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DURATION OF DEVELOPMENT, BIOMASS AND RATE OF PRODUCTION OF THE DOMINANT COPEPODS (CALANOIDA AND CYCLOPOIDA) IN LAKE TANA, ETHIOPIA

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ABSTRACT: Data on zooplankton development and production rates are relatively scarce for copepods in large turbid tropical lakes like Lake Tana, Ethiopia. We determined the duration times of instars of the dominant planktonic copepods - *Thermodiaptomus galebi lacustris* (Calanoida), *Thermocylops ethiopiensis* and *Mesocyclops aequatorialis similis* (Cyclopoida) in laboratory algal cultures enhanced with growth media and maintained at 20 and 25°C. Development times were temperature and food-dependent. These laboratory results together with field abundance data collected monthly for two years were used to estimate biomass and production rates with the growth summation (Winberg) method. The calanoid *T. galebi* was 50% more abundant than each cyclopoid species (average 20.4/L) with a mean biomass of 20.92 mg DW m^{-3} and daily and annual production rates of 1.04 mg DW m^{-3} day^{-1} and 380 mg DW m^{-3} yr^{-1}, respectively. *T. ethiopiensis* and *M. aequatorialis* had lower abundances (9.59/L and 7.22/L) and biomass (7.33 mg DW m^{-3} and 6.18 mg DW m^{-3}) but similar daily (~ 0.42 mg DW m^{-3} day^{-1}) production rates. All the three copepods have close daily (P/B ~0.05 - 0.08 d^{-1}) biomass turnover rates. Production was continuous for all copepods with peaks during the post and pre-rainy seasons, and was regulated predominantly by food availability. Copepod production and biomass turnover rates are low for Lake Tana when compared to other tropical lakes. Turbidity showed depressed effect on biomass and production rates only during the late-rainy season. The contribution of cladocerans and rotifers to secondary production and energy flow in the Lake Tana ecosystem will be reported elsewhere.

Key words/phrases: Biomass, duration of development, Lake Tana, large-turbid lake, rate of production

INTRODUCTION

Secondary production estimates are useful indications of the fundamental role of zooplankton in lake ecosystems. Secondary production may be considered an ecological link for the flux of material and energy through trophic levels, and present a path between populations and ecosystem ecology (Benke, 1993). As the zooplankton populations in tropical regions are continuously recruiting and growing, the more simple cohort approach cannot be used for estimation of secondary production (Rigler and Downing, 1984). Instead, such analysis requires culturing of zooplankton at temperatures similar to those in nature (Vijverberg, 1989; Seyoum Mengistou and Fernando, 1991; Mavuti, 1994; Amarasinghe *et al.*, 1997a,b), besides the use of field population census data. In the present study, the production rates and P/B ratio of the dominant copepod species in Lake Tana, Ethiopia, were evaluated based on their reproductive and population characteristics.

The only zooplankton production study in Ethiopia is the report of Seyoum Mengistou and Fernando (1991) on Lake Awassa. In Lake Tana, there have been some previous studies on preliminary survey of zooplankton production and distribution by Tesfaye Wudneh (1998) and spatial and temporal distribution by Eshete Dejen *et al.* (2004). However, in these studies, information on growth and recruitment were not included. The duration times of the various developmental stages, which are necessary to calculate production, were not determined. Besides, these studies were done only in the southern gulf area of L. Tana, which represent only a tenth of the total lake surface area. Therefore, the production estimate done by Tesfaye Wudneh (1998) is relatively crude because the biomass distribution and duration times of individual species and age/size classes was not taken into consideration, and the estimate was made from P/B ratio given in the literature for temperate and tropical water bodies. Previous studies (Tesfaye Wudneh, 1998;

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Eshete Dejen *et al.*, 2004) suggested high biomass for the zooplankton in Lake Tana, and therefore assumed a critical trophic role for the zooplankton in the system. But, high zooplankton biomass does not necessarily mean high productivity without some knowledge of the biomass turnover rates of the populations. Developmental time, biomass production rate and biomass turnover rate should be determined at least on an annual basis in order to assess energy flow to higher trophic levels.

This study is therefore set out to make a more reliable estimate of the copepod production in Lake Tana. We further addressed three questions: (a) what is the pattern of spatial and temporal distribution of the three copepod species? (b) What is the level of copepod production in this turbid, large lake and how does it compare with results from other tropical lakes? (c) Is the copepod productions in the lake mainly regulated by turbidity or are biotic factors also important?

STUDY AREA

Geographically, the Lake Tana basin is bounded between latitudes 10°58`-12°47`N and longitudes 36°45`-38°14`E and at an altitude of 1830 m, a.s.l. The lake is shallow (average depth 9 m, maximum 14 m) covering a surface area of 3200 km^2 and it is the source of the Blue Nile (Tesfaye Wudneh, 1998). The lake is well mixed and a thermocline is lacking (Gasse, 1987). The catchment area of the lake (16,500 km^2) has a dendritic type of drainage network. Five major permanent rivers, Gilgel Abay (Small Blue Nile), Gumara, Rib, Megech and Dirma, as well as more than 30 seasonal streams feed the lake. The littoral zone of the lake is poorly developed, highly degraded and most of the wetland areas have been converted to agricultural and grazing lands (Birru Yitaferu *et al.*, 2004).

The seasonal rains cause the lake level to fluctuate regularly and during the dry season, its level decreases by up to 2 m. Winds are predominantly southerly from January until July, and mostly northerly from August until November (Gassè, 1987). The climate of L. Tana is characterized by a main rainy season with heavy rains during July-August, a dry season during November-April, and two minor rainy seasons during May-June (pre-rainy season) and September-October (post-rainy season) (After Tesfaye Wudneh, 1998; Eshete Dejen *et al.*, 2004).

MATERIALS AND METHODS

Sampling methods

Sampling was carried out monthly between July 2003 and June 2005. Weekly sampling was also carried out in May/June 2005. Qualitative and quantitative zooplankton sampling was carried out at 6 sites, which were evenly distributed over the lake, namely Gumie tirs, Zegie, Gelda, Gumara, Gorgora and Gilgel Abay (Fig. 1). At each site, two stations were fixed, one at the inshore (*ca.* 250 m from the shore, depth < 3 m) and another one at the open water (*ca.* 1500 m from the shore, depth ca. 10 m). Three replicates were taken at each station and all sampling was carried out during the daytime, generally during the morning between 9 AM to noon.

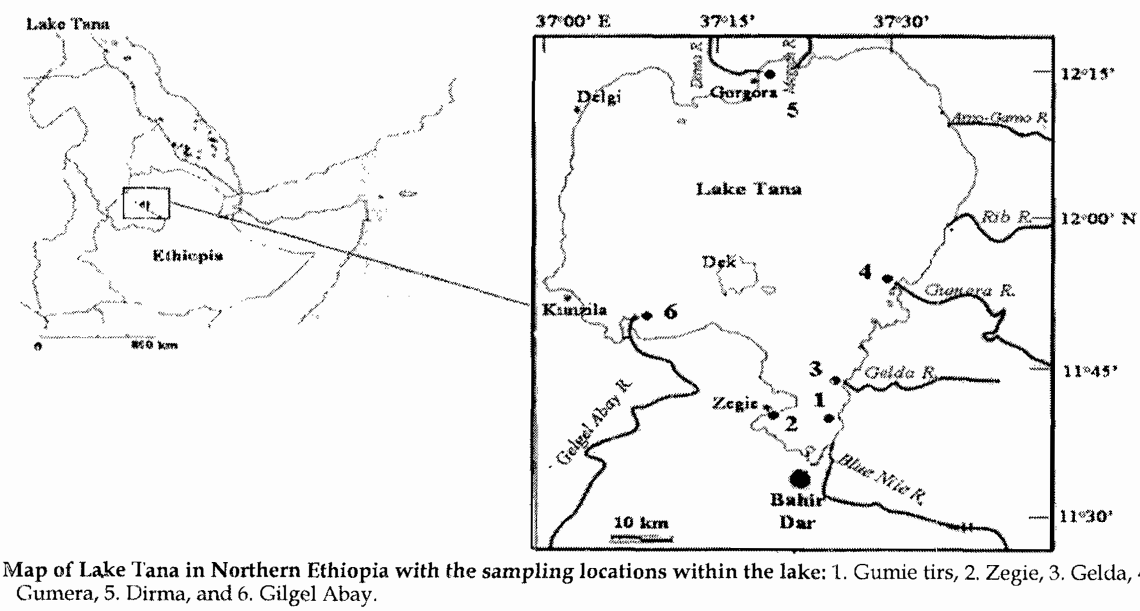


Fig 1. Map of Lake Tana in Northern Ethiopia with the sampling locations within the lake: 1. Gumie tirs, 2. Zegie, 3. Gelda, 4. Gumera, 5. Dirma, and 6. Gilgel Abay.

