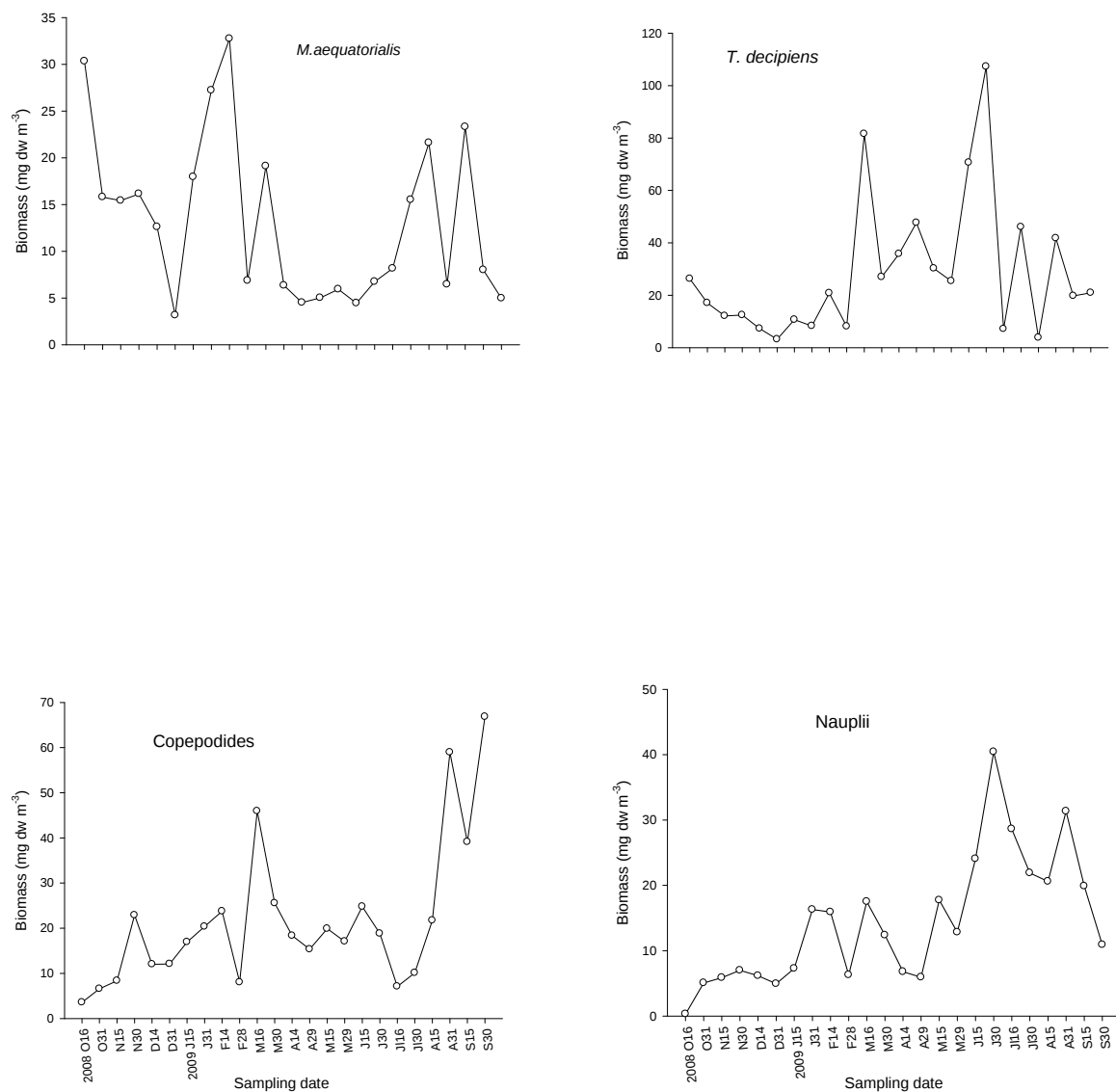


Fig. 2.31. Seasonal variation of copepod developmental stages biomass.

Discussion

Environmental conditions

Conductivity, turbidity, water transparency (secchi depth), inshore dissolved oxygen and Chlorophyll a concentration showed pronounced fluctuations. On the other hand, water temperature, offshore dissolved oxygen and pH showed little temporal variation. The water column was well oxygenated throughout the study period. The maximum variation between the upper 0,5 m water stratum and the bottom 2,5 m at the offshore station was less than one mg l^{-1} (range: 0,02 - 0,94 mg l^{-1}); this was the result of wind-induced mixing. On the other hand, the frequent fluctuations in the dissolved oxygen in the inshore station could be due to the presence of dense macrophyte stands in the inshore station. Progressive increase in the conductivity during the dry period and a decline towards the rainy season could be explained by lake level fluctuation and more evaporative concentration of ions during the dry period and dilution for the decline of conductivity. The conductivity ranged between 389 and 458 μScm^{-1} and was well in the range of values from the long-term records (372-427 μScm^{-1} recorded in 1937/38 by Cannicci and Almagia (1947); 300-400 μScm^{-1} by Martens and Tudorancea (1991) and 295-468 μScm^{-1} by Zinabu *et al.* (2002)).

The brown color throughout the study period is the result of the influence of wind induced turbulences that keep sediment particles suspended in the water column. Frequent wind-induced turbulence together with sediment laden inputs from surface run off and river inflows during the main rainy season have substantial impact on the turbidity and on the water transparency of the lake. The high turbidity (maximum up to 342 FTU) was the major cause for the decline in most abiotic and biotic components of the lake during the rainy season. The lowest records of secchi depth, dissolved oxygen and sharp decline in Chlorophyll a concentration were recorded during the time of high turbidity. The increase in turbidity following rainfall is clearly a basic limnological feature of the lake. At the same time physical, chemical and biological parameters showed a general decline. Abiotic conditions such as water temperature, dissolved oxygen, conductivity and pH did not correlate significantly with zooplankton abundance. This could be attributed to the low spatio-temporal variation of abiotic factors. The increase in Chlorophyll a following the rainfall was well explained by the associated increase in nutrient availability through the inflows into the lake. During the main rainy season a decline in Chlorophyll a concentration was observed. This

could be attributed to the reduction in the water transparency which affects the underwater light climate. Chlorophyll a increased with the increase in water transparency shortly after the peak turbidity. The absence of depth distribution pattern in Chlorophyll a concentration is the result of frequent mixing of the lake and a homogenous distribution of algae over the water column. Viable algae may settle and accumulate in the lower water column but are brought up again by the resuspension. The mean Chlorophyll a ($23,4 \mu\text{g l}^{-1}$) during the present study is low compared to previous records from the lake (e.g. $91 \mu\text{g l}^{-1}$ Belay and Wood, 1984; $186,8 \mu\text{g l}^{-1}$ Tilahun, 1988; $154,2 \mu\text{g l}^{-1}$ Kebede *et al.*, 1994; $82,4 \mu\text{g l}^{-1}$ Zinabu *et al.*, 2002). The decline in Chlorophyll a in the recent studies is not clear. Nutrient limitation could not be the reason since there is an increase in the nutrient like soluble reactive phosphorus (see Zenabu *et al.*, 2002). High turbidity of the lake could contribute for such low records.

Plankton community composition

Phytoplankton

Besides the information on physico-chemical variables, information on the phytoplankton community is essential to evaluate the fluctuation in composition and abundance of the herbivorous plankton organisms. The phytoplankton community was dominated by large colonial forms like *Microcystis* species and filamentous *Anabaena* and *Oscillatoria* species. *Microcystis* earlier reported with 80% of the phytoplankton biomass (Schröder, 1984) contributed even higher percentages during the present study. Among the diatoms, *Fragilaria* and *Synedra* species were dominant during the dry season. *Microcystis* species dominated throughout the study period where as *Anabaena* and *Oscillatoria* co-dominated following the short wet periods through the rainy season. Most phytoplankton species however were present following the short wet periods in May, June and through the main rainy season. Green algae showed low abundance compared to the blue greens and diatoms which might be due to the different mechanisms in coping with the turbid waters. Previous studies on phytoplankton of Lake Ziway also documented the dominance of blue green algae, mainly large filamentous and colonial forms (Schröder, 1984; Wood and Talling, 1988; Kebede and Willen, 1998; Dagne *et al.*, 2008). Absence of large filter feeders from the lake could contribute to their dominance in such turbid environment. However, the response of phytoplankton is not only the result of grazing pressure and nutrient availability. The change in the light climate due to

suspended sediments, self shading, wind, seasonal hydrological events can lead to temporal changes in the composition of phytoplankton. According to Tilman *et al.* (1986) blue greens are able to grow under low light intensities or more turbulent conditions (Allanson *et al.*, 1990; Scheffer, 1998). Large herbivorous zooplankton species are rare in the tropics as compared to the temperate zones (Fernando, 1994, Sarma *et al* 2005) and small bodied zooplankton with low grazing pressure do not have the capacity to control the large colonial and filamentous blue greens (Lazzaro, 1997) and they are inedible for many herbivorous zooplankton (Lampert, 1987). Even the filter feeding Nile *Tilapia* had no effect on the biomass of large algae (Okun *et al.*, 2008).

In shallow lakes like Lake Ziway, continuous stirring of the bottom sediments by benthic feeding fish (e.g., catfish and *Gara* sp.) and the turbulences could ensure the availability of nutrients in the water column and help the blue greens to dominate. Dominance of blue greens with increasing nutrient concentration is also reported by Elser (1999). Internal recycling of phosphorous via *Tilapia* excretion is also reported to contribute to the external total phosphorous load in a reservoir in Brazil (Starling *et al*, 2002) which may be the case in Lake Ziway too. It could be possible that *Hippopotamus* populations contribute to nutrient pool as they graze in the littoral in the evening and defecate in the lake. Together with high temperature and no marked seasonal variation the above mentioned factors could favour blue greens to dominate all year round in Lake Ziway.

Zooplankton

The species composition of zooplankton reflects typical tropical aspects, with rotifers being by far the dominant taxa (Green, 1993; Fernando, 1994; Dagne *et al.*, 2008). 49 rotifer species were identified in the present study but only 10 crustaceans. The rotifer species number is not only planktonic, more than fifty percent were identified from the littoral macrophyte beds. The methodological approach, using small mesh size plankton net (40 µm) that can retrieve the smaller rotifers and sampling from offshore and the littoral with dense macrophyte belt, does lead to high species numbers. The rotifer species composition in the present study agrees very well with previous records (Dagne *et al.* 2008). Most species, particularly Brachionidae (*B. angularis*, *B. calyciflorus*, *B. caudatus*, *Anuraeopsis coelata*, *Keratella tropica*, and *Plationus patulus*), and Lecanidae (*L. furcata*, *L. luna*, *L. aculeata* and *L. closterocerca*), are already reported from 1927 (Bryce, 1931). From a biogeographical perspective, wide-ranging rotifers are dominant, with the large majority being cosmopolites, in many cases with a range

including the Antarctic and/or Pacific region, some are tropicopolitan (Dagne *et al.*, 2008). Rotifer species numbers dominating over the ones of crustaceans is in agreement with reports from other African lakes (Table 2.12). The smaller zooplankters are in general known to be less impacted by blue green algae (Pinel-Alloul, 1993; Bouvy *et al.*, 2000). In his studies on zooplankton communities from East African lakes, Green (1993) found that rotifers have more species in the plankton than copepods and cladocerans. Green and Mengestou (1991) found that the mean momentary rotifer species number from Ethiopian water samples is higher than the mean for the rest of the world. It can also be possible that rotifers benefited from the high turbidity of the lake as they are less affected than larger filter feeders (Hart, 1988; Kirk, 1991). The correlation analysis for the Ziway data (Table 2.9) also revealed that the highest significant coefficient for copepods and rotifers was with chlorophyll. Cladocerans however correlated weakly and negatively with chlorophyll but strongly with secchi depth.

