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SEASONAL VARIATION OF BIOMASS AND SECONDARY PRODUCTION OF *THERMOCYCLOPS* (CYCLOPOIDA) AND *BRACHIONUS* (ROTIFERA) SPP. IN A SHALLOW TROPICAL LAKE KURIFTU, ETHIOPIA

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ABSTRACT: Monthly net samples were taken at inshore and midlake sites in Lake Kuriftu from August 2008 to May 2009 to estimate biomass of the dominant zooplankton, the cyclopoid copepod (*Thermocyclops consimilis*, 71% in abundance) and the rotifer *Brachionus calyciflorus* (12%). *T. consimilis* was cultured in the laboratory to obtain life history data on duration of embryonic and post-embryonic development at 20 and 25.9°C, fed mixed algal food enhanced with F/2 culture medium. Laboratory duration times were close to biomass turnover rates calculated from field data for both species. Laboratory results and field data were used to estimate production of *T. consimilis* with the growth increment method. The mean biomass and production of *T. consimilis* were 23.8 mg dry weight (DW) m^{-3} and 0.78 mg DW $m^{-3}d^{-1}$, respectively, and daily and annual P:B ratios were 0.033 and 13.10, respectively. Cyclopoid production was highest during the post-rainy month of November enhanced by a month lag of decomposed detrital food in October. For *B. calyciflorus*, its dry mass, determined from biovolume, and recruitment rates of new individuals, were used to calculate secondary production. The mean biomass and production of this species were 629.66 µg DW m^{-3} and 180.38 µg DW m^{-3} d^{-1}, respectively, with daily and annual P:B ratios of 0.29 and 104.6, respectively. Rotifer production was highest during the dry months of December – March with high temperature and chl a. Overall, secondary production rates in Lake Kuriftu were low compared to other tropical lakes and related cyclopoids and rotifers, and some reasons for this observation are discussed.

Key words/phrases: **Biomass, *Brachionus calyciflorus*, Lake Kuriftu, secondary production, *Thermocyclops consimilis***

INTRODUCTION

Limnological studies of tropical freshwater ecosystems are not extensive when compared to temperate ones; nevertheless East African lakes have been studied fairly well in comparison with other regions of Africa. Hecky (1984) noted that East African lakes are regarded as among the world's most productive ecosystems. For example zooplankton biomass and production of some African lakes is exceptionally high, such as Lake Nakuru, Kenya (Vareschi and Jacobs, 1984). However the contribution of different zooplankton taxa to secondary production, or the factors that critically regulate the production rates have not been intensively elaborated, despite the fact that zooplankton are important food items for juveniles and adults of many fish species (*e.g.*, Gophen *et al.*, 1988; Tudoracea *et al.*, 1988).

The only studies on secondary production in Ethiopian lakes include the work of Seyoum Mengistou and Fernando (1991) in Lake Hawassa and Ayalew Wondie and Seyoum Mengistou (2006) in Lake Tana. These two lakes represent contrasting ecosystems—Lake Hawassa is moderately-sized and moderately-deep lake (A_0 = 88 km^2; Z_{max} ~ 22 m) and Lake Tana is the largest lake in Ethiopia (A_0 = 3156 km^2) but relatively shallow (Z_{max} = 8 m). It was noted that secondary production in Lake Hawassa was dominated by copepods and cladocerans, while in Lake Tana, Rotifera also contributed about 24% of the annual secondary production. Secondary production was highest during the rainy months in Lake Hawassa, but during the post-rainy months in Lake Tana. Zooplankton productivity was associated with high primary productivity enhanced by inflow of nutrients

through runoff and deep mixing in Lake Hawassa (Seyoum Mengistou and Fernando, 1991), while in Lake Tana, decomposed detrital particles and bacteria appeared to contribute the major nutrition to zooplankton during the post-rainy months of October-November, enhanced by re-suspension and mixing by wind. Secondary production of zooplankton was lowest during the rainy months of July – September in Lake Tana. The total annual zooplankton production in Lake Hawassa was slightly higher (2.5 $gDW/m^3/yr$) than in Lake Tana (1.49 $gDW/m^3/yr$), but the annual biomass turnover rate (P:B) was slightly higher in Lake Tana (67.8 to 55.8 in Lake Hawassa). The higher biomass turnover rate in Lake Tana was attributed to Rotifera and Cladocera, but no such analysis was done for Lake Hawassa. We opted to include a different lake system to assess which factors are of over-riding importance for secondary productivity in Ethiopian lakes. In this study, we considered a small and shallow polymictic Lake Kuriftu to determine the biomass and seasonal variation of secondary production of the dominant zooplankton taxa. Thus the main objective of this study was to estimate the magnitude of production rates by the dominant zooplankton and identify the major seasons associated with peaks of secondary production. We also compared our results with data of secondary production rates of cyclopoids and rotifers from other tropical Ethiopian and African lakes. Because Lake Kuriftu is shallow (max. depth 6 m), only seasonal hydrological and biological factors, rather than hydrographical (stratification) patterns in the lake were considered.