At each sampling station, zooplankton was sampled with a zooplankton net (64 μm mesh size, 30 cm mouth opening, 1.2 m cod end), which was hauled along the entire water column (from just above the bottom up to the surface). Since the lake is turbid, one net was used for only 4 months in order to avoid clogging by silt, and filtration efficiency was generally assumed to be 100%, based on the net design (Duncan Associates, UK). The total number of females in the adult population and the % of females carrying eggs was estimated from adult female counts. Adult males were included in the adult population counts. The fecundity as eggs per female was also determined each month. The mean size and weight of naupliar, copepodite and adult stages were immediately measured from field samples. Direct weighing was used to measure dry mass. The algal chlorophyll a concentration (μg/L) was also measured during the fieldwork using standard spectrophotometric method.

Developmental times

Developmental times of the copepods were measured in culture experiments using mixed algal culture and natural seston from filtered, concentrated (45 μm mesh sieve) lake water. Algal samples taken from the lake were enhanced with inorganic growth nutrients (Guillard's F/2 media) and maintained in laboratory cultures until fed to zooplankton. Before release into the culture media, zooplankton were filtered through a 150 μm sieve so that the larger stages were retained on the sieve and the developmental stages of copepods, cladocerans and rotifers passed into the filtrate. The sieve was gently immersed in filtered lake water to release the large individuals. Then, 20 ovigerous females were pipetted out individually into small test tubes (glass jars) containing pre-filtered lake water, and incubated in a thermostatically controlled water bath. They were subsequently observed for hatching and the adult females were immediately removed leaving the newly hatched nauplii. The water containing the nauplii was then transferred into large beakers (1–2 liters capacity). The juvenile stages were observed twice daily. The culture water was changed every three days and replenished with filtered lake water and mixed algal culture. We realize that the animals were given food in excess (not so natural feeding regime), but the objective of this experiment was to ensure unfailing survival of laboratory cohorts until completion of one generation cycle.

The duration times were determined by direct observations of times taken to develop from egg to nauplii for at least 100 eggs, from nauplii to copepodites for 80 nauplii, and copepodites to adults for at least 30 copepodites. The duration times of the three copepods were measured under manipulated conditions (20/21°C) with a 12 hour photoperiod. Additional culture experiments were carried out at 25/26°C to assess the relative duration and growth of individual species and stages at higher temperatures.

Zooplankton counting and determination of dry weight biomass (DW)

Each sample was concentrated to a volume of 150 ml and preserved in 4–5% formaldehyde and sucrose. The zooplankton samples brought from each sampling station were sub-sampled to 50 ml after thorough mixing. Specimens were sorted into species, developmental stages, and then counted in the laboratory under stereoscopic microscope (mag. 40X) using grid glass counting chamber.

Body length of copepodites and adults was measured with an ocular micrometer from the apex of the head to the base of the spine and to the tip of the furcal rami (Culver *et al.*, 1985). From each sample, 20–30 individuals of each species were measured and measurements were carried out once a month.

Individuals of each copepod species were separated into lumped age classes, and were transferred to aluminium-coated dishes and dried at 60°C for 24 hours in an oven. Biomass of the lumped age classes of nauplii, copepodites and adults was determined by direct weighing on a Mettler MT-5 micro analytical balance (accuracy 0.1μg). Individual dry weight was calculated from at least 50 adults and 100 juveniles, and as many as 15 replicates. Analyzing the sample immediately after collection minimized weight loss as a result of preservation.

Production estimation

The biomass increment method (growth-increment summation model) (Winberg *et al.*, 1971b) for the calculation of production of species with continuous reproduction was used. The production of the whole population can be regarded as the sum of the production of the different age classes.

$$P = (N_e \Delta W_e) T_e^{-1} + (N_n \Delta W_n) T_n^{-1} + (N_c \Delta W_c) T_c^{-1}$$

where P is the total production estimate in weight per unit volume and time. N_e, N_n and N_c are the mean population densities of eggs, nauplii and copepodites, respectively, in numbers per the same unit volume. ΔW_e is the mean weight of an egg (initial weight of nauplii), ΔW_n and ΔW_c are the mean weight increments of the nauplii and copepodite stages from the smallest to the largest sizes, respectively. T_e, T_n and T_c are the mean duration of development of the eggs, nauplii and copepodites, respectively. Naupliar and copepodite production estimates are somatic, while adult production is reproductive (eggs).

The daily and annual production/biomass (P/B) ratio was also determined by taking mean biomass as the denominator.

Data analyses

Differences in spatial and temporal variations in density, biomass and production of each group were tested using analysis of variance (ANOVA). Since the counts were not normally distributed, they were log transformed. Each parameter was analysed for differences among years, seasons, sites, stations and zones (inshore, open water). Regression and correlation analysis was used for relating the structure of copepod species with environmental variables. For all data analyses, the SPSS version 11.0 was used.

RESULTS

Duration of development

Table 1 summarizes the developmental data of each species raised under laboratory conditions. *Thermodiaptomus galebi* (Calanoida) showed significantly longer developmental time than the cyclopoids, and took about 25 days to complete a generation at 20°C, whereas the cyclopoids took 18-20 days. All copepods had slightly shorter development times at 25°C, with the calanoid completing a generation in 17 days.

Copepod numerical density

Fig. 2 compares temporal variation in mean monthly numerical density (ind/L) of the three copepod species in the lake during the two study years (July 2003– June 2005). The calanoid *T. galebi* showed the maximum density (~ 50 ind/L) while cyclopoid densities were always below 20 ind/L. The two cyclopoids showed more or less stable population numbers throughout the two years. *T. galebi* however showed peak abundance during October (post-rainy season) in both years.

Numerically *T. galebi* were higher by more than 50% of both cyclopoid species. The mean density was 20.40 ind/L for *T. galebi*, and 9.59 ind/L and 7.22 ind/L for *T. ethiopiensis* and *M. aequatorialis*, respectively. In general, copepods increased during pre-rainy (May-June), reached peaks in the post-rainy season (Oct and Nov) and decreased during early dry season (Dec–Feb). Only 11% of the changes in copepod density is explained by turbidity in the lake ($r^2 = 0.11$, $P > 0.05$, $N=288$) (Fig. 2).

Table 1. Developmental time (days) of different stages of *Thermodiaptomus galebi, Thermocyclops ethiopiensis* and *Mesocyclops aequatorialis* raised under laboratory conditions (20 and 25 ± 1°C SEM).