Most studies on zooplankton of the Ethiopian water bodies are qualitative (taxonomic description and faunistic lists) and usually the result of expeditions (Lowndes, 1930; Dumon, 1983; Van de Velde, 1984; Green, 1986 and Defay, 1988). The zooplankton species inventory from Ethiopian water bodies is still not complete and in general the taxonomy of species from some of earlier studies from African water bodies are under revision; e.g. Van de Velde, 1984 - revision of the African species of the genus *Mesocyclops*; Jeje, 1988 - revision of the Nigerian species of *Mesocyclops* and *Thermocyclops*; Jeje, 1992 - redescription of *Diaphanosoma senegal*; recently Kotov and Taylor, 2010- re-described *Daphnia obtusa* as new species *Daphnia izpodvala* sp. nov.. Among the cladoceran species *Moina micrura*, *Ceriodaphnia cornuta*, *Ceriodaphnia dubia*, *Daphnia barbata*, *Daphnia carinata*, *Daphnia hyalina*, *Daphnia lumholtzi*, *Daphnia longispina*, *Daphnia magna*, *Daphnia pulex*, *Alona diaphnia*, *Diaphanosoma excisum*, *Diaphanosoma mongolianum*, *Diaphanosoma sarsi* and *Pseudosida szalay* are reported from most lakes in Ethiopia (Cannicci and Almagia, 1947; Wodajo and Belay 1984; Belay, 1988; Mengestou and Fernando, 1991a; Dumont, 1994; Dejen *et al.*, 2004; Dagne *et al.*, 2008; Dejenie *et al.*, 2008; Fetahi, 2010 and this study). The presence of vast altitudinal ranges among the inland waters of Ethiopia and the variation in salinity among the water bodies (Kebede *et al.* 1994; Zinabu *et al.*, 2002) are of great interest for faunistic and ecological studies. Besides typical tropical crustacean representatives earlier studies reported the presence of some temperate species from Ethiopian water bodies like *Daphnia obtusa* (Löffler, 1978) and member of the genus *Arctodiaptomus* (Dussart, 1974) in the highland mountain lakes. However, *Daphnia obtusa* is recently re-described as new species by Kotov and Taylor as *Daphnia izpodvala* sp. nov. (Kotov and Taylor, 2010).

Table 2.12. Crustacean species numbers from African lakes

Lake	Rotifera	Cladocera	Copepoda	Reference
Abijata	13	-	4	Wodajo and Belay, 1984
Naivasha	12	11	3	Mavuti and Litterick, 1981
Kivu	12	4	3	Isumbisho <i>et al.</i> , 2006
Guiers	14	5	9	Kâ <i>et al.</i> , 2006
Ziway	49	7	3	Dagne <i>et al.</i> , 2008; this study
Awassa	40	5	8	Green and Mengestou, 1991 & Mengestou and Fernando, 1991a

Recent studies indicated a pronounced variation in zooplankton species composition in Lake Ziway. *Ceriodaphnia cornuta* and *Daphnia barbata* which were not reported in earlier studies (e.g. Belay, 1988 and Fernando *et al.*, 1990) were reported by Dagne *et al.* (2008) and completely disappeared after half of the present sampling period. *Pseudosida szalay* and the invertebrate predator *Chaoborus* sp. which were not reported in the previous studies (Belay, 1988; Fernando *et al.*, 1990; Dagne *et al.*, 2008) could be identified in this study. Compared to rotifers and cladocerans, species composition of copepods showed no fluctuation in their composition; three cyclopoid species *Afrocylops gibsoni*, *Mesocyclops aequatorialis* and *Thermocyclops decipiens* reported in the earlier studies (e.g. Belay, 1988; Dagne, 2004) were identified in the present study. Copepod species identified from most water bodies in Ethiopia include the calanoid species *Lovenula africana* (Daday), *Thermodiaptomus galebi lacustris* and other calanoid species from a highland reservoir (above 3000m a.s.l. personal observation) and the cyclopoid copepods *Afrocylops gibsoni*, *Mesocyclops aequatorialis*, *Mesocyclops salinus*, *Microcyclops varicans*, *Thermocyclops ethiopiensis* (Defay, 1988), *Thermocyclops decipiens*, *Thermocyclops consimilis*, *Cryptocyclops bicolor breviramus*, *Ectocyclops rubescens*, *Eucyclops* cf. *serrulatus*, *Tropocyclops confinis* (source: Dussart, 1974; Wodajo and Belay 1984; Van de Velde, 1984; Defay, 1988; Belay, 1988; Mengestou and Fernando, 1991a; Dejen *et al.*, 2004; Dagne, 2004 and this study).

Spatio-temporal distribution and abundances of zooplankton in relation to abiotic and biotic factors

The distribution patterns of aquatic organisms vary as a function of the scale of investigation. Sampling over long time interval may not reflect the short term events in the pelagic communities (Twombly, 1983; Pinel-Alloul, 1995). Comparison between the distribution patterns of total zooplankton in Lake Ziway from two different sampling intervals (biweekly and monthly) indicates how sampling intervals could affect the final results. In the monthly sampling short-term fluctuations in the population were masked, but becomes obvious from the biweekly taken samples. This strengthens the importance of a sampling strategy which considers the development times of the various plankton organisms (Twombly, 1983; Avois *et al.*, 2000).

The spatial distribution pattern of zooplankton was another distinct feature observed in the present study. The littoral species *Alona* reported to be dominant in the open water of lakes Ziway and Awassa (Fernando *et al.*, 1990) was not confirmed in the present study. *Alona* occurred in higher densities inshore. *Alona* contributed 12,1% of the total crustaceans during its peak abundance at the inshore station but hardly reached 1% in the open water. Such distribution pattern, littoral species being in the open water could be due to the violent and frequent turbulence in Lake Ziway. Two to five fold abundances of zooplankton inshore compared to offshore of Lake Ziway also support the presence of variation in the spatial distribution. Dense macrophytes in littoral could provide a refuge against predation (see also Laurdisen and Buenk, 1996; Burks *et al.*, 2002). According to Moss (1998) structural complexity (dense emergent, submerged and floating macrophytes) has an important role in the diel horizontal migration of zooplankton. On the contrary size variation in the distribution of copepod species was evident in the present study, larger adults and egg carrying *Mesocyclops aequatorialis* females were almost absent from day samples and rare in the inshore station. From 24 sampling cruises conducted only 14 *Thermocyclops decipiens* and 1 *Mesocyclops aequatorialis* egg carrying females were recorded which indicates avoidance of the macrophytes by the larger sized copepods. This could probably be due to high predation pressure from benthic and ephiphytic invertebrate predators (Sih *et al.*, 1998). According to Cattaneo *et al.* (1998) the macro-invertebrate density often increases with surface area and structural complexity of the macrophytes and hence may lead to a high impact by predators. Another possible reason for the avoidance of macrophytes by *Mesocyclops* could be the presence of juvenile *Tilapia* in the littoral throughout most of the sampling period which may pose a significant predation on the larger adult copepods or they avoid the macrophytes due to chemical cues from the fish. It is difficult to explain such fluctuations (presence and/or absence) in species composition due to a lack of extensive and long-term studies and different methodological approaches like in the case of *Chaoborus* which could stay in the bottom sediments during day time and is missed in the plankton samples. On the other hand dominance of the small sized *Thermocyclops decipiens* in all stations throughout the sampling period could be the result of its omnivorous feeding habits; this species is reported to feed on *Microcystis* and nauplii in Lake George Uganda (Burgis, 1969). It may have gained an advantage from the dominance of blue green algae and the fact that it is less attractive for a predator due to its small body size (average total length 641µm) in Lake Ziway. *Thermocyclops* is the only crustacean which developed peak abundance at the time of peak phytoplankton development.

The consistency in the absence of large adults and egg carrying copepods from day samples drew the attention to conduct diel vertical sampling in this highly turbid shallow system. A clear vertical distribution gradient mainly by the larger and egg carrying copepods became obvious. Numbers of egg carrying females and their clutch size were larger from night samples and increased with depth in the day samples. Vertical distribution of zooplankton according to the light intensity to avoid visual predators has been indicated in several experimental and field observations (e.g. Gliwicz, 1986; Ballons and Frost, 1991; Lampert, 1993; Ringelberg, 1995). Staying in the deeper and darker water during the day time and migrating into the surface waters at night is mainly performed to avoid predation. However, in shallow lakes where the water transparency is generally low, diel vertical migration may hardly been observed. Rather in such shallow lakes, large bodied zooplankton such as *Daphnia* species migrate horizontally from the open water to the littoral into the macrophytes seeking a refuge against predators (Burks *et al.*, 2002).

There exists some support for the presence of diel vertical migration by the larger size copepods mainly egg carrying *Mesocyclops*. Temporal length-frequency distribution of this species indicates that larger individuals were absent from day samples but were present in night samples. Predation by fish (catfish) and the invertebrate predator *Chaoborus* could be the major cause for the diel vertical migration. Migration of egg carrying *Mesocyclops* to the greatest water depth is also reported by Guisande *et al.* (1991). Several studies indicate *Chaoborus* as a major component of the limnetic food web in tropical lakes (e.g. Lake Chad - Saint-Jean, 1983; Lake Malawi - Irvine, 1997; or in shallow reservoirs (Aka *et al.*, 2000; Pagano *et al.*, 2003) which can be confirmed by the data from Lake Ziway. *Chaoborus* can eliminate 2-90% of the population of its prey per day (Pastorok, 1980) or 20-29 prey items per individual per day (Pagano *et al.*, 2003). An experimental study on *Chaoborus* predation on zooplankton indicated that large zooplankton like cladocerans, and adult *Mesocyclops* species are significantly affected. Consistent high selection of *Chaoborus* for cyclopoid *Mesocyclops aequatorialis* is reported from Lake Malawi (Irvine, 1997) and an increase in vulnerability of *Mesocyclops* with an increase in size from Lake Valencia (Lewis, 1979).

The abundance of some rotifer species declined at times of low water transparency (e.g. *Keratella tropica*). On the other hand, the highest peak of *Brachionus angularis* was attained at the time of peak turbidity. This could be the result of an increase in bacterial density during this episodic event. Cladocerans showed a progressive decline in the abundance towards the rainy season which was associated with the progressive decline in the water transparency.

Cladocerans generally occurred in very low abundance. Their contribution to the total crustaceans as well as total zooplankton was low throughout the investigation period. It is also evident that the standing stock of cladocerans declined despite an increase in Chlorophyll a concentration following the decline in water transparency.

From six major abundance peaks in total zooplankton only two (mid March and end of June) supported maximum zooplankton biomass and the third peak biomass occurred two weeks after the maximum zooplankton abundance peak in mid August. The discrepancy in this case was due to the difference in the species that contributed to the peak abundance, rotifers and pre adult stages of copepods comprised 96% but adult copepods only 1,3%. The first sharp decline in zooplankton biomass between end of March and May coincided with the increase in the mean water transparency and the second from June to mid August during the reverse. The relative increase in the adult copepod abundance during the high turbidity could be the result of turbidity providing some sort of refuge against predators and/or the increased detrital food associated with the rainfall favours these species. Abundance peaks developing shortly after the peak turbidity was observed by different species and as chlorophyll increased as well, food might be the major reason.

The temporal pattern in zooplankton abundance is characterized by seasonal variation. Close examination on the peak abundances attained by 30 zooplankton species and stages on the bases of hydrological cycles indicated that 53,3 and 46,7%, of the species showed their peak abundances in the dry and rainy season, respectively. Analysis of variance of zooplankton abundances also revealed the presence of seasonal variation. Rotifers abundances during dry, pre-rainy and rainy seasons were significantly different from post-rainy season. There was no significant difference in rotifers abundances between dry and rainy season. Cladocerans abundance varied significantly within seasons except between the pre-rainy and rainy and pre-rainy and post rainy season. Abundance during the dry season showed highly significant difference with the ones in the rainy season, the former being the maximum and the latter the minimum. Copepods abundances during dry and post-rainy, pre-rainy and rainy seasons were not significantly different. Highly significant difference in copepods abundance was between pre-rainy and post-rainy, between rainy and post-rainy and a weak variation between dry and rainy season. The absence of significant variation in the abundances of rotifers between dry and rainy season and only weakly by the copepods unlike the highly significant difference in the cladocerans could reveal the differential impact of turbidity and food quality among zooplankton groups.

The difference in the response of cladoceran species to an increase in turbidity (e.g. disappearance of *Daphnia barbata* and *Ceriodaphnia cornuta* at low water transparency but an increase of *Moina micrura* and *Diaphanosoma excisum*) could reveal differences in the susceptibility of the species (c.f. Threlkeld, 1986). Generally, cladocerans seem to be affected by the high turbidity of the lake and the food quality. Blue greens mainly large colonial and filamentous such as *Microcystis*, *Anabaena* and *Oscillatoria* were dominant throughout the study period. It has been indicated in several studies that the formation of large colonies or filaments limits their exploitation by zooplankton through physical constraint on ingestion, nutritional inadequacy and toxicity (DeMott and Moxter, 1991; Haney *et al.*, 1994, Gilbert, 1990). The strong inhibitory effect of *Microcystis aeruginosa* on the feeding of daphnids and increased mortality is also evident from laboratory studies (Lampert, 1987). The dominance of copepods and rotifers over cladocerans in Lake Ziway could be the result of their competitive advantage over cladocerans. Feeding experiment did show that rotifers and smaller zooplankton were dominant in the presence of blue green filament *Anabaena* (Fulton, 1988). The correlation analyses of Cladocera, Copepoda and Rotifera abundances with algal food (chlorophyll) in the present study also indicated similar result (Table 2.9). The phenology of *Ceriodaphnia cornuta* is difficult to be explained; probably *Chaoborus* predation is responsible for population losses. Lewis (1977) discusses *Chaoborus* switching from daily feeding on copepods to night feeding on cladocerans.