MATERIALS AND METHODS

The study area

Lake Kuriftu (8° 47′ N and 39° 00′E, Fig. 1) is one of the crater lakes found in Bishoftu (also called Debre zeyt) town some 47 km southeast of Addis Ababa at an altitude of 1860 masl. It is a shallow (≈6 m) artificial lake formed by diverting and damming Belbela River for irrigation purposes. Groundwater inflow plays a minor role in the water balance of this lake as the static water level in the area is well below the lake and the occurrence of loss of water through seepage is not well known (Seifu Kebede *et al*., 2001). The only seasonal water influx into the lake is thus rainfall and surface runoff during June-September and March-April (small rains).

The region has two rainy periods, the minor one extending roughly from March to April and the major one beginning in June and ending in September. During 2006, monthly total rainfall varied from 2.9 mm in November to 186.7 mm in August (Girum Tamire, 2006). During this study period, highest rainfall was recorded during August (250 mm) and September (150 mm) but no measurement or sampling was done in June and July, 2008. Very small rain was recorded in October 2008 which was followed by higher rainfall in Nov. (~ 40 mm). December – March was mostly dry (except January) and was followed by the small rains in April 2009 (data from the National meteorological Service of Ethiopia). During 2006, surface water temperature of the lake was reported to be between 20°C and 27.4°C while the bottom temperature was almost constant (19.2°C to 19.3°C) (Girum Tamire, 2006). Similar result of surface to bottom lake temperature between 20–24.5°C was measured during this study period (Table 1).

Table 1. Physico-chemical features of Lake Kuriftu (After Brook Lemma *et al*., 2001, Zinabu Gebremariam *et al*., 2002, and this study).

Parameter (unit)	Values and ranges
Area (Km^2)	0.4
Max. depth (m)	6
Mean depth (m)	2
pH	7.9-8.4, 8.2 – 8.93 *
Volume (m^3)	$3.0x10^6$
Secchi depth (m)	0.15-0.20, 0.37 – 0.56 *
Conductivity (mS cm/1)	3.19
Salinity (g/l)	0.26
Cations (meq/l)	3.19
Anions (meq/l)	3.46
Na^{1+} (meq/l)	1.00
Ka^{1+} (meq/l)	0.15
Ca^{2+} (meq/l)	1.25
Mg^{2+}(meq/l)	0.78
Total Alkalinity (meq/l)	2.89, 1.90 – 2.0- *
Cl^- (meq/l)	0.57
SO_4^{2-} (meq/l)	0.000
NO_3 – N (ug/l)	32.6 – 44.6 *
PO_4 – P (ug/l)	8.64 – 37.4 *
SiO_2 (mg/l)	7.0 – 10.5 *
Chl a (mg/m^3)	13.6 – 63.5 *
Temperature at surface (°C)	19.4 – 24.8 *