Developmental time	*Thermodiaptomus galebi*	*Thermocyclops ethiopiensis*	*Mesocyclops aequatorialis*
Stages	20°C	20°C	20°C
Egg to nauplii I (De)	2.8 ± 0.8	2.4 ± 0.7	2.4 ± 0.9
Nauplii I to Copepodite I (Dn)	7.72 ± 1.8	5.0 ± 1.0	5.5 ± 1.2
Copepodite I to Adult (Dc)	13.6 ± 2.4	10.36 ± 1.5	12.98 ± 1.7
Stages	25°C	25°C	25°C
Egg to nauplii I (De)	2.2 ± 0.9	1.95 ± 0.8	1.95 ± 0.8
Nauplii I to Copepodite I (Dn)	5.00 ± 1.5	3.5 ± 1.1	3.9 ± 1.4
Copepodite I to Adult (Dc)	9.98 ± 1.8	7.36 ± 1.3	8.36 ± 1.5

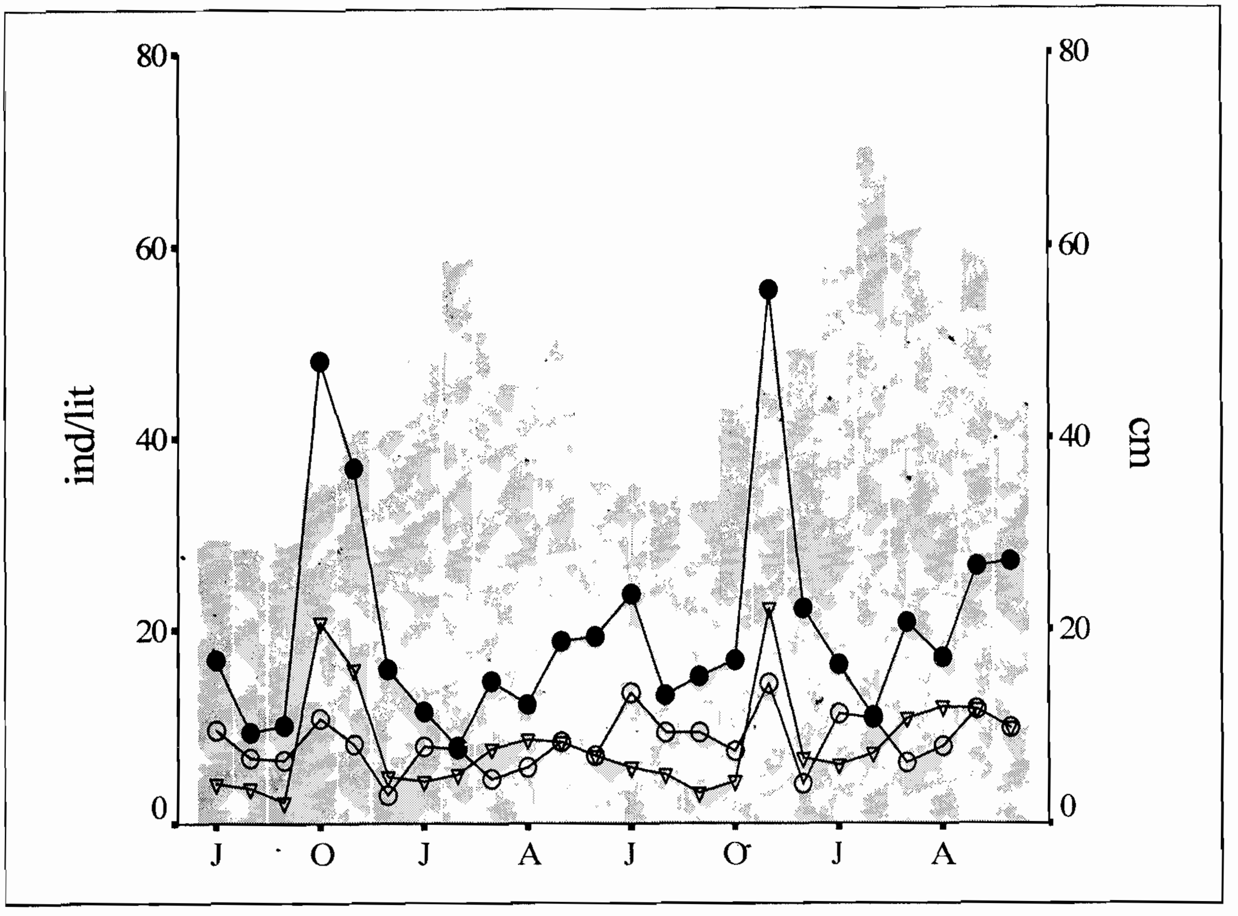


Fig. 2. Temporal variation in mean numerical densities (ind/L) of the dominant planktonic copepod species: *T. galebi* (•), *T. ethiopiensis* (o) and *M. aequatorialis* (∇) in Lake Tana for the period July 2003 to June 2005. Water transparency measured as Secchi depth (cm) is shown as bars.

The numerical density of the copepods was significantly higher in the inshore zone as compared with the open water zone (Mann-Whitney U-test $P < 0.001$, $N = 288$). When we compared all sites, significant differences were observed between North-west (Gorgora and Gilgel Abay) and South-east (Gumie, Zegie, Gelda and Gumara) of the lake (Mann-Whitney U-test, $P= 0.035$, $N=288$). The greatest density values were observed in the Gumara (av. 25.64 ind/L) for *T. galebi*. For *T. ethiopiensis*, numerical density peaks occurred in Zegie areas (av. 11.4 ind/L). For *M. aequatorialis*, the highest density was observed in Gumietirs (av. 9.51 ind/L). Though copepods in the north western sites were less abundant, they were larger in size as compared to the southeastern species.

The numerical density (ind/L) of each stage of development (nauplii, copepodites and adults) for each copepod species is shown in Fig. 3. In general, numbers of nauplii surpassed that of other stages for all the three species. For the cyclopoids, there is no apparent seasonal trend in distribution so that cohorts could not be identified even if all instars were enumerated separately. Densities of both copepodites and nauplii of *T. galebi* and *M. aequatorialis* were higher in the post-rainy season and adults increased also during the pre-rainy season. There is erratic variability in the naupliar densities recorded for *T. ethiopiensis*.