The analyses of gut contents from fish species of Lake Ziway point into the direction of zooplanktivory on larger copepods. *Clarias gariepinus* fed mainly on copepods and *Carassius carassius* to a lesser extent. Observation of the gut content revealed that larger adults were the major prey item. Culture experiment on catfish revealed that this opportunist feeder can graze on zooplankton by creating a strong suction pressure (Rahman *et al.*, 1992). It has also been reported from Lake Kinneret, Israel (Gophen, 1988; Gophen *et al.*, 1990) that zooplanktivory by fish was significantly high on adult *Mesocyclops* species but not on *Thermocyclops* species. On the other hand phytoplankton (mainly blue green algae) and detritus were found to form the entire stomach contents of juvenile stages of *Tilapia*. However, the juvenile stages of *Tilapia* are reported to feed on zooplankton (Tudorancea *et al.*, 1988; Chapman and Fernando, 1994; Elhigzi *et al.*, 1995). A recent study on Lake Hashenge, one of the highland Ethiopian lakes also indicated the presence of abundant zooplankton species in the stomachs contents of *Oreochromis niloticus* (Tadesse, 2010). There is also evidence from an experimental study that *Tilapia* selectively feed on large cladocerans (Okun *et al.*, 2008) which may have a negative impact on phytoplankton and zooplankton biomass (Menezes *et*

al., 2010). It is very likely that predation pressure of fish and *Chaoborus* on the larger zooplankton organisms (e.g. *Daphnia barbata* and *Mesocyclops*) shifted zooplankton community structure in Lake Ziway towards the dominance of the smaller sized *Thermocyclops*, pre-adult copepods and rotifers.

Population dynamics of crustaceans

The method of calculating the numbers of individuals that pass through each instar into the next development stage appeared to be applicable to the Ziway data. Theoretical number of individuals that passes through each developmental stage into the next stage was calculated using Southwood's graphical method (Southwood, 1978). The wide gap between the number of *Moina* neonates passing into the adult stage and the adults found in the period March to April coincided with increased water transparency and could be the result of the loss of adults due to predation by fish and *Chaoborus*. In the cyclopoids, a much wider gap between the numbers of copepodides based on the theoretical input coming from nauplii and the actual numbers of copepodides being present was observed between May and June. Low food quality seemed to affect the copepodid stages. Although phytoplankton biomass increased continuously in these periods, more species of blue greens (e.g. *Anabaena* and *Oscillatoria* spp.) were dominant together with *Microcystis* sp. It was also evident that egg production and nauplii density were increasing in this period but copepodid numbers were lower. Nauplii seem to be less influenced by the food situation than the later developmental stages. This is in agreement with experimental results where copepodid stages were more dependent on food than nauplii (Hart, 1991). The theoretical number of copepodides developing into adult stages agreed well with the number of adults found in the samples except in the last two samplings where counts of adults were lower than the recruits coming from the copepodid stage. This could be the result of counting error. The samples were mainly *Thermocyclops* and adults could be considered as last copepodid stage.

Multiple factors seem to regulate egg production of cyclopoids: temperature, food, turbidity and predation. Egg production was continuously decreasing during the relatively cold dry period end of October to mid January. The second similar decline in egg production occurred from mid March to end of April and coincided with an increase in the secchi depth and hence predation on the larger egg carrying females may have increased. The maximum egg production by *Mesocyclops* and *Thermocyclops* occurred in mid July which was due to the

presence of more ovigerous cyclopoids in the samples. The reduced water transparency could provide a refuge for the ovigerous females from their predators and hence more female with eggs were in the plankton. Proportion of ovigerous females and clutch sizes of *Mesocyclops* were very low during the dry period when the lake water was relatively transparent and increased during the wet period. Temporal fluctuation in clutch size was much higher in *Mesocyclops* close to 30 times than in *Thermocyclops* where the maximum was only 3 fold; this might reflect the predation pressure upon them (e.g. maximum size of *Thermocyclops* was 890 μm but 1525 μm for *Mesocyclops*). The recruitment was much higher during the rainy season; availability of algal food following the rainfall as well as the presence of more females with eggs in the samples could be the reasons. Similar results are reported from Lake George (Burgis, 1974) and Lake Naivasha (Mavuti, 1994). Although samplings were conducted from the near bottom of the lake, the numbers of females with eggs could be underestimated. As discussed above, their presence in high numbers in the night samples and the possibility that ovigerous females could migrate deep (Guisande *et al.*, 1991) could result in such low numbers of ovigerous females in the samples.

Continuous production of eggs by *Thermocyclops* compared to *Mesocyclops* could lead to the dominance of *Thermocyclops* over the larger clutch sized *Mesocyclops* throughout the sampling period. Ovigerous *Mesocyclops* was almost absent from most samples, the maximum proportion was 3 % of the adults but 20% by *Thermocyclops*. The omnivorous feeding habits of *Thermocyclops* could favour the development of this species. This species is reported to feed on *Microcystis* in Lake George Uganda (Burgis, 1969). It may have gained an advantage from the dominance of blue green algae in Lake Ziway and the fact that it is less attractive for predators due to its smaller size. This was also evident from the peak abundance of *Thermocyclops* that occurred following the peak in algal food (Chlorophyll a). *Mesocyclops* however, was under predation pressure from fish and *Chaoborus* and hence developed in low numbers in the plankton.

Zooplankton biomass

The annual variation in zooplankton biomass was low, i.e. the average maximum to minimum ratio was 4,5 (offshore 3,2; and inshore 9,9). Much larger variation was observed among individual species and between sampling stations. *Moina* showed a 60 and 45 fold annual variation in the inshore and offshore station, respectively. The largest difference between

maximum and minimum biomass ratio was estimated for *Thermocyclops* (275 fold inshore, but only 10 fold offshore). The biomass variation of *Mesocyclops* was lower (7 fold in the offshore but 30 fold in the inshore station). The factors responsible for the maximum and minimum biomass of the three species vary. *Moina* showed lowest biomass during high turbidity, while *Thermocyclops* respond well with the increase in algal food (Chlorophyll a), offshore *Mesocyclops* biomass was maximum during high turbidity which could be due to reduced predation pressure from fish and *Chaoborus*. The occurrence of *Mesocyclops* in high density during reduced predation pressure but not in the case of *Thermocyclops* could be explained by the difference in body size (e.g. maximum size 1525 mm and 890 mm, respectively and clutch size maximum 64 and 26). A maximum/minimum ratio of <10 for zooplankton biomass is reported from other tropical lakes (e.g. Awassa: Mengestou and Fernando, 1991b; George: Burgis 1974; Chad: Saint-Jean 1983). High seasonal fluctuation 13-99 is reported from Lake Valencia (Saunders and Lewis, 1988), variation in the abiotic factors and predation pressure from *Chaoborus* are mentioned as major factors. In Lake Ziway, it seems that interacting factors (high turbidity, low food quality and predation) could be the reasons for the observed high biomass maximum to minimum ratios among individual species.

Biomass estimates of tropical zooplankton reveal large variability. The mean total zooplankton biomass of Lake Ziway (91 mg dwt m⁻³) is about 4 times lower than the one from Lake George (Burgis, 1974), 3,7 times lower than from Lake Chad (Caramouze *et al.*, 1983) and 2,4 times lower compared with Lake Naivasha (Mavuti and Litterick, 1981). But it is 2 times higher than the report from the Rift Vally Lake Awassa (Mengestou and Fernando, 1991b). Even though some species were found to be common among these lakes, the species which contributed most to the biomass differ. The common feature of these lakes is the absence of larger *Daphnia* species which results in lower biomass. Most tropical lakes are dominated by either one or a few copepods (e.g. Burgis, 1974; Mavuti and Litterick, 1981; Hart, 1987; Mengestou and Fernando, 1991b; Irvine and Waya, 1999; Wondie and Mengestou, 2006; Isumbisho *et al.*, 2006; Dagne *et al.*, 2008).

The results from Lake Awassa were of special interest because they dealt with similar species and are from the same region in the Rift Valley (Ethiopia). However, the major contributor to the total biomass differs, i.e. adult *Mesocyclops* contributed 44% in Lake Awassa, but an equal amount (40%) was contributed by pre adult cyclopoids in the present study. Although the larger *Mesocyclops* was the dominant in Lake Awassa the biomass is lower because of

lower numbers. *Mesocyclops* density in Lake Awassa is 3 times greater than the density of the same species in Lake Ziway but 3 times lower than cyclopoids nauplii or 6 times lower than copepodides. The major factors which could have impacted the zooplankton in lakes Ziway and Awassa were also different. In the present study high turbidity, low food quality (mainly large colonial and filamentous species which dominate throughout the year) and predation from fish and *Chaoborus* were the major factors affecting zooplankton species composition, distribution and standing stocks in Lake Ziway.

Total cladocerans biomass and population density showed contrasting difference between the relatively less turbid periods and the time of very low water transparency. Between January and April when secchi depth ranged between 34,3 and 41,7 cm, the total cladoceran density and biomass were 3 and 2,1 fold higher, respectively than when the water transparency declined to a range of 15-29 cm in the period June to September. In contrast, an increase in the total copepods density (1,4 fold) and biomass (1,3 fold) were observed during the high turbid conditions from June to September.

Chapter 3

Development times and production of dominant crustaceans

Introduction

Presence of seasonality and variation in the species composition and population densities of tropical zooplankton have been described and discussed by several authors as reviewed in the previous chapter. Information about population dynamics is still limited. Although the importance of secondary production studies for the understanding of the functional role of organisms (Amarasinghe *et al.*, 1997), of energy or material transfer and the rational management of aquatic resources (Downing, 1984) is known, such studies from tropical water bodies are generally scarce (see review by Amarasinghe *et al.*, 1997). Despite a growing body of limnological studies from tropical water bodies, zooplankton production studies are far less compared to studies on fisheries and primary production (Burgis, 1974; Carmouze *et al.*, 1983; Gras and Saint-Jean, 1983; Vareschi and Jacobs, 1984; Hart, 1987; Kimmerer and McKinnon, 1987; Mengestou and Fernando, 1991b; Mavuti, 1994; Irvine and Waya, 1999). The situation is even worse for Ethiopian water bodies where only a few studies on zooplankton production are reported so far (Mengestou and Fernando, 1991b; Wondie and Mengestou, 2006). Lack of laboratory facilities (e.g. culturing chambers with controlled temperature, micro balance and appropriate microscope), laborious intensive field sampling and laboratory processing are the limits for studies on secondary production from tropical water bodies.

Reliable estimates of the development time of the population under study are essential for the estimation of secondary production which needs culturing the animals at temperatures similar to those in their natural habitats (Vijverberg, 1989). Sampling strategy should consider short sampling intervals roughly equal to the embryonic duration of the animals for proper estimates of population birth and death rates (Keen and Nassar, 1981). According to Herzig (1983) the accurate estimation of population dynamics requires 2 or 3 times sampling per week for most entomostracan crustaceans in a water body with water temperature above 20 °C.

Despite the fact that any study of zooplankton secondary production is laborious, knowledge on population dynamics and identifying the driving forces of change is crucial in understanding aquatic ecosystems and their management (e.g. fisheries management and water quality monitoring). Such studies are important in countries like Ethiopia where an increasing human population and an increasing demand for fish especially in the Rift Valley areas need a wise management of water bodies. Different computational models are suggested to estimate secondary production. However, the population under study needs to satisfy the assumptions in the models. Recruitment and growth in tropical zooplankton are continuous and therefore, a simple cohort approach cannot be used (Rigler and Downing, 1984). For such population independent information on growth and recruitment is needed together with field population structure, density and fecundity data. It can be obtained through culturing of the animals in the laboratory (Vijverberg, 1989). In the present study I conducted laboratory experiment on development times of common crustaceans. For the production calculations field data on population densities, length measurements and fecundity data together with laboratory determined dry weights and durations of development were used.

The objective of this part of my study is therefore to generate information on the development times of crustaceans and to estimate their production.