***Data from this study**

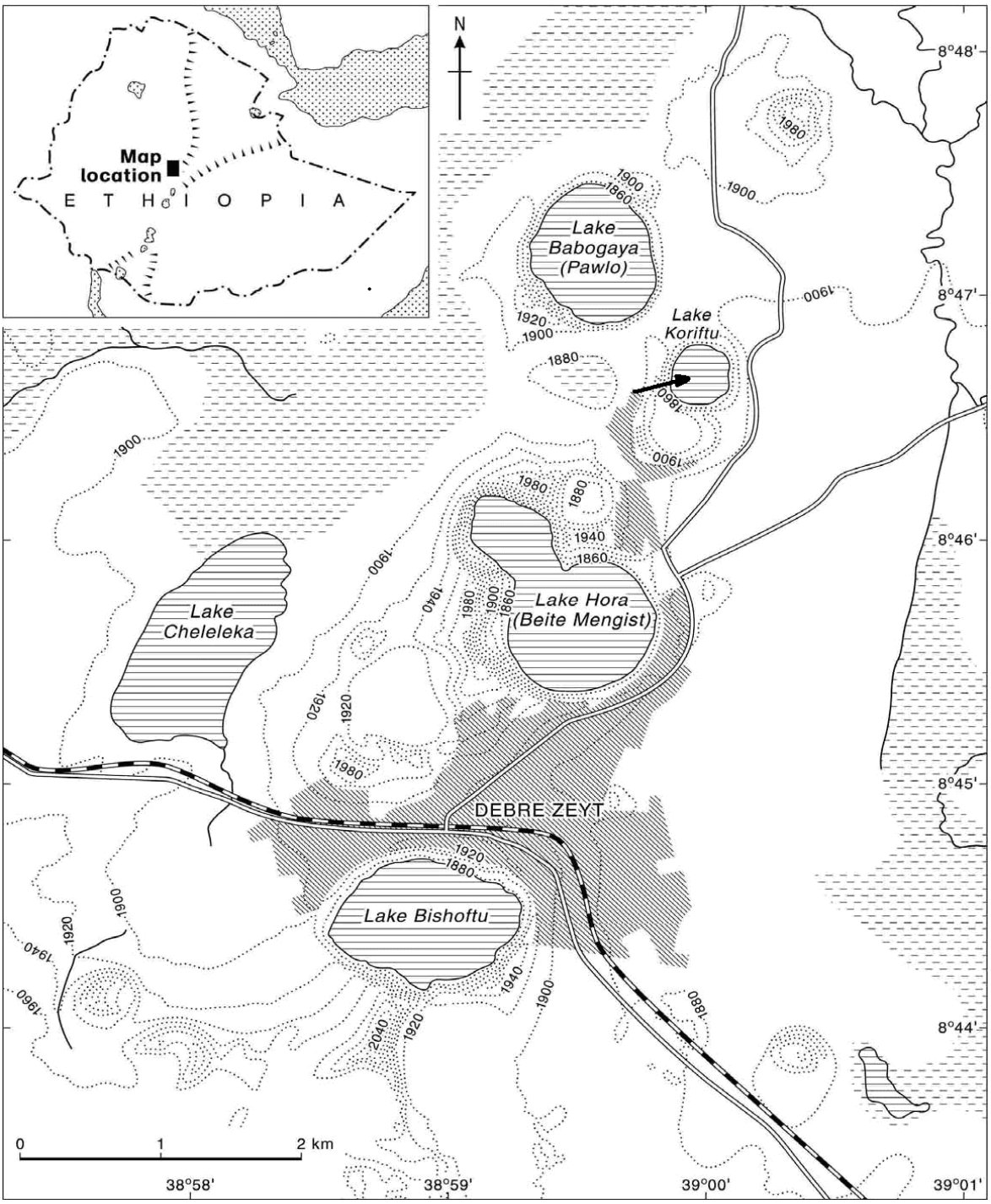

Fig. 1. Map of Bishoftu (Debre zeyt) crater lakes, including Lake Kuriftu shown with an arrow.

The chemical composition of the lake (Zinabu Gebremariam *et al*., 2002) and some physical parameters (Brook Lemma *et al*., 2001) are shown in Table1. According to Girum Tamire (2006) the phytoplankton species composition of the lake is mainly represented by colonial algae and filamentous cyanobacterial forms. The dominant species during this study were *Anabaena circinalis, Cylindrospermopsis africana, C. curvispora* and *Microcystis aeuruginosa.* Zelalem Dessalegn (2007) identified 25 species of phytoplankton during his study, which consisted of the dominant Cyanobacteria and Chlorophyceae and Bacillarophyceae (diatoms). *Oreochromis niloticus*,

Cyprinius carpio and *Barbus* species are known to occur in the lake, but very little study has been done on fish biology in Lake Kuriftu; as a result we did not consider predation factors in our analysis of the seasonal dynamics of secondary production in the lake.

Sampling protocol

Two sampling stations, one from an area of high human impact (near-shore station, ca. 8 m from the shore, depth 2 m) and the second from a relatively less impacted area (mid-lake station, ca. 500 m from the shore, depth 5 m) were selected. Quantitative zooplankton samples were collected at least once a month from the two stations with nets of mesh size 64 µm and 30 cm mouth opening which was hauled along the entire water column (from the desired depth up to the surface). No calibration was done for net efficiency because of the shallow depths sampled. As the mesh size used in this study was too wide for Rotifera and nauplii, it is possible that the biomass and production values for these groups are under-estimated. This calls for some caution in interpreting the data on biomass and production rates given here for Rotifera. Three replicates were taken at each site and all samples were preserved in 4% formaldehyde. Sampling was carried out during the day time, generally during 11 am to noon and water samples were also collected for phytoplankton composition analysis and live zooplankton for laboratory culturing at the same sites.

Measurement of physico-chemical parameters in the field

Depth