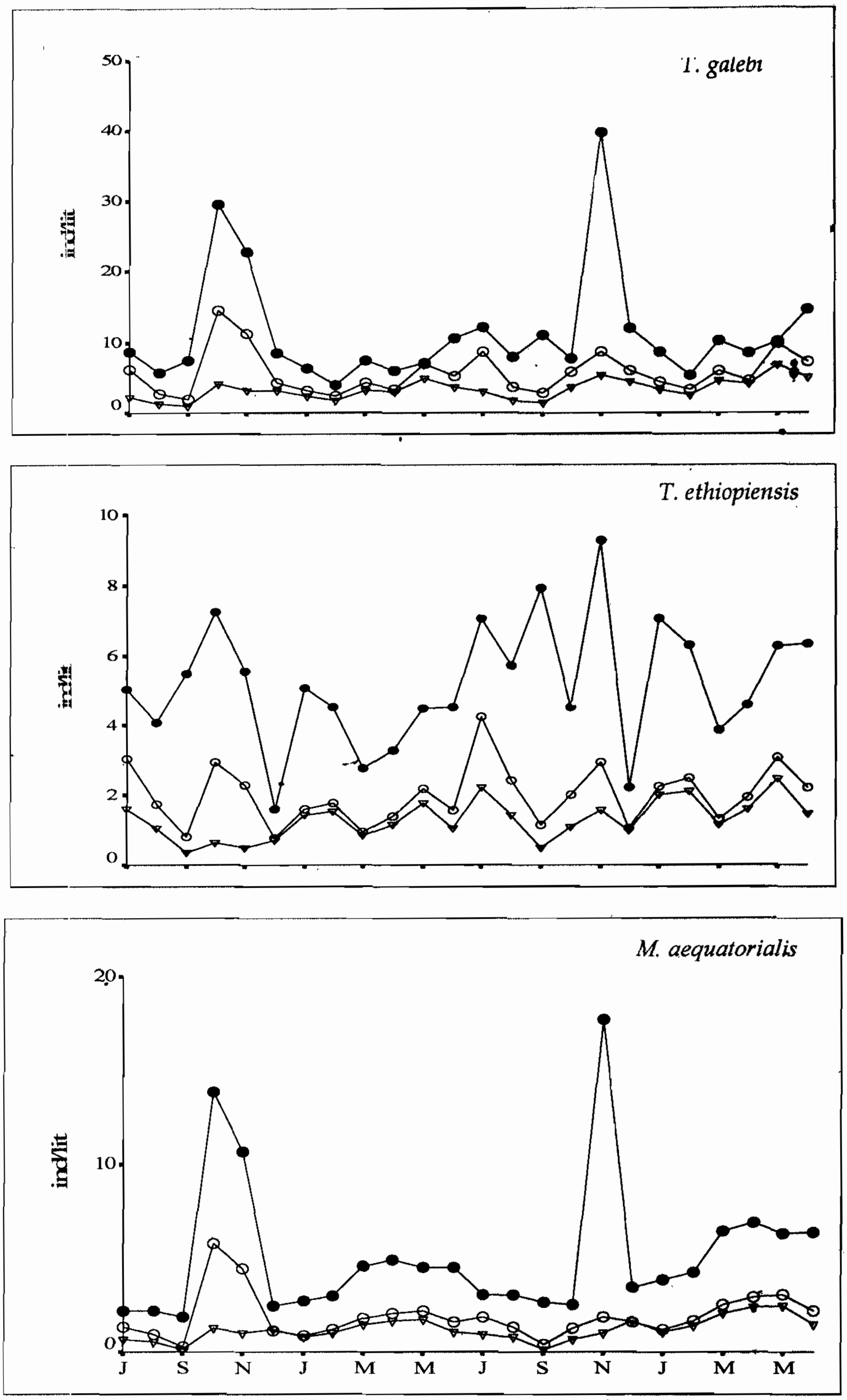


Fig. 3. Numerical density of nauplii(•), copepodites (o) and adults (∇) for each species of copepoda (*T. galebi*, *T. ethiopiensis*, and *M. aequatorialis*) in Lake Tana for the period July 2003 to June 2005.

The mean percentage of adult females relative to the total number of adults was 75% for *T. galebi*. 85% and 84% for *T. ethiopiensis and M. aequatorialis*, respectively (Fig. 4). In pre-rainy season, the population of adult copepods increased to more than 90%, including the adult females. Low percentage (*ca.* 60%) occurred during the rainy season for *T. galebi.* while *T. ethiopiensis and M. aequatorialis* showed the lowest percentage of females during the post rainy and dry seasons, respectively (Fig. 4A). The post-rainy period coincides with the period of maximal fish growth (juvenile zooplanktivores) and with the period of highest fish predation. The fecundity (as eggs/female) for the three copepods was continuous throughout the study period, with the mean highest ratio (1.8 eggs/female) recorded for *T. galebi* during the rainy season (Fig. 4B). The average clutch size of individual female calanoids did not exceed 10 eggs/sac, while for the cyclopoids; clutch sizes were more than 20 eggs/ind.

The highest clutches and fecundity occurred during the rainy season, after which they decreased to a minimum at the end of the rainy period through post-rainy season. For *T. ethiopiensis*, fecundity was variable among seasons with several peaks (max. 7.1 egg female^{-1} in November). Fecundity of *M. aequatorialis* varied from 0.03 to 6.45 egg female^{-1} with maximum values in March.

Copepod biomass estimates

Table 2 shows the body lengths and dry weights for the different stages of development of the three copepods in Lake Tana. Fig. 5 shows seasonal variations of biomass (as mg DW m^{-3}) of each stage of development (nauplii, copepodites and adults) of the three-copepod species in Lake Tana.

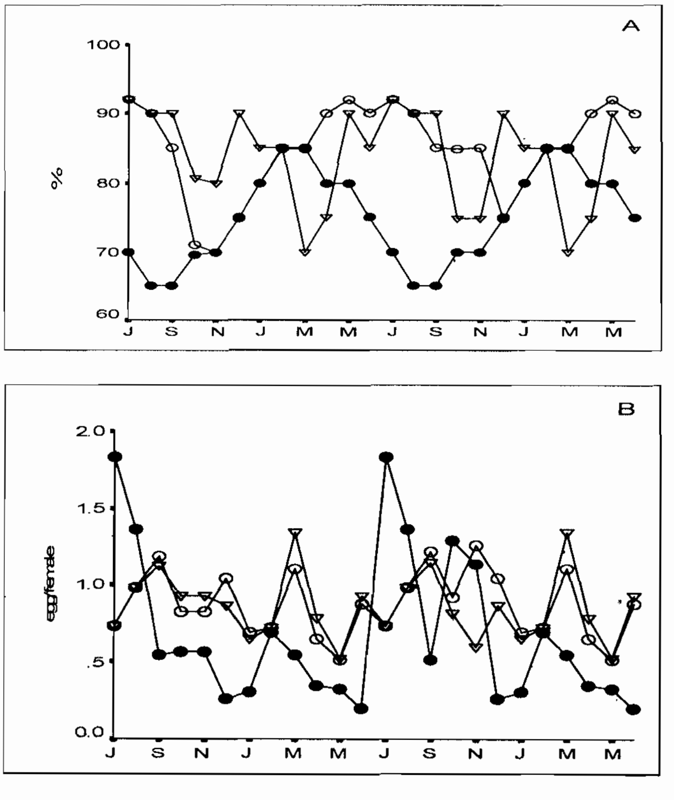


Fig. 4. Percentage of total females (A) and mean number of eggs per female(B) for *T. galebi* (•), *T.ethiopiensis* (o) and *M. aequatorialis* (∇) in Lake Tana for the period July 2003 - June 2005.

Table 2. Mean lengths (mm) and weight (µg) of copepod age classes in Lake Tana. Error bars represent 1 SD. All values are the results of monthly field samples.

Age class	*Thermodiaptomus galebi*		*Thermocyclops ethiopiiensis*		*Mesocyclops aequatorialis*	
	Length	DW	Length	DW	Length	DW
Egg	-------	0.14 ± 0.1	---------	0.08 ± 0.05	------------	0.12 ± 0.1
Nauplii	0.32 ± 0.3	0.21 ± 0.2	0.17 ± 0.13	0.11 ± 0.1	0.18 ± 15	0.15 ± 0:12
Copepodite	0.45 ± 0.4	1.79 ± 1.6	0.35 ± 0.2	1.62 ± 1.45	0.4 ± 0.3	1.68 ± 1.6
Adult male	0.92 ± 0.75	2.48 ± 2.42	0.8 ± 0.65	2.30 ± 2.2	0.93 ± 0.8	2.31 ± 2.2
Adult female	0.98 ± 0.85	2.51 ± 2.48	0.82 ± 0.72	2.32 ± 2.3	0.97 ± 0.7	2.36 ± 2.3

For *T. galebi*, the mean biomass of all stages is 20.92 mg DW m^{-3} (range 0.83–118.02 mg DW m^{-3}). The mean values are 7.33 mg DW m^{-3} (range 0.32–39.17 mg DW m^{-3}) and 6.18 mg DW m^{-3} (range 0.13–33.43 mg DW m^{-3}) for *T. ethiopiensis* and *M. aequatorialis*, respectively. Higher biomass values (> 25%) were recorded in the year 2004/2005 than in 2003/2004 for all three species. Peaks were observed in post- (Oct and Nov) and pre-rainy season (April-June) for *T. galebi* and *M aequatorialis*. *T. ethiopiensis* has highest biomass during the rainy season (June) and shows less seasonal variation in biomass fluctuations. Generally, copepodites had the highest biomass for all three copepods throughout the two years, except for higher adult cyclopoid biomass during the dry season in 2005 (Fig. 5B, C).