Material and Methods

Sample collection

Zooplankton sampling and biomass measurement methods are as described in chapter 2. Animals for the laboratory experiments were collected from the lake using 100 µm mesh plankton net during the routine sampling. The filtered sample was transferred into plastic container with lake water. More lake water was filtered with 40 µm mesh plankton net for latter use as food. Samples were immediately transported to the laboratory which is located at the shore of the lake. Fresh food (filtered lake water) was collected every third day from the lake.

Cultures

Four cladocerans *Ceriodaphnia cornuta*, *Moina micrura*, *Daphnia barbata* and *Diaphanosoma excisum* and two cyclopoids *Mesocyclops aequatorialis* and *Thermocyclops decipiens*, were cultured. After two days of acclimatization, experimental animals were sorted individually under a stereomicroscope into culturing jars filled with 20 ml filtered lake water. Because of lack of laboratory facility, culturing was carried out at room temperature and culture temperatures were noted from a thermometer placed within the culture jar in a hourly interval. Filtered lake water was changed twice a day (morning and evening) to reduce food shortage since there was no additional food supply.

Development times of crustaceans

Embryonic and post-embryonic development times of *Ceriodaphnia cornuta* and *Moina micrura* were followed from individually and batch cultured females with eggs. Cultures were checked every half to one hour intervals and the newly hatched neonates were counted. Cultures of *Diaphanosoma excisum* and *Daphnia barbata* could not be completed successfully. Embryonic development times of *Mesocyclops* and *Thermocyclops* were followed from ovigerous females cultured individually and in batches. Individual ovigerous females within the culture jar were checked under stereomicroscope at hourly and a maximum of 2 hour intervals and the time from extrusion of eggs in the egg pouch till hatching was noted. Among ovigerous females in batches, the decline in the numbers of egg carrying females were closely followed up at the same time interval with the individual until all eggs hatched. The numbers of hatched females with time were noted. Newly hatched nauplii from individually cultured ovigerous females were transferred into new culture medium. Batches of the remaining nauplii from which each individual was taken were kept separately in a large petridish with the same medium and used as stock population source to replace the dead and/or missed individuals during handling in the process of microscopic checkup. Among the cladocerans, the procedure is similar. Mean development times of eggs for each species were calculated from a number of observations.

For determination of post-embryonic development times of *Mesocyclops* and *Thermocyclops* nauplii of the respective species were obtained from individually cultured ovigerous females. Individual nauplius transferred into fresh medium was checked every hour under stereomicroscope and compound microscope to identify each developmental feature using depression slides. Follow up of each copepodid stage continued from each last nauplius stage with similar procedure only the checking time interval varied between 1 to 2 hours and maximum of 4 hours. Monitoring continued until all animals developed to the final copepodid stage. The generation time is taken as the sum of embryonic and post-embryonic development times. The limitation of the present experiment is that data on those eggs laid and hatched during the night were lacking as the observation was from early morning to late evening. The problem for night observation was beyond the investigator.

The relationship between temperature and development time was described by a quadratic equation (equation 3.1), for the regression calculation only the mean durations per temperature were used,

$$\ln D = a + b(\ln T) + c(\ln T)^2 \quad (3.1)$$

where D is duration of development (hours or days) and T is temperature ($^{\circ}\text{C}$)

Crustacean production estimates

Growth increment (Winberg 1971)

Production was estimated for dominant cladocera (*Moina micrura*) and cyclopoid copepods (*Mesocyclops aequatorialis* and *Thermocyclops decipiens*) by growth increment (Winberg) method using equation 3.2. This method gives an estimate of the daily production of the population on a particular sampling occasion as the sum of the daily production of each age class present on that day. It assumes a linear growth between age classes.

$$P_d = (N_1 \cdot \Delta W_1) / D_1 + (N_2 \cdot \Delta W_2) / D_2 + \dots + (N_n \cdot \Delta W_n) / D_n \quad (3.2)$$

where P_d is production per day, $N_1 \dots N_n$ average density of each age class analyzed, ΔW was calculated from the difference between the maximum and minimum weights of each age class and $D_1 \dots D_n$ development times of the different size class/development stage. Production rates of pre adult stages of cyclopoids were not calculated at species level, but as cyclopoid nauplii

and copepodides. For the calculation of production, the field data on densities and fecundity were combined with laboratory determined length weight relation and embryonic and post – embryonic development times in relation to temperature. Adult production in copepods was estimated as the production of eggs since growth is ceased after adulthood. Egg production was calculated by dividing egg biomass by the embryonic development time. Weight of egg was assumed to be equal to the weight of the first nauplius. To estimate monthly integrated production the arithmetic mean daily production between each sampling date was calculated and multiplied by the time interval between the two sampling dates. Annual production is then calculated by summing up the monthly integrated productions. Crustacean biomass turnover rate (P/B) was calculated based on the annual production and annual mean biomass.

Results

Embryonic and Post-embryonic development times

Embryonic and post-embryonic development times of cladocerans and cyclopoid copepods are presented in tables 3.1 and 3.2. Fig. 3.1 shows the temperature-embryonic duration- response of cladoceran species from tropical water bodies. The mean temperature during the experiment (which is used to calculate the regression) varied between 21,3 and 25,1 °C. The results from these experiments were not sufficient to calculate a regression between the development times and temperature because of the rather narrow temperature range. However, the results from this study were comparable with the results from other tropical lakes (Figs 3.1-3.4). Data from these lakes with the best fit to own data were used for the calculation of the regression equations. The regression equations presented in Table 3.3 are best fitted with quadratic equations (equation 3.1). Embryonic durations of *Moina micrura* and cyclopoid copepods (*Mesocyclops aequatorialis* and *Thermocyclops decipiens*) showed a decline with an increase in temperature (Figs 3.1; 3.2). Similar declining trend in post-embryonic duration of *Mesocyclops* was observed. However, post-embryonic duration of *Thermocyclops* showed an increasing trend at higher temperature (Figs 3.3; 3.4).

Table 3.1. Embryonic and post-embryonic development times in days (mean $\pm$ SD.), temperature ($^{\circ}\text{C}$) and numbers of experiments (n) of cladoceran species

	Temperature ($^{\circ}\text{C}$)	Mean $\pm$ SD. (days)	n
<i>Ceriodaphnia cornuta</i>			
Embryonic:	23,3	1,85 $\pm$ 0,15	3
	24	1,54 $\pm$ 0,19	9
	24,5	1,35 $\pm$ 0,09	6
	24,8	1,34 $\pm$ 0,11	5
	25,1	1,17 $\pm$ 0,06	2
Post-embryonic:	24	2,75	1
	24,2	2,69 $\pm$ 0,08	2
<i>Moina micrura</i>			
Embryonic:	22,8	1,95 $\pm$ 0,06	4
	23,7	1,76 $\pm$ 0,15	7
	24,1	1,62 $\pm$ 0,14	8
	24,4	1,5 $\pm$ 0,08	3
	25	1,42	1
Post-embryonic	24	3,5	2

Table 3.2. Embryonic (D_e) and post-embryonic development times (D_n and D_c) of cyclopoid copepods

Species	Temperature ($^{\circ}\text{C}$)	Mean $\pm$ SD. (days)	n
development stages			
<i>Mesocyclops aequatorialis</i>			
D_e	23,4	$1,72 \pm 0,24$	7
	24,4	$1,44 \pm 0,45$	7
D_n	21,3	$8,2 \pm 0,97$	9
	22	7,5	1
	22,9	$6,6 \pm 0,52$	13
D_c	22,3	$13,2 \pm 2,21$	11
	22,6	$12,3 \pm 1,1$	13
<i>Thermocyclops decipiens</i>			
D_e	23	$1,8 \pm 0,15$	4
	23,3	$1,58 \pm 0,07$	4
	23,9	$1,59 \pm 0,12$	7
	24,2	$1,54 \pm 0,11$	13
D_n	23	$8,17 \pm 0,71$	9
	23,8	$11,67 \pm 1,5$	9
D_c	23,4	10	1
	24	$15 \pm 1,73$	3
	24,4	$16 \pm 1,63$	4

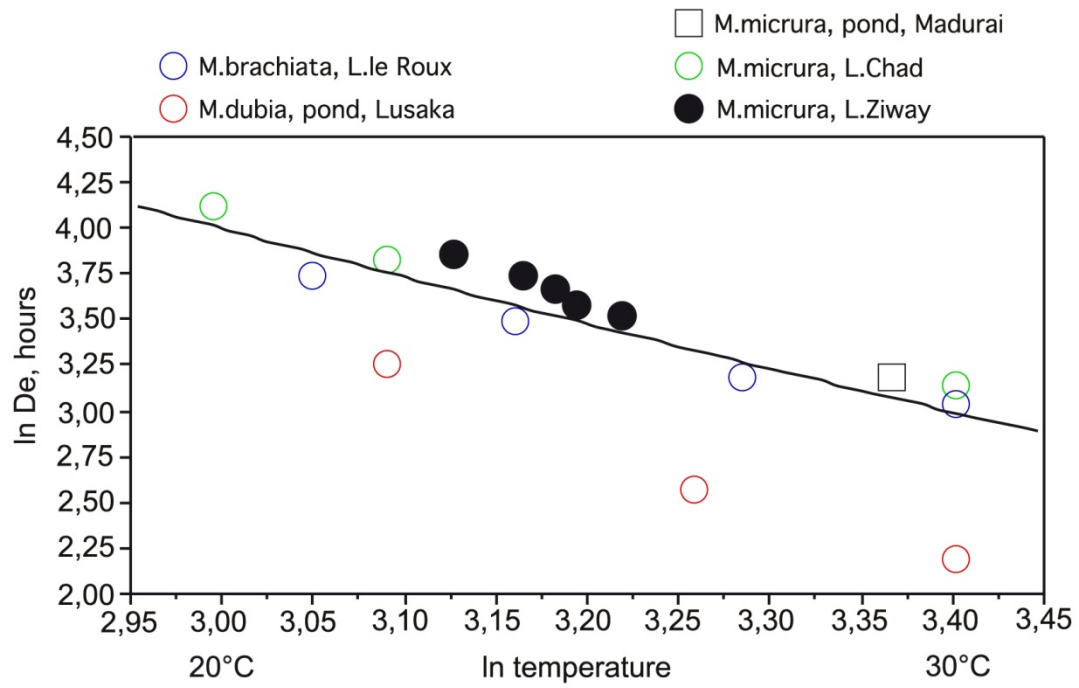


Fig. 3.1. Temperature vs embryonic development times of *Moina* species from tropical water bodies.

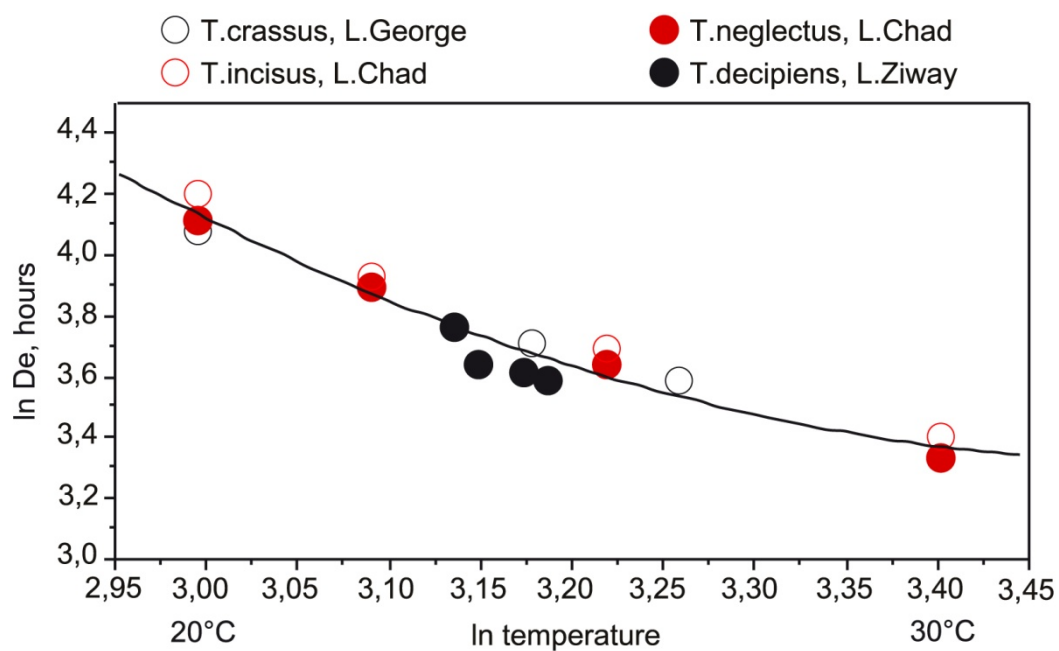
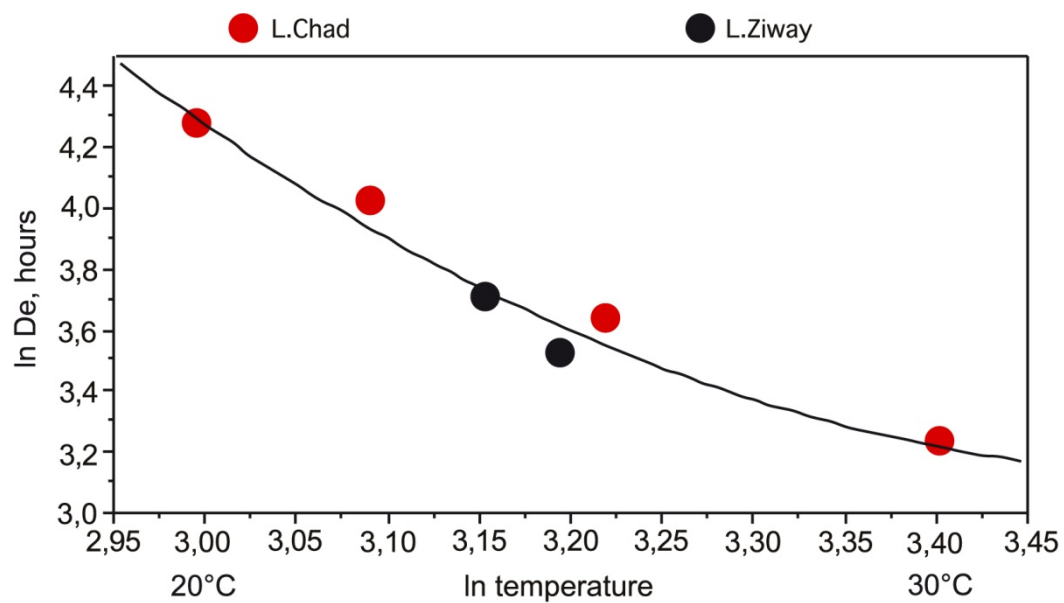