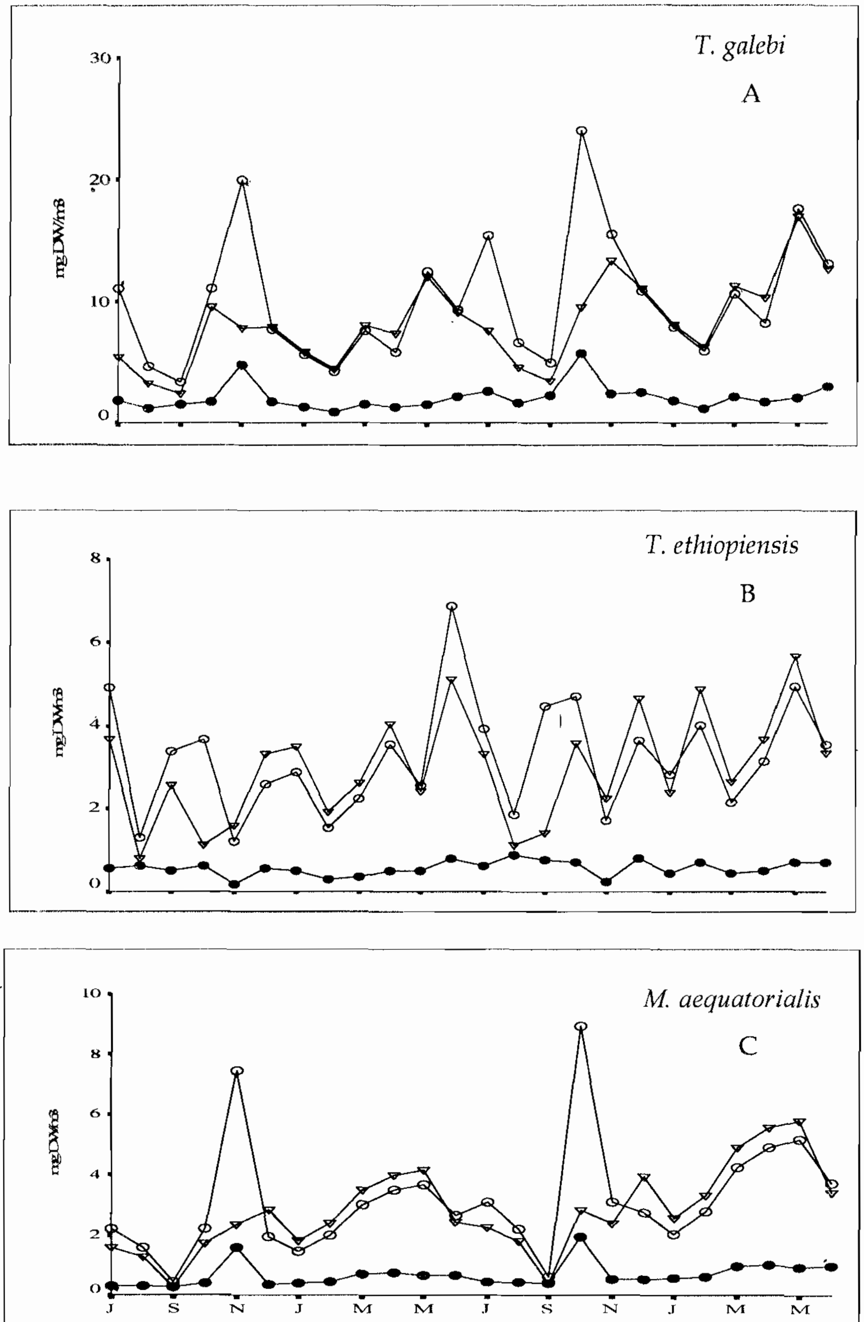


Fig. 5. Standing biomass (mg DW m^{-3}) of nauplii (•), copepodites (o) and adults (∇) for each species of copepoda (*T. galebi*, *T. ethiopiensis*, and *M. aequatorialis*) in Lake Tana for the period July 2003 to June 2005.

Production estimates and P/B ratios

Fig. 6 shows daily production rates (mg DW m^{-3} day^{-1}) of nauplii, copepodites and adults (eggs) of the three copepods in Lake Tana

For *T. galebi*, the mean production rate was 1.04 mg DW m^{-3} day^{-1} (range 0.05-7.16 mg DW m^{-3} day^{-1}), while for *T. ethiopiensis* and *M. aequatorialis*, the mean production rates were 0.42 mg DW m^{-3} day^{-1} (range 0.02-2.44 mg DW m^{-3} day^{-1}) and 0.43 mg DW m^{-3} day^{-1} (range 0.01-3.21 mg DW m^{-3} day^{-1}), respectively. The highest rate of production is observed during the post-rainy season for *T. galebi* and *M. aequatorialis* and pre-rainy season for *T. ethiopiensis.*

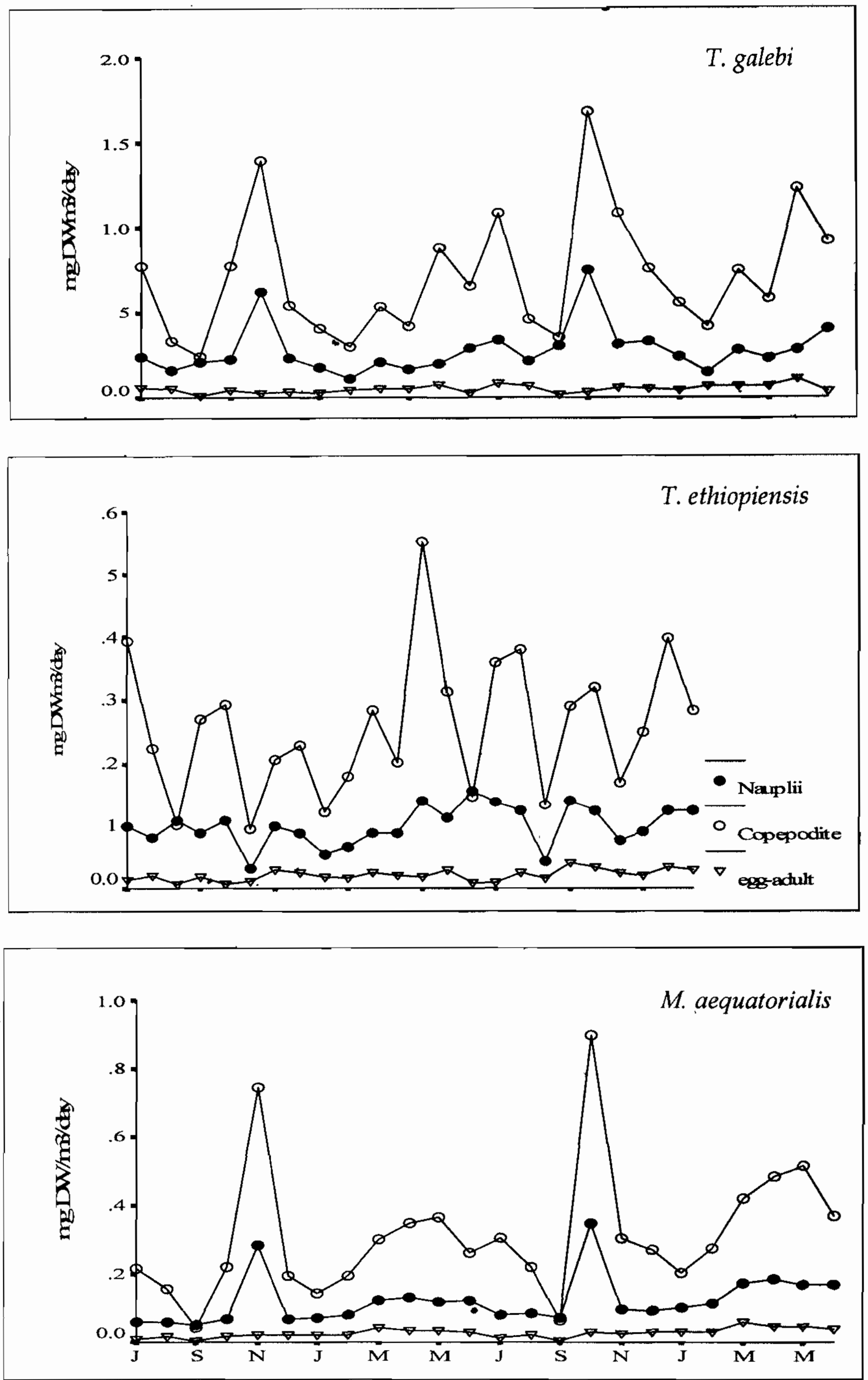


Fig. 6. Production (mg DW m^{-3} day^{-1}) of nauplii (•), copepodites (o) and egg- adults (∇) for each species of copepoda (*T. galebi, T. ethiopiensis,* and *M. aequatorialis*) in Lake Tana for the period July 2003 to June 2005.

The relative contribution of each developmental stage to total copepod production is presented in Fig. 7. Copepodites contribute 68.5% (ranging from 0.04 to 8.43 mg DW m^{-3} d^{-1}) of the total copepod production and nauplii and eggs (adults) contribute 26.5% (ranging from 0.008 to 4.78 mg DW m^{-3} d^{-1}) and 5% (ranging from 0.005 to 0.6 mg DW m^{-3} d^{-1}), respectively. The contribution of the eggs to the total production was very low (<10%) in all seasons. However, all the three copepods did not show period with zero egg production (see Fig. 4). At the end of the dry and during the pre-rainy season (March-June), the proportion of egg production to the total copepod production was relatively higher for all the three copepods species (Fig. 7).

The mean daily P/B ratio is 0.054 for *T. galebi* (range 0.03 to 0.11), and for *T. ethiopiensis* and *M. aequatorialis*, it is 0.06 (range 0.02 to 0.12) and 0.08 (range 0.03 to 0.14), respectively. The P/B ratios were seasonally stable for all copepods, with few exceptions (September). The turnover time (days) of biomass for *T. galebi* was 19.9 (range 9.00 to 34.21, and 18.0 (range 8.31 to 44.6) and 14.5 (range 7.39 to 35.06) for *T. ethiopiensis* and *M. aequatorialis*, respectively. This is in close agreement with the generation times obtained from culture experiments for all three copepods.

The maximum daily copepod production was 10.45 mg DW m^{-3} day^{-1} (Av. 2 mg DW m^{-3} day^{-1}). More than 50% of the production can be attributed to the copepodite stage (Fig. 7). However, copepodites had a relatively low productivity, with daily P/B ratio of 0.08 (range 0.07 to 0.09). Nauplii and eggs showed higher daily P/B values of 0.15 (range 0.13 to 0.17) and 0.39 (range 0.36 to 0.41), respectively. The relative temporal contribution of each species to the total copepod production is presented in Fig. 8. *T. galebi* contribute 55% of the total copepod production while *T. ethiopiensis* and *M. aequatorialis* contribute 20% and 25%, respectively. Despite the considerable seasonal fluctuation in production, a substantial amount of mean daily production was maintained throughout the year for the cyclopoids. There is no relationship between rainfall, and the algal biomass and copepod production in the lake (Fig. 8, lower panel).

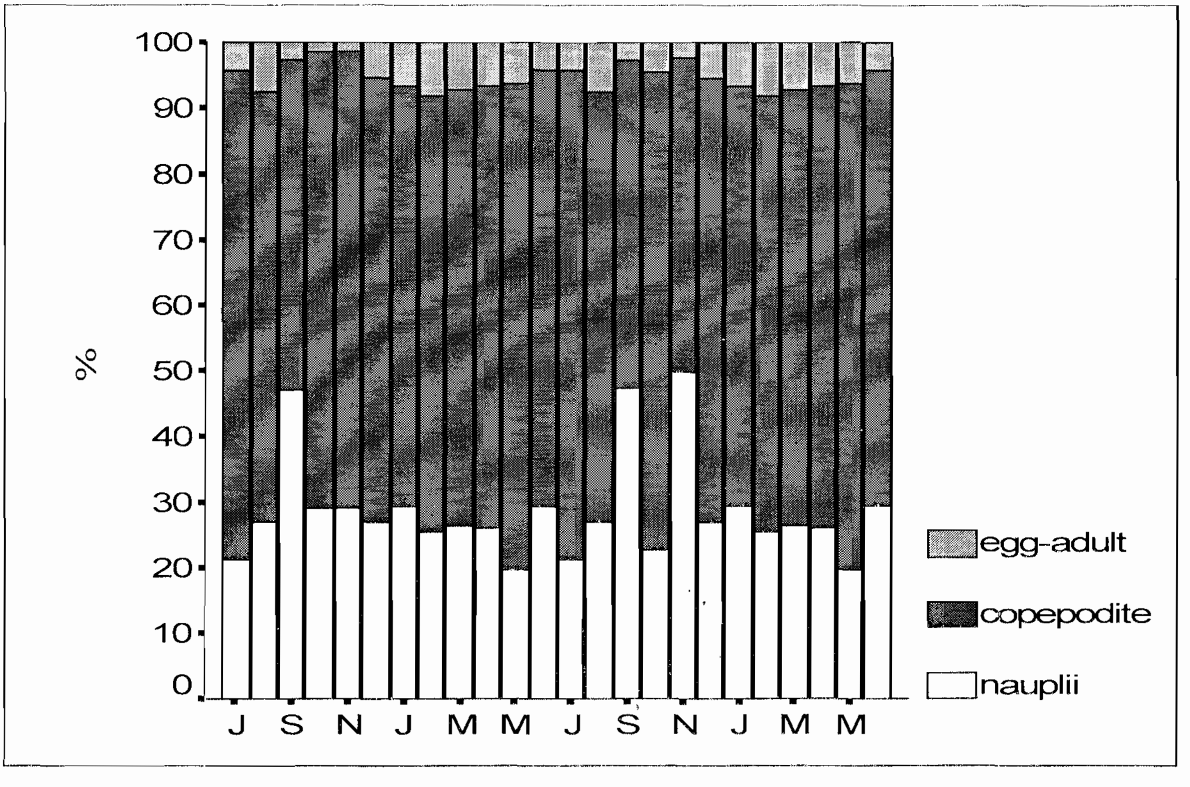
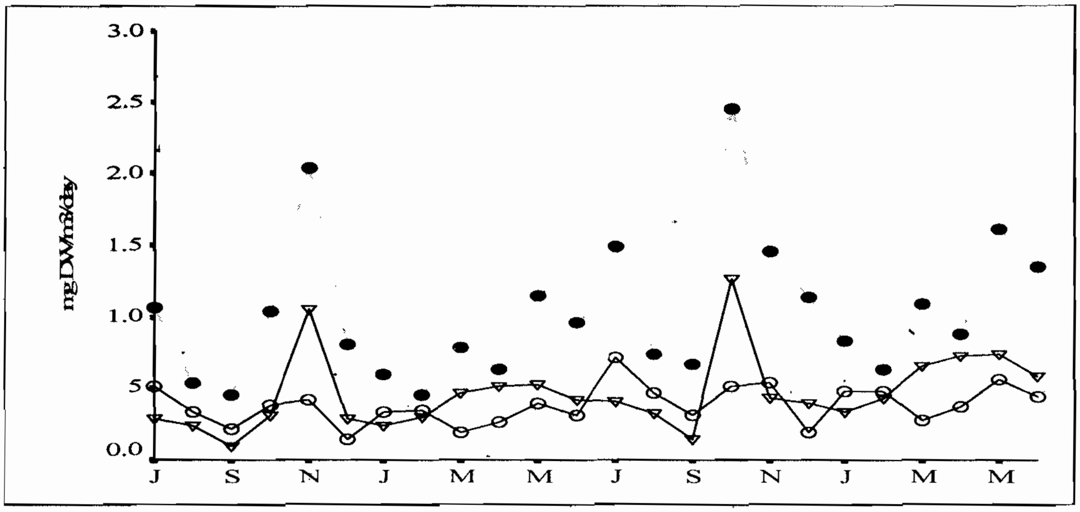


Fig. 7. Temporal variation in the contribution of each developmental stage to total copepod production in Lake Tana for the period July 2003 to June 2005.