Fig. 3.2. Temperature vs embryonic development times of cyclopoid copepods from tropical lakes (a) *Mesocyclops* species and (b) *Thermocyclops* species.

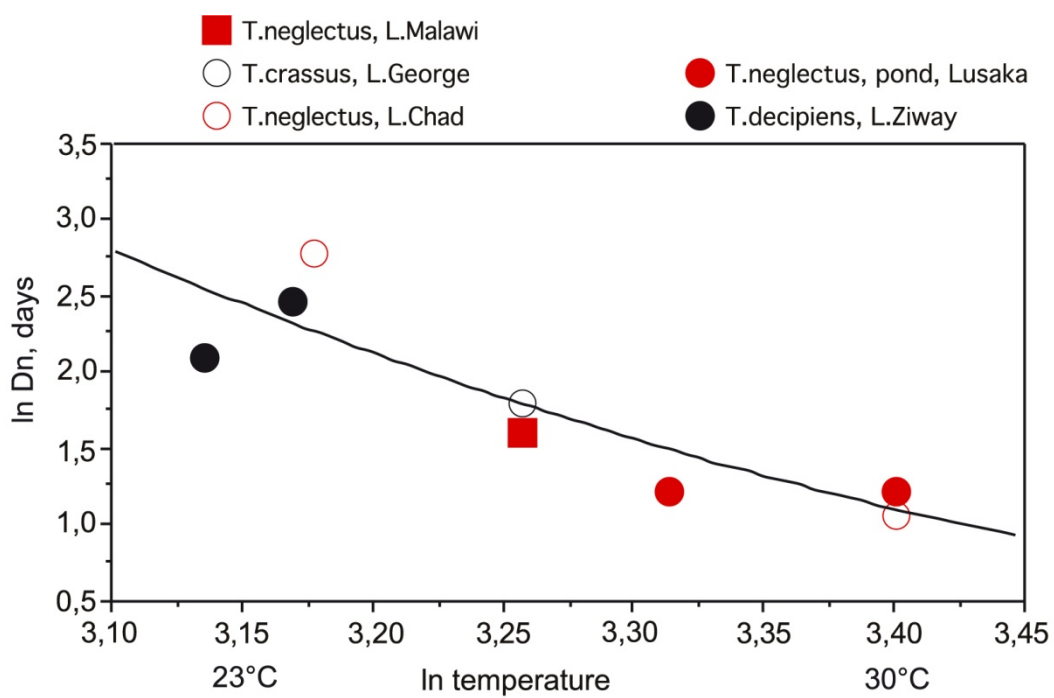


Fig. 3.3. Temperature vs cyclopoid naupliar development times from tropical lakes.

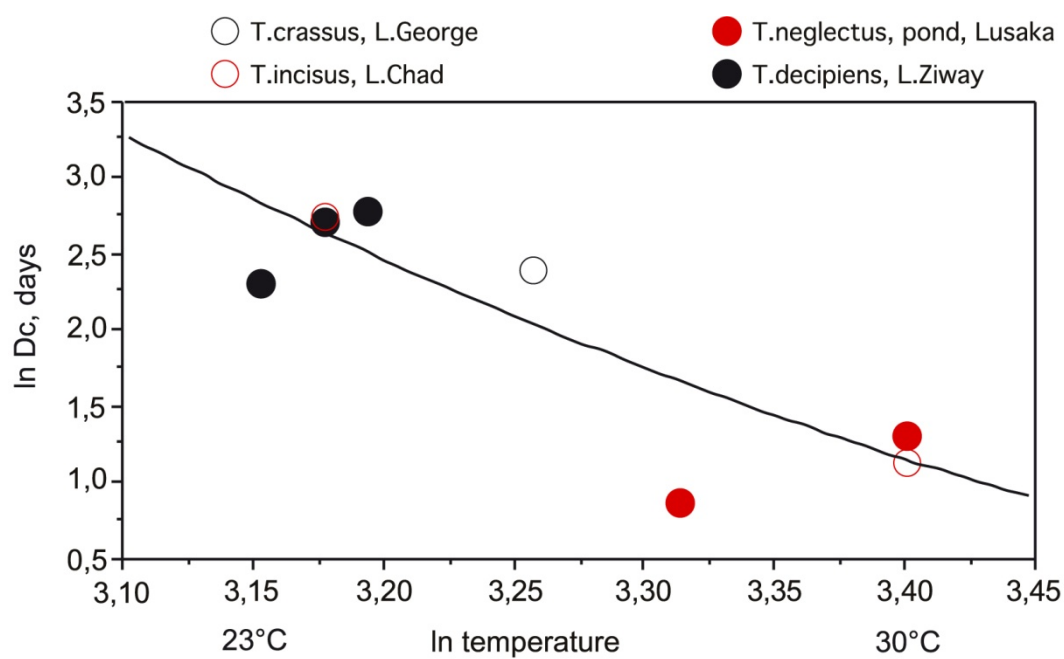


Fig. 3.4. Temperature vs cyclopoid copepodites development times from tropical lakes.

Table 3.3. Regression equations for the relationship between temperature and development times

Species	Regression equation	Remarks
development stages		(data from lakes)
<i>Moina micrura</i>		
	$\ln D_e = 16,387 - 5,488(\ln T) + 0,466(\ln T)^2$	Ziway and Chad
	$\ln D_{\text{post}} = 212,3 - 125,96(\ln T) + 18,7(\ln T)^2$	„
<i>Ceriodaphnia cornuta</i>		
	$\ln D_e = 36,497 - 18,31(\ln T) + 2,501(\ln T)^2$	Ziway and Chad
<i>Mesocyclops aequatorialis</i>		
	$\ln D_e = 49,73 - 26,21(\ln T) + 3,69(\ln T)^2$	Ziway and Chad
	$\ln D_n = 179,16 - 111,42(\ln T) + 17,5(\ln T)^2$	Ziway and Malawi
	$\ln D_c = 150,25 - 91,11(\ln T) + 14,02(\ln T)^2$	Ziway, Malawi and Kinneret
<i>Thermocyclops decipiens</i>		
	$\ln D_e = 7,9 - 19,56(\ln T) + 2,77(\ln T)^2$	Ziway, George (<i>Thermocyclops hyalinus</i>) and Chad (<i>Thermocyclops incisus</i> and <i>Thermocyclops neglectus</i>)
	$\ln D_n = 76,22 - 40,15(\ln T) + 5,31(\ln T)^2$	„
	$\ln D_c = 83,38 - 42,98(\ln T) + 5,52(\ln T)^2$	„

where D_e embryonic, D_n naupliar, D_c copepodid development times and T temperature in ($^{\circ}\text{C}$).

D_e in hours, D_{post} , D_n and D_c in days.

Crustacean zooplankton production estimates and P/B ratios

Production of crustaceans was seasonally variable (Fig. 3.5). Monthly and annual productions of crustaceans are presented in Table 3.4. Cladocerans showed greater production during the dry season. Maximum daily production of *Moina* 5 mg dw m^{-3} was recorded in March and the minimum ($0,14 \text{ mg dw m}^{-3}$) in July (Fig. 3.6). The mean daily production during the dry period was two times greater than the one of the wet period. During the dry period *Moina* comprised 12,6 % of the daily total crustacean production and 3,5 % during the wet period. The annual production was $510,1 \text{ mg dw m}^{-3}$. The daily P/B ratios of *Moina* during the dry and wet period were about the same ($0,35$ and $0,36 \text{ d}^{-1}$), and the annual P/B ratio was 121,7.

Egg production estimates of *Mesocyclops* and *Thermocyclops* were generally low, the daily maximum being $0,14$ and $0,48 \text{ mg dw m}^{-3} \text{ d}^{-1}$ for the two species, respectively. Higher mean daily and maximum egg productions of the two cyclopoids were recorded during the wet period (Fig. 3.5). *Mesocyclops* mean daily egg production during the wet period was 10 times greater than the daily mean during the dry period. No *Mesocyclops* females were found with eggs for 50% of the sampling dates during the dry period (Fig. 3.7). Nauplii and copepodid stages of cyclopoids showed the highest mean daily production rates ($3,43$ and $4,34 \text{ mg dw m}^{-3}$, respectively) of all age classes. The maximum daily production by nauplii was in mid June (17 mg dw m^{-3}) and copepodides end of September ($15,2 \text{ mg dw m}^{-3}$). The mean daily production of nauplii and copepodides was $6,17 \text{ mg dw m}^{-3}$ during the dry and $5,5 \text{ mg dw m}^{-3}$ during the wet period. Nauplii contributed 17 % to the total crustacean daily production during the dry period and 24% during the wet period. Copepodides comprised 26 and 24 % of the total crustacean daily production during the dry and wet periods, respectively. These pre adult stages together contributed 83 % of the total annual crustacean production (Table 3.7). The mean daily P/B ratios of nauplii and copepodides were $0,24$ and $0,2 \text{ d}^{-1}$, respectively. Total annual crustacean zooplankton production of Lake Ziway was $3202,6 \text{ mg dw m}^{-3} \text{ year}^{-1}$ and had an overall annual P/B ratio of 38,7.

Table 3.4. Monthly and annual production (mg dw m⁻³) of crustaceans

Sampling date	<i>Moina</i>	Adults		Cyclopoid	
		<i>Mesocyclops</i>	<i>Thermocyclops</i>	nauplii	copepodides
2008 Oct.	18,3	0,18	0,88	28	12
Nov.	52,5	0,3	2,3	51,4	72,4
Dec.	40,8	0,1	0,4	25,0	68,3
2009 Jan.	49,6	0,0	1,9	50,8	85,0
Feb.	37,0	0,1	2,7	133,1	133,9
Mar.	76,6	0,0	5,6	81,2	209,3
Apr.	82,0	0,0	2,1	65,2	161,9
May	62,4	0,0	5,7	95,6	121,7
Jun.	14,0	0,2	6,8	311,4	104,8
Jul.	6,7	2,4	8,8	107,0	32,5
Aug.	27,9	0,3	2,2	117,6	125,1
Sept.	42,3	0,3	1,7	140,6	313,9
Annual	510,1	4,0	41,2	1206,4	1441,0
%	15,9	0,1	1,3	37,7	45,0

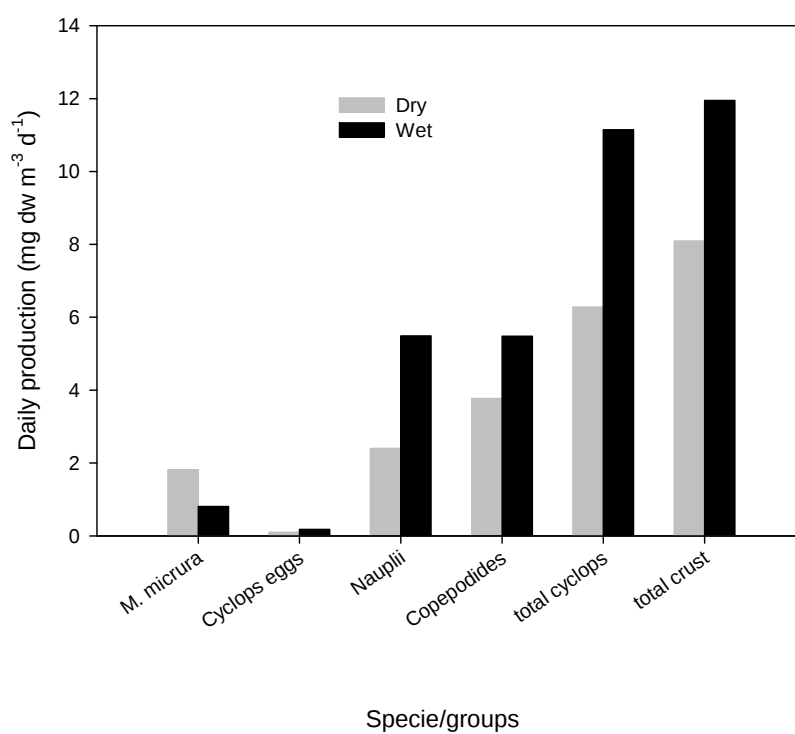


Fig. 3.5. Seasonal mean daily production of crustacean zooplankton.

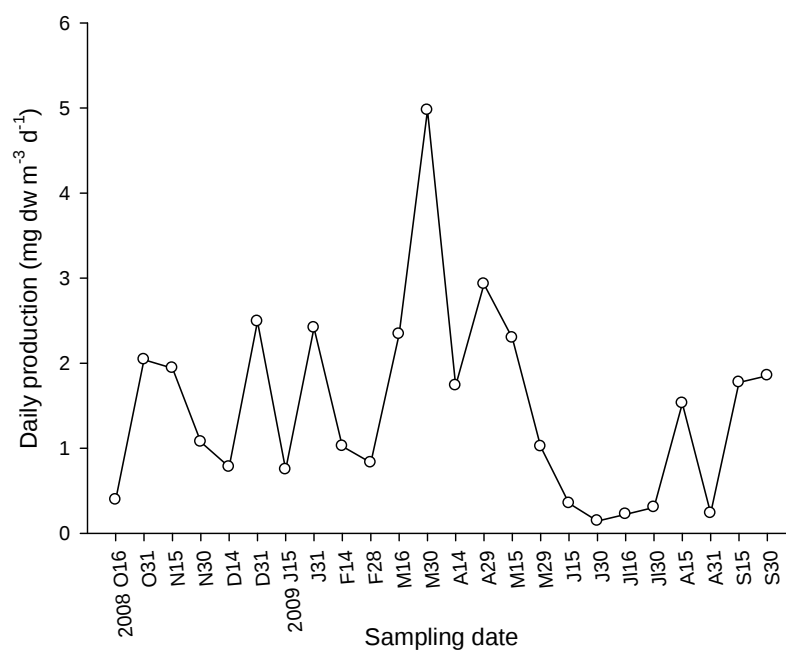


Fig. 3.6. Daily production rate of *Moina micrura*.

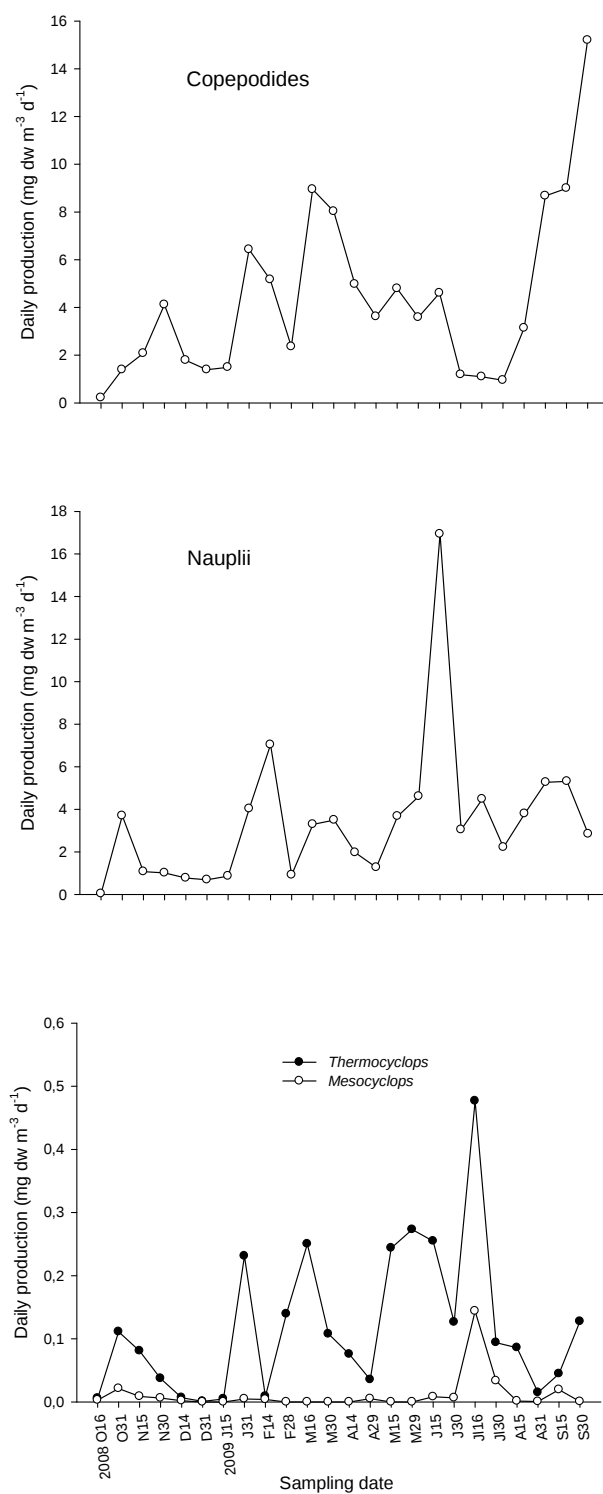


Fig. 3.7. Daily production of copepodites, nauplii and adults (*Thermocyclops decipiens* and *Mesocyclops aequatorialis*).

Discussion

Development times of crustaceans

The present observations on *Moina micrura* embryonic development times agree very well with the results for the same species from Lake Chad (Gras and Saint-Jean, 1969) (Table 3.5). Embryonic development data for *Moina brachiata* from Lake le Roux (Hart, 1985) reveal shorter durations in the temperature range of 21,1-26,7 °C. Even shorter development times for *Moina micrura* are reported from a pond in South India in the temperature range of 28-30 °C (Murugan, 1975). Among the *Moina* species the embryonic development times reported for *Moina dubia* (Magazda, 1977) are much shorter than reported for *M. micrura* from lakes Chad, Maduraia and Ziway or the results of *M. brachiata* from Lake le Roux at similar temperature range. On the other hand the embryonic development times of *Ceriodaphnia cornuta* from Lake Ziway are shorter than reported from Lake Chad (Gras and Saint-Jean, 1976). Attempts of culturing *Daphnia barbata* and *Diaphanosoma excisum* were not successful for two reasons: *Daphnia* was very rare in the samples and completely disappeared after half of the study period and in the case of *Diaphanosoma* high mortality occurred during culturing.

Much time was devoted to the culture of the two cyclopoids, *Thermocyclops decipiens* and *Mesocyclops aequatorialis*, because the two cyclopoids contributed 86% to the total zooplankton biomass. Embryonic and post-embryonic development times showed inverse relationships to temperature. At high temperatures naupliar and copepodid development times of *Thermocyclops* increased with increasing temperature (Table 3.2), however the differences were not significant because of higher variance in the data. According to Amarasinghe *et al.* (1997) temperature and food conditions affect instar durations in cladocerans as well as the duration of nauplii and copepodid stages. Two to three fold variations in copepodid development times and a less pronounced effect on nauplii duration due to food level variation is reported from experimental studies by Hart (1991). Embryonic development times of *Mesocyclops aequatorialis* and *Thermocyclops decipiens* from Lake Ziway were faster compared to the results for the same and/or similar species from other tropical lakes (Table 3.6). The embryonic development times of *M. aequatorialis* in Lake Malawi cultured at 26 °C (Irvine and Waya, 1999) and Lake Tana at 20 °C (Wondie and Mengestou, 2006) are longer than the result of the present study (cultured at 23,3 and 24,4 °C). The post-embryonic durations from Lake Malawi at 26 °C and Lake Ziway (21,3 to 22,9 °C) were comparable.

Embryonic development times of *Mesocyclops leuckarti* from Lake Chad fit well with the present observation for *M. aequatorialis* (Fig. 3.1). The embryonic development time of *T. decipiens* from Lake Ziway compares with *T. neglectus*, *T. incises* from Lake Chad and *T. hyalinus* (= *T. crassus*) from Lake George. The results from Lake Awassa (Mengestou and Fernando, 1991b) on both embryonic and post-embryonic durations using filtered lake water revealed faster development than in the present study and elsewhere for the same species and a comparable temperature range (Table 3.6). The post-embryonic development times of *Thermocyclops* were generally longer than the ones of *Mesocyclops*. However, the results are comparable with other species (e.g. *T. neglectus* from Lake Chad). Because of the limited temperature range and low maximum temperature further comparison was not possible.

Table 3.5. Mean embryonic development time of cladocerans from tropical lakes

Species	Temp. (°C)	Mean duration (range) (days)	Lake	Reference
<i>Moina micrura</i>	22,8	1,95	Ziway	This study
„	23,7	1,76	„	„
„	24,1	1,62	„	„
„	24,4	1,5	„	„
„	25	1,42	„	„
„	20	2,58	Chad	Gras & Saint-Jean (1976)
„	22	1,92	„	Gras & Saint-Jean (1969)
„	25	1,42	„	„
<i>Moina brachiata</i>	21,1	1,73	Le Roux	Hart (1985)
„	23,6	1,36	„	„
„	26,7	1,02	„	„
<i>Ceriodaphnia cornuta</i>	23,3	1,85	Ziway	This study
„	24	1,54	„	„
„	24,5	1,35	„	„
„	24,8	1,34	„	„
„	25,1	1,17	„	„
„	20	2,42	Chad	Gras & Saint-Jean (1976)
„	25	1,38	„	„

Table 3.6. Mean embryonic and post-embryonic development times of copepods from tropical lakes

Species	Temp. (°C)	Mean duration (days)			Lakes	Reference
		D _e	D _n	D _c		
<i>M. aequatorialis</i>	21,3	-	8,2	-	Ziway	This study
„	22	-	7,5	-	„	„
„	22,3	-	-	13,2	„	„
„	22,6	-	-	12,3	„	„
„	22,9	-	6,6	-	„	„
„	23,4	1,72	-	-	„	„
„	24,4	1,44	-	-	„	„
„	26	2,5	7	13,6	Malawi	Irvine & Waya (1999)
„	20	-	2	3,5	Awassa	Mengestou & Fernando (1991b)
„	23	-	2	4	„	„
„	25	0,92	2,3	5,7	„	„
„	20	2,4	5,5	13	Tana	Wondie & Mengestou (2006)
„	25	1,95	3,9	8,4	„	„
<i>M. leuckarti</i>	20	3	-	-	Chad	Gras & Saint-Jean (1976)
„	22	2,33	-	-	„	Gras & Saint-Jean (1969)
„	24	-	17	15	„	„
„	25	1,58	-	-	„	„
„	22	-	15,5	12,5	Kinneret	Gophen (1981)

	(°C)	D _e	D _n	D _c		
<i>M. decipiens</i>	26,5	-	8,4	11,6	Valencia	Saunders & Lewis (1988)
<i>T. decipiens</i>	23	1,8	8,17	14,9	Ziway	This study
„	23,3	1,6	-	10	„	„
„	23,8	-	11,7	-	„	„
„	23,9	1,6	-	-	„	„
„	24	-	-	15	„	„
„	24,2	1,5	-	-	„	„
<i>T. decipiens</i>	24,4	-	-	16	„	„
<i>T. hyalinus</i>	20	2,5	-	-	George	Burgis (1974)
„	22	2,0	-	-	„	„
„	24	1,7	-	-	„	„
„	26	1,5	6	11	„	„
<i>T. neglectus</i>	20	2,5	6,6	-	Chad	Gras & Saint-Jean (1976)
„	22	2,0	-	-	„	Gras & Saint-Jean (1969)
„	24	-	16	15,5	„	„
„	25	1,6	2	-	„	Gras & Saint-Jean (1976)
„	26	1,8	-	19	Malawi	Irvine & Waya (1999)
<i>T. ethiopiensis</i>	20	2,4	5	10,4	Tana	Wondie & Mengestou (2006)
„	25	1,9	3,5	7,4	„	„

Production estimates and P/B ratios of crustaceans

Production was estimated for the dominant Cladocera (*Moina micrura*) and cyclopoid copepods (*Mesocyclops aequatorialis* and *Thermocyclops decipiens*) as these crustaceans together contributed >90% of the total crustacean biomass in Lake Ziway. Production was estimated using growth increment (Winberg) method, because the data fulfills the requirement of this method. Daily production of *Moina micrura* ranged between 0,14-5 mg dw m⁻³ d⁻¹ (mean: 1,5 mg dw m⁻³ d⁻¹) values which are lower than from Lake Chad (2-20 mg dw m⁻³ d⁻¹). The seasonal difference in daily production of *Moina* was well expressed, the daily production being 2,3 times higher in dry period than in the wet. Such a difference could be expected if there is a temperature difference between the seasons. However, there was no significant difference in mean temperature between dry (23,4 °C) and wet periods (22,2 °C). At high tropical latitude the temperature factor is responsible for a marked seasonal variation. In Lake Chad reduction of specific growth rate and production and increase of stage-duration was observed in the cooler season (Gras and saint-Jean, 1983). Chlorophyll a increased during the wet period but food quality (mainly blue green algae) does not favour the development of Cladocera. The change in the species composition of cladocerans i.e. absence of *Daphnia barbata* and *Ceriodaphnia cornuta* at times of increased turbidity and low food quality (mainly blue greens) could also reflect the stress on cladocerans. This agrees well with the results from other tropical lakes: the absence of daphnids in years with a high level of inorganic turbidity in Lake le Roux in South Africa (Hart, 1986), the negative impact of turbidity on daphnids abundance in Lake Tana (Dejen *et al.*, 2004) and interference of resuspended sediments in *Daphnia* grazing in Lake Waiholo, New Zealand (Levine *et al.*, 2005). However, cladocerans are reported as major contributors to the crustacean production of tropical lakes, e.g. daily production of *Diaphanosoma excisum* in Lake Awassa ranged between 0,2 and 20 mg dw m⁻³ (Mengestou and Fernando, 1991b) and in Lake Chad between 1 and 18 mg dw m⁻³ (Gras and Sant- Jean, 1983).

Production of adult cyclopoids (eggs) was very low in the present study, only less than 2% of the total copepod production. The maximum contribution of eggs to the total production was 7,5%. Similar low production of eggs is reported from Lake Awassa where the egg production by *Mesocyclops* was 1,6 and 3,7 % by *Thermocyclops consimilis* (Mengestou and Fernando, 1991b). The absence of the larger clutch sized *Mesocyclops* from the samples could underestimate the total egg production (c.f. high nauplii numbers throughout the sampling). Low contribution of adults (eggs) to the total copepod production is reported from different

tropical lakes, e.g. 5,3% in Lake Awassa (Mengestou and Fernando, 1991b), 5% in Lake Tana (Wondie and Mengestou, 2006), 5% in Lake Naivasha (Mavuti, 1994). Similar low contribution of egg production to the total copepods production is reported from temperate Lake Tjeukemeer (Vijverberg and Richter, 1982). Lower egg production than the production of nauplii and copepodid stages is also reported by Gophen (1978). In contrary a high contribution of adult production (15%) is found for *Thermocyclops hyalinus* in Lake George (Burgis, 1974) and greater than 50% of the total production of the calanoid copepod *Paradiaptomus africana* in Lake Nakuru (Vareschi and Jacobs, 1984).

Unlike cladocerans, cyclopoids (all development stages) showed greater daily production during the wet period than in the dry period (Fig. 3.7). The difference to the cladocerans is that copepods can do well in turbid systems (Hart, 1988). The turbidity also seems to provide copepods a refuge from their predators. As a result the maximum egg stocks and increased individual clutch sizes (mainly by the large body sized *Mesocyclops*) are found during the wet period. The dependence of fecundity upon food availability and the presence of more breeding females in the samples (i.e. increased turbidity reduced predation pressure) could also contribute to the seasonal variation. *Thermocyclops* is found to feed on *Microcystis* in Lake George (Burgis, 1969) and the high positive correlation with Chlorophyll a concentration in the present study could be the reason for the observed difference in cyclopoids production compared to cladocerans. Nauplii and copepodides of the two cyclopoids were the major contributors to the total copepod production (45% and 53,5%, respectively). Similar high contribution of nauplii and copepodides 27 and 68%, respectively to the total copepod production is reported from Lake Awassa (Mengestou and Fernando, 1991b). The relatively constant high temperatures throughout the year and the corresponding short development times of the nauplii and copepodid do result in a high production. In contrary the contribution of nauplii to the total production in Lake George (8%) is much lower than the one of copepodid (77%) (Burgis, 1974). Most likely mortality in the Lake George population is more pronounced in the nauplii stage.

Tabele 3.7. Mean daily and annual production (mg dw m⁻³) and P/B ratios of crustaceans

Species/stages	Daily P	Annual P	Daily P/B	Annual P/B	Lakes	Reference
<i>Moina micrura</i>	1,48	501,1	0,35	121,7	Ziway	1
„	-	283,5	0,29	105	Lanao	2
„	-	-	0,95	-	Cote d'Ivoire P	3
„	-	-	0,37	-	Sri Lanka R	4
„	2,4-20,4	3148,1	0,52	190,8	Chad	5
<i>Moina brachiata</i>	0,48	174,5	0,17	60,7	le Roux	6
Cyclopoid copepods	7,9	2692,5	0,1	34,3	Ziway	1
Cyclopoid copepods	-	535,2	-	14,5	Awassa	7
Cyclopoid copepods	0,85	313	0,06	23,3	Tana	8
Copepods	66-210*	49**	-	36	Malawi	9
<i>T. hyalinus</i>	19,6	7154	0,08	28,8	George	10
<i>T. hyalinus</i>	-	6886,2	0,13	46	Lanao	2
<i>T. decipiens</i>	-	-	0,25-0,3	-	Sri Lanka R	4
<i>M. thermocyclopides</i>	-	-	0,15-0,19	-	„	„
<i>M. leuckarti</i>	-	-	0,1-0,17	37,2	Kinneret	11
„	-	876,3	-	53,5	Tjeukemeer	12

1-This study; 2- Lewis, 1979; 3- Saint-Jean and Bonou, 1994; 4- Amarasinghe *et al.*, 1997; 5- Gras & Saint-Jean, 1983; 6- Hart, 1987; 7- Mengestou and Fernando, 1991b; 8- Wondie and Mengestou, 2006; 9- Irvine and Waya, 1999; 10- Burgis, 1974; 11- Gophen, 1978 and 12- Vijverberg & Richter, 1982.

* mg dw m⁻², ** g dw m⁻², R-reservoir, P-pond

According to Waters (1977) most annual production values reported for individual copepod species range from 0,2 to 10 g dw m⁻². In lake Ziway, a total annual production of 6,7 mg dw m⁻² is estimated for the two cyclopoids (*Mesocyclops aequatorialis* and *Thermocyclops decipiens*). The variation of the production estimates of zooplankton species in the literature from tropical lakes is high (Tables 3.7; 3.8). The annual production of the two cyclopoids in Lake Ziway is 3,6 times higher than the values reported from Lake Awassa for *Mesocyclops aequatorialis* and *Thermocyclops consimilis* (Mengestou and Fernando, 1991b). The daily production of *Thermocyclops hyalinus* (= *T. crassus*) in Lake George (Burgis, 1974) is 2,3 times greater than the daily production of the two cyclopoids in Lake Ziway. These variations may be partly caused by the variation in the food conditions (phytoplankton quantity, quality as well as suitable size) of those lakes. Change in phytoplankton species composition is seen to favour at times one species and at another times another (e.g. mean daily production of *Moina micrura* during dry period was 2,3 time greater than the of the wet but cyclopoid copepods showed about 2 times greater mean daily production during the wet period). Phytoplankton biomass is also seen as a moderately good predictor of the total microcrustacean zooplankton production explaining 43% of the observed variance (Amarasinghe *et al.*, 1997). Nevertheless, zooplankton production will depend not only on the phytoplankton but also on predation and other abiotic factors. In the present study, together with food quality, turbidity and predation by fish and *Chaoborus* were found as the main determining factors for the zooplankton standing stock of Lake Ziway.

On geographical scale, P/B ratios of a single species seem to be primarily a function of temperature and at the same temperature, a function of food availability (Morgan *et al.*, 1980). The mean daily P/B ratio for *Moina micrura* is lower when compared to results from other tropical water bodies (e.g. Lake Chad and a pond in Cote d'Ivoire). The mean water temperature (maximum $\leq 25^{\circ}\text{C}$) during the investigation did not reach the high values of 30°C at which high values of P/B were reported from Lake Chad and a pond in Cote d'Ivoire and could partly be the reason. However, daily P/B ratios of *Moina* from Lake Ziway (0,1- 0,89 d⁻¹) is well in the range calculated for the small bodied cladocerans (maximum length ca. 1 mm) such as *Moina micrura*, *M. brachiata*, *Ceriodaphnia cornuta* and *Bosmina fontalis* (i.e. mean 0,41; range 0,12-0,95) (Amarasinghe *et al.*, 1997). Daily P/B ratios of cyclopoid copepods in Lake Ziway ranged between 0,004 and 0,17 d⁻¹. The minimum P/B value in the cyclopoids is much lower than the range for the biomass turnover rates of copepods reported from different tropical and subtropical water bodies (0,03-3 d⁻¹) (Amarasinghe *et al.*, 1997). Very low adult

Table 3.8. Mean biomass, annual production and annual P/B ratios of zooplankton population from tropical lakes

Lake	Biomass (mg dw m ⁻³)	Production (g dw m ⁻³ yr ⁻¹)	P/B (yr ⁻¹)	Reference
Malawi	1,6*	49**	30,6	1
George	248,4	7,2	28,7	2
Chad	333	21,2	63,7	3
Lanao	222	9,1	41	4
Ziway	82,5	3,2	38,7	5
Sibaya	50,8	2	40,6	6
Awassa	44,9	2,5	55,8	7
Tana	34,4	0,7	21,4	8

*mg dw m⁻² and **g dw m⁻² for biomass and production, respectively

References: 1- Irvine and Waya (1999); 2- Burgis (1974); 3- Carmouze *et al.* (1983); 4- Lewis (1979); 5- This study; 6- Hart and Allanson (1975); 7- Mengestou and Fernando (1991b); 8- Wondie and Mengestou (2006)

production 0,001 and 004 mg dw m⁻³ d⁻¹ due to predation and hence low numbers of ovigerous females in the samples contributed for the overall low cyclopoid P/B ratio. The overall annual P/B ratio for the crustaceans in Lake Ziway was 38,7; it compares well with literature data; but the annual production rate is low compared to other shallow tropical lakes like Lake George and Lake Chad (Table 3.8). The dominance of small sized zooplankton as well as high contribution of post-embryonic stages to the total copepod production and relatively uniform high temperature throughout the year and correspondingly short development times could lead to such high turnover rate. It is also indicated by Brylinsky (1980) that smaller organisms have larger P/B ratios.

Generally, sampling frequency should consider the generation time of the dominant zooplankters, taking into account that this varies with temperature and food conditions. Whenever possible, development times of zooplankton should be measured for the dominant species in a water body, and measurement should be made over a wide temperature range. A curvilinear logarithmic relationship appears to be a suitable model for the prediction of the relationship between rate of development and temperature. Results of production estimate depend on accuracy of biomass measurement and development times. Direct measurement of dry weight gives a good definition of individual size in all groups of planktonic animals, a pre-request for biomass determination. Further studies on the effects of food and temperature on the post-embryonic development time of zooplankton are required for the better understanding of the population dynamics in unpredictable shallow, turbid tropical lakes.

Chapter 4

General discussion

Phytoplankton communities of shallow lakes are usually dominated by blue green algae (Scheffer, 1998). Records from Lake Ziway, a shallow turbid lake revealed this hypothesis. Dominance of blue greens among the phytoplankton of Lake Ziway has been indicated in various papers (e.g. Schröder, 1984; Kebede & Willen, 1998; Dagne *et al.*, 2008 and this study). Algal bloom however, was not reported and neither observed during the present study. It might be due to the frequent turbulence and well mixing of the lake that blooms are not common in such lakes (Schefer, 1998). But such mixing could favor blue greens through continuous recycling of nutrients.

Species composition and abundances of plankton communities of shallow tropical lakes seem to be governed mainly by hydrological associated impacts (like water level fluctuation, turbidity and nutrient input). The change in the species number following turbidity and water level fluctuation of shallow lakes is documented by various authors (e.g. Lakes: Chilwa Kalk, 1979; Chad Gras and Saint-Jean, 1983; le Roux Hart, 1986; Ziway this study). Absence of species mainly cladocerans during periods of high turbidity (Hart, 1986; Levine *et al.*, 2005; this study) is the result of direct negative effects of turbidity on cladocerans (e.g. feeding interference) or, indirectly, through low food quality caused by light limited growing phytoplankton. *Daphnia* abundance is found to be inversely correlated with turbidity (Hart, 1986, Dejen *et al.*, 2004; this study). In the absence of *Daphnia*, rotifers and copepods dominate the plankton (Sarma *et al.*, 2005; Dagne *et al.*, 2008) and copepods are the major contributor to the total zooplankton biomass in such shallow lakes (Burgis, 1974; Mengestou and Fernando, 1991b; this study). In Lake George Uganda, *Thermocyclops hyalinus* contributed about 68% of the total crustacean biomass. In the present study, *Thermocyclops decipiens* contributed about the same percentage to the total crustacean biomass. The ecological factor that helped this species to dominate could be related to its omnivorous feeding habits and prey-predator interaction. Although rotifers occurred with the highest species number in Lake Ziway, the density of the dominant rotifer was very low. According to Morgan *et al* (1980) lowest rotifer density was found in shallow, turbid tropical lakes. Shallow lakes seem to be numerically dominated by a few copepod species (Burgis, 1974; Hart, 1986; Dagne *et al.*, 2008 and this study). The dominant copepod species are herbivorous

which are reported to feed on the blue greens and they are better performing in such turbid blue green dominated lakes than the cladocerans and/or the rotifers.

In shallow lakes vertical gradients in the abiotic factors are not as strong as in deep lakes to structure zooplankton distribution (Burks *et al.*, 2002). The littoral zone with structural complexity (typical features of most shallow lakes) will have a structuring role in zooplankton species composition and distribution pattern. Results of the present study revealed that densities of most zooplankton species were higher in the littoral with its dense macrophyte stands. This is in agreement with literature that in shallow lakes macrophytes provide zooplankton a refuge from their predators (e.g. Timms and Moss 1984; Lauridsen and Buenk, 1996). However, large sized adults and egg carrying females of *Mesocyclops aequatorialis* did not show horizontal migration into the macrophytes. Avoidance of the macrophytes especially by the large sized adults could be due to high predation pressure from predators (fish and *Chaoborus*) within the macrophytes (e.g. Burks *et al.*, 2002).

There was also some striking result by the larger adults and ovigerous females of *Mesocyclops* in the present study. Usually in shallow turbid lakes where the water transparency is generally low vertical migration of zooplankton is hardly observed. In the present study, however, *Mesocyclops* showed diel vertical migration. The presence of the invertebrate predator *Chaoborus* and catfish which are found to feed mainly on copepods could be the major trigger for the observed diel vertical migration.

In most of the shallow tropical lakes herbivorous fish like *Tilapia* dominate the fish community. Dominance of rotifers and copepods in such shallow tropical lakes will have negative impact on fish production. First, direct competition for resources (i.e. the algal food) with the herbivores fish and the second is indirectly through energy transfer in the food chain to the predator fish will decrease. In most tropical lakes the invertebrate predators like *Chaoborus* will be the major predator of zooplankton communities and hence will package energy to fish (i.e. the energy available to higher consumers will decrease). According to Brylinsky (1980) the energy transfer efficiency of herbivorous zooplankton is about two orders of magnitude, but only about one order of magnitude for carnivorous zooplankton. Low secondary production is reported from lakes where copepods are the dominant zooplankters (Mengestou and Fernando, 1991b; Wondie and Mengestou, 2006; this study). According to Moore *et al.* (1996) low production at the time of copepod dominance on the zooplankton could be due to less efficiency of copepods to harvest carbon in the microbial loop compared to cladocerans. The dominance of blue green algae in most tropical lakes

(Burgis, 1974; Haande *et al.* 2007; Dagne *et al.*, 2008, this study) could also be the potential factor to suppress production. It has been indicated in various papers that blue greens are considered as inedible or low food quality (Lampert, 1987; Fulton, 1988), they interfere with zooplankton grazing (DeMott & Moxter, 1991) and some species are known to produce toxins (Oh *et al.*, 2000) which can lead to increased mortality (Lüring, 2003), lower reproduction and population growth rate (Tillmanns *et al.*, 2008). Predation by fish and invertebrates (e.g. *Chaoborus*) predators could not be ruled out to be one of the contributors to low production.

Management of water bodies in Ethiopia seems to be far off being effective. Many water bodies are threatened by human activities. Increasing agricultural activities in and around the water bodies are contributing to increasing turbidity and reduction in the water level. The increasing floriculture especially around the Rift Valley lakes and rivers which includes direct usage of waters from the rivers and lakes and damping the effluents back into the water bodies needs special consideration and thorough investigation. Sediment dragging both legal and illegal from rivers and Rift Valley lakes is also a potential threat to the water bodies.

“Study of tropical lakes will be essential if tropical inland waters are to be protected and used in the wisest possible way” Lewis, 1996.

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Appendix

Abbreviations and units in the text

L-Length in μm

W-Weight in μg

SD- Standard deviation

Chl a –Chlorophyll a

$\ln W$ or $\ln L$ -Natural logarithm of, weight or length

$\ln D$ or $\ln T$ -natural logarithm of, development time or water temperature

DW- Dry weight in μg or mg

Ind.l^{-1} -Individual per liter

Mgm^{-3} -Miligram per cubic meter

Mg dw m^{-2} -Miligram dry weight per meter square

$\text{Mg dw m}^{-3} \text{ d}^{-1}$ - Milligram dry weight per cubic meter per day

D- Development time

D_e - Embryonic development time (hours or days)

D_n - Nauplii development time (hours or days)

D_c - Copepodid development time (hours or days)

N - Density of species or age classes

P_d - Production per day

P/B- Production to biomass ratio

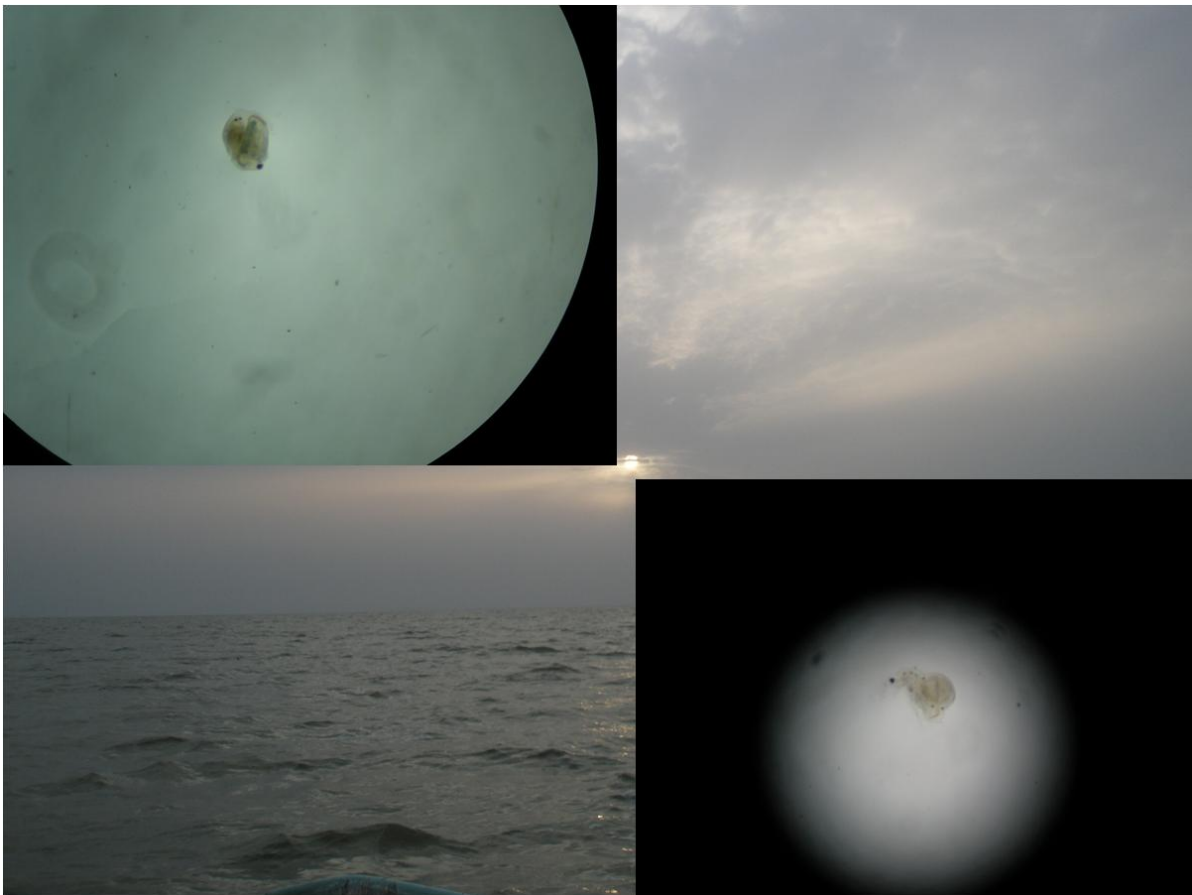
Pictures



Picture 1. Brown colour of Lake Ziway during high turbidity.



Picture 2. Top left the investigator while calibrating the pH meter, top right filtered lake water (food) for the experiment, lower left microscopic investigation with the super visor (Prof. Alois HERZIG) while he was in Ethiopia for field visit and lower right the experimental setup.



Picture 3. Top left *Ceriodaphnia cornuta* and lower right *Moina micrura* seen under microscopic field about to hatch. Back ground picture is the lake during the early morning taken during night sampling.



Picture 4. Cyclopoid developmental stages.



Picture 5. *Chaoborus* sp. which was not reported in Lake Ziway before.

Curriculum Vitae

Personal information:

Name: Adamneh Dagne Admassie

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Educational background:

October 2007 - December 2010: Studied PhD in biology, Universität Wien, Austria

Thesis title: Zooplankton community structure, population dynamics and production and its relation to abiotic and biotic factors in Lake Ziway, Ethiopia

February 2003- October 2004: Studied MSc in Environmental Science and Technology, IPGL Mondsee-Austria and UNESCO-IHE, Institute for Water Education, The Netherlands

Thesis title: Zooplankton abundance and species composition in the Ethiopian Rift Valley Lake, Lake Ziway

January 1999 - March 2001: Studied Bachelor of Sciences in Agriculture (Animal Production and Rangeland Management), Debub University-Awassa College of Agriculture

December 1991- October 1993: Studied Diploma in Animal Production and Rangeland Management, Addis Ababa University-Awassa College of Agriculture

Work experience:

Since April 2001 researcher at the Ethiopian Institute of Agricultural Research-National Fisheries and Other Aquatic life Research Center, Sebeta-Ethiopia

April 1995-January 1999 development agent at Awi Zone-Enjibara Woreda Agricultural Office

On job training:

Planning, monitoring and evaluation

Biometrical methods and SPSS software packages, scientific paper writing

Publications

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Adamneh D., Aschalew L., Fasil D. and Abeba W.G. (2007) Growth performance and economic returns of male monosex and unsexed tilapia (*Oreochromis niloticus* L.) cultured in pods fed on wheat bran. In: Live stock systems: Opportunities and challenges as a livelihood strategy, D. Tamerat and F. Fekede (eds), pp. 172-179. Proceedings of the 15th annual conference of the Ethiopian Society of Animal production (ESAP), Addis Abeba-Ethiopia.

Adamneh D., Herzig A. and Schiemer F. Zooplankton community structure and standing stocks and their relation to abiotic and biotic factors in shallow turbid tropical Lake Ziway (in preparation)

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- Association of Ethiopians Educated in Austria
- SIL-AUSTRIA ‘‘Fresh Blood for Freshwater Young Aquatic Science’’
- UNESCO-IHE alumni
- OeAD alumni