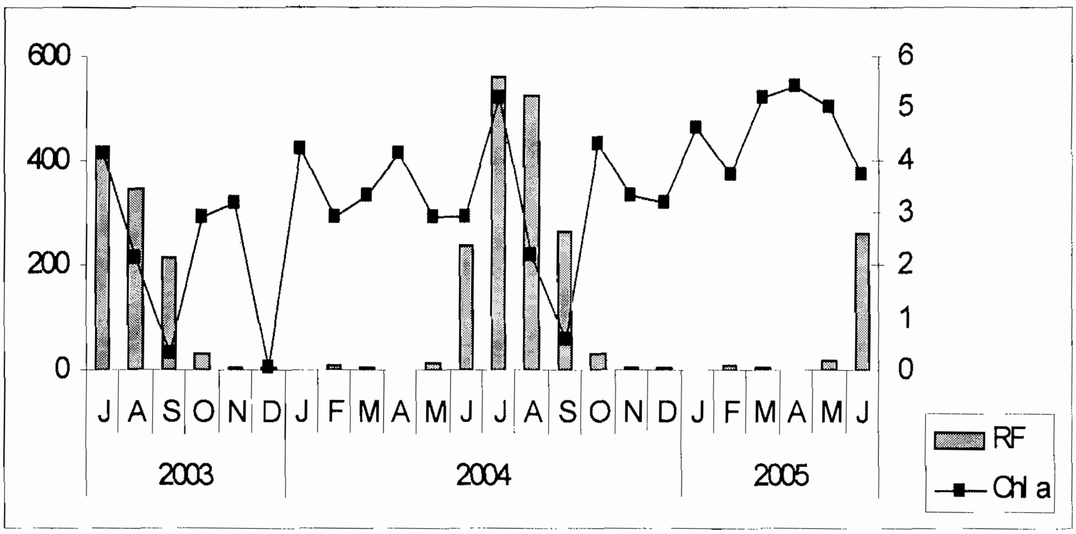


Fig. 8. Temporal changes of daily production of the three dominant limnetic zooplankton: *T. galebi, T. ethiopiensis,* and *M. aequatorialis.* Lower panel shows changes in mean monthly chlorophyll a concentration and rainfall (RF, in mm) in Lake Tana for the same period.

DISCUSSION

Duration of development

The duration of embryonic development in planktonic freshwater copepods is primarily a function of temperature. Life history data are limited for copepods from tropical regions. Our data (Table 1) were close to those obtained from other tropical species and follow an inverse relationship between temperature and developmental time or longevity (Léveque and Saint-Jean, 1983; Burgis, 1974; Seyoum Mengistou and Fernando, 1991; Mavuti, 1994; Irvine and Waya, 1999). However, longer developmental times were observed for all copepods in Lake Tana as compared to reports from other tropical lakes.

Post-embryonic duration is mainly affected by temperature and quality/quantity of food (Vijverberg, 1989; Amarasinghe *et al.*, 1997b). Since our experimental study was under non-limiting food levels, postembryonic development times were highly dependent on temperature. The relatively longer developmental time for each stage in our experiments probably reflects the low culture temperature (20°C) that was used in this study.

Copepod pattern of distribution

The zooplankton community in Lake Tana has shown a shift from dominance by Cyclopoida (Tesfaye Wudneh, 1998) to Calanoida in recent years (Eshete Dejen *et al.*, 2004), and this trend was also observed in the present study. In comparison with the earlier report (Tesfaye Wudneh, 1998), copepod densities were higher in the study of Eshete Dejen *et al.* (2004) and also in this study because different age classes (nauplii and copepodites) were considered in the counts.

Although highly abundant, calanoids were poorly utilized in Lake Tana. Eshete Dejen (2003) reported that although calanoids represent >50% of the total zooplankton density and biomass in Lake Tana, they represent only from 2.7–9.6% (by biovolume) of the diet of zooplanktivorous small barbs. This may be because catching calanoids is difficult as they are fast swimmers-even against water currents (Drenner and McComas, 1984).

Species abundance in number and biomass vary with temperature, and quality and quantity of food. Regulation of zooplankton populations is frequently observed to be due to predation (top-down) or/and to food availability (bottom-up). *T. ethiopiensis* was numerically higher than *M. aequatorialis* during the post-rainy season. This is probably because algae were an important food source for this herbivore species. However *M. aequatorialis* had also relatively high abundance during October and November (post-rainy season), and April and May (pre-rainy season), possibly due to an increased density of animal foods such as cladocerans, insect larvae and protozoans, and algae and detritus.

We conducted a preliminary study on the feeding ecology of these copepods in Lake Tana. *T. galebi and T. ethiopiensis* were found to be herbivorous and sometimes where there is limitation of food during February, July and August, they feed on detritus and silt (Personal Observation). *M. aequatorialis* is omnivorous during its juvenile stages while adults are mainly carnivorous (Lampert, 1988). The numerical dominance of *M. aequatorialis* over *T. ethiopiensis* is probably due to its predatory nature on rotifers and cladocerans. The omnivorous nature of *M. aequatorialis* was also recognized in cultures where they grew well with a mixture of algae, ciliates and rotifers as food source. In general, the seasonal abundance of the copepods coincided primarily with high prey density, water level and temperature. The effect of turbidity was not critical for copepods as also reported by Eshete Dejen *et al.* (2004), although some cladocerans were found to be negatively affected by turbidity in previous studies.

In post-rainy and pre-rainy seasons, intensified production and decomposition following nutrient release stimulates secondary production. Primary production seems to be the main limiting factor for zooplankton growth, as it is also the source of detritus. Primary production in pre-rainy season was associated with wind-driven mixing and efficient small-sized algae compared to the post-rainy months, where it depends on rain-fed production. *T. galebi* mainly depends on algal and detritus foods rather than animal prey (cf. Lampert, 1988).

Of the different copepod age classes, nauplii had the highest abundance for all three copepods (Fig. 3), while adult numbers were low. This is in contrast to the findings of Seyoum Mengistou (1989) in Lake Awassa where nauplii were very low, and cannibalistic predation was suggested as a possible reason for the observation. In Lake Tana, *M. aequatorialis* apparently has other food sources to exclude nauplii in its diet. Peak recruitment of nauplii occurred in the rainy season for this cyclopid and the calanoid, but not for *T. ethiopiensis*, which showed erratic nauplilar recruitment (Fig. 3). Although adults are low for all three copepods, there was continuous reproduction as shown by the high % of females in the adult population and consistent fecundity throughout the two years of study (Fig. 4).

Eshete Dejen *et al.* (2004) associate strong reduction of some cladocerans' densities with turbidity in Lake Tana. This study found that copepod densities were positively correlated with phytoplankton biomass and productivity and weakly correlated with suspended silt concentration. We observed large seasonal and spatial changes in turbidity (as Secchi depth). Secchi depth varied from stations with 70 cm while at the river mouth it was 5 cm. Therefore, we conclude that it is unlikely that turbidity has a profound effect on the dynamics of the copepod community in Lake Tana.

Copepod biomass estimates

Biomass data for tropical copepods so far investigated show large variability. Burgis (1974) recorded a mean annual biomass value of 559 mg DW m^{-2} for *Thermocyclops hyalinus*, in Lake George (Uganda), Léveque and Saint-Jean (1983) estimated biomass values ranging from 13.6 to 243.9 mg DW m^{-2} for the cyclopoids in Lake Chad. The estimated biomass of copepods in Lake Tana was in the same range as the figures reported above. Mean biomass of *T. galebi* (integrated for a water column of 9 m depth) was 188.11 mg DW m^{-2} (ranging from 7.47 mg DW m^{-2} to 1.06 g DW m^{-2}). For *T. ethiopiensis* and *M. aequatorialis* the corresponding values were 65.97 mg DW m^{-2} (ranging from 3.15 to 352.53 mg

DW m^{-2}) and 55.62 mg DW m^{-2} (ranging from 1.17 to 300.87 mg DW m^{-2}), respectively. Total copepods mean biomass was 310 mg DW m^{-2} (ranging from 11.7 mg DW m^{-2} to 1.57 g DW m^{-2}). Although calanoid copepods represent more than 50% of the total zooplankton biomass in Lake Tana, they accounted only for 2.7 to 9.6% of the zooplankton biomass in the diet of small barbs (Eshete Dejen, 2003). This indicates that the higher biomass of *T. galebi* throughout the year is possibly due to its poor consumption by the small zooplanktivorous barbs.

High variability in mean dry mass of tropical copepods is reported (Table 3). In Lake Naivasha (Kenya), Mavuti (1994) found an annual mean biomass of 120.45 mg DW m^{-3} for *Thermocyclops oblongatus*. Seyoum Mengistou and Fernando (1991) obtained lower mean biomass of 44.85 mg DW m^{-3} for the dominant crustaceans in Lake Awassa. Léveque and Saint-Jean (1983) report closer value of 56.4 mg DW m^{-3} for *T. neglectus* in Lake Chad. The mean annual biomass of copepods in Lake Tana is 34.43 mg DW m^{-3}, which is low compared to all of the data above.

The percent contribution of the different age classes of the copepods is similar with copepodites contributing the most. In Lake Lanao, Lewis (1979) estimated biomass of the different stages of development of *T. hyalinus* (nauplii, copepodites, adults and eggs) as 31.8, 67.5, 25.15 and 0.9 mg DW m^{-3}, respectively. Seyoum Mengistou and Fernandó (1991) recorded a maximum value of 2, 15 and 70 mg DW m^{-3} for nauplii, copepodites and adults of *M. aequatorialis* in Lake Awassa, Ethiopia. Values of 2, 10, 8 mg DW m^{-3} was estimated for the same stages of development of *Thermocyclops consimilis* in the same lake. Burgis (1974) found mean values of 10, 164, 74 and 4 mg DW m^{-3} for nauplii, copepodites, adults and eggs, respectively, of *T. hyalinus* in Lake George. In the present work, the mean biomass values of nauplii, copepodites, adults and eggs of *T. galebi* are 2.37, 10.24, 8.3 and 0.13 mg DW m^{-3}, respectively, and the respective values for *T. ethiopiensis* and *M. aequatorialis* are 0.67, 3.58, 3.09 and 0.05 mg DW m^{-3}, and 0.66, 2.82, 2.7 and 0.06 mg DW m^{-3}, which is consistent with data obtained from most tropical lakes studied. Lower values in September and December in all developmental stage was probably due to unfavourable feeding conditions in September and perhaps due to poor quality of the phytoplankton as food source and lower mean temperature in December. The soup of large-sized *Melosira sp.* is not easily ingested by zooplankton. During this period, fishermen also complained about the clogging of their fishing nets due of the heavy sedimentation of blooms of *Melosira*-dominated algal soup (personal observation).

Table 3. Comparison of production of *Thermodiaptomus spp.*, *Thermocyclops spp.* and *Mesocyclops spp.*, from 6 tropical African lakes. Biomass (mg DW m^{-3}), mean daily production (mg DW m^{-3} day^{-1}); total annual production; mean daily and total annual P/B ratio, respectively.

Taxa	Lake mean T (°C)	B	Daily production	Annual production	Daily P/B ratio	Annual P/B	Locality (Lake)	Reference
Mesocyclops aequatorialis	23/24	—	—	—	0.18	14.3	Awassa	Seyoum Mengistou (1989)
Thermocyclops consimilis	23/24	95	6.9	535.2	0.044	14.6	Awassa	Seyoum Mengistou (1989)
Thermocyclops oblongatus	22	120.0	11.0	4022	0.09	73.5	Naivasha	Mavuti (1994)
Thermocyclops hyalinus	25	248.0	18.6	7154	0.08	28.8	George	Burgis(1974)
Thermocyclops neglectus	26	56.4	9.6	3580	0.17	63.5	Chad	Leveque and Saint Jean (1983)
Mesocyclops aequatorialis	—	—	3.2-7.0*	—	—	—	Malawi	Irvine and Waya (1999)
Mesocyclops aequatorialis	21/22	6.18	0.43	157	0.07	25.4	Tana	Present study
Thermocyclops ethiopiensis	21/22	7.33	0.42	156	0.06	21.3	Tana	Present study
Thermodiaptomus galebi	21/22	20.9	1.04	380	0.05	18.2	Tana	Present study

*depth integrated value.

Production and P/B ratios

Productivity measurements are more realistic than abundance or biomass measurements in describing the contribution of each species to energy flow in ecosystems. There are several estimates of zooplankton production in African lakes. Léveque and Saint-Jean (1983) estimated the daily production of crustacean zooplankton (cyclopoid copepod) in Lake Chad as 1.3 to 60.6 mg DW m^{-2}. Seyoum Mengistou and Fernando (1991) recorded integrated production of cyclopoid copepod in Lake Awassa as 16.04 mg DW m^{-2} d^{-1}. Burgis (1974) recorded mean production of 44 mg DW m^{-2} d^{-1} for *T. hyalinus* (Lake George). Irvine and Waya (1999) reported production values ranging from 3.2 to 7.0 mg DW m^{-2} d^{-1} for *M. aequatorialis* in oligotrophic Lake Malawi. In Lake Tana, mean daily production of total copepods was 17.28 mg DW m^{-2} d^{-1}, which is almost equal to the integrated production in Lake Awassa. The presence of the calanoid of *T. galebi* has not increased secondary production level in Lake Tana.

The percentage contributions of the developmental stages of the three copepods were similar (Fig. 7). The relative low contribution of egg production to total production was reported earlier for copepods in tropical lakes. In Lake Awassa (Ethiopia), Seyoum Mengistou and Fernando (1991) observed minor contribution of eggs to total production of the cyclopoids- eggs (5.3%), nauplii (27%) and copepodites (67.7%). Mavuti (1994) reported contribution of 5% for eggs, 48% for nauplii and 47% for copepodites in Lake Naivasha (Kenya). Burgis (1974) observed a different proportion of 15% for eggs, 8% for nauplii and 77% for copepodites of *Thermocyclops hyalinus* in Lake George, Uganda. On the other hand, Vareschi and Jacobs (1984) reported an exceptionally high value (>50%) of egg production for the Calanoid copepod *Paradiaptomous africanus*, in Lake Nakuru (Kenya).

The P/B ratio is the biomass turnover rate on a daily or annual basis. Seyoum Mengistou and Fernando (1991) estimated a daily P/B ratio of 0.18 and 0.04 for *M. aequatorialis* and *T. consimilis*, respectively, in Lake Awassa. The annnual P/B value of cyclopoids in Lake Awassa was 14.3 for *M. aequatorialis* and 14.6 for *T. consimilis*. Léveque and Saint-Jean (1983) estimated a daily P/B ratios ranging from 0.10 to 0.25 for the cyclopoids in Lake Chad, while Mavuti (1994) obtained a daily P/B ratio of 0.09 (turnover time of 11.1 days) and annual P/B of 73.5 for *T. oblongatus* in Lake Naivasha. Burgis (1974) found a daily P/B ratio of 0.078 (turnover time of 12.8 days or 8% of the biomass replacement every day) for *T. hyalinus* in Lake George. Lower daily and annual P/B ratios and longer turnover times were observed for the Lake Tana copepods (Table 3), which suggest that they show relatively low turnover rates in the food chain.

The biomass and production values recorded in this study are much lower (ca. 6.3 g DW m^{-2} yr^{-1}) when compared to previous reports (ca. 14.6 g DW m^{-2} yr^{-1}) (Tesfaye Wudneh, 1998). It is likely that previous results obtained were overestimated because they sampled only a small representation of the lake (one site), limited only to the gulf area (10% of the lake) while this study represents the whole lake area (6 sites and 12 stations). Moreover, generalized conversion factors were previously used while in this study, we considered individual species and stages and their development rates to estimate biomass and production.

In Lake Tana, an annual biomass turnover rate of 19year $^{-1}$ was calculated for *T. galebi*, 22 year $^{-1}$ for *T. ethiopiensis* and 27 year^{-1} for *M. aequatorialis*. The total copepods had an annual P/B of 21.4 year^{-1}. This is low turnover rate, but in spite of the low P/B values and longer turnover times, they had relatively high seasonal biomass and productivity. The highest P/B value and the shortest biomass turnover times of *T. galebi* were recorded in October/November when both production and biomass were high.

This paper dealt only with the rates of development and production of the dominant copepods in Lake Tana. Similar studies on the cladoceran and rotifer communities are underway. The interactions between phytoplankton and zooplankton communities, and the role of detritus, silt and the microbial loop need to be elucidated in this large-turbid tropical lake.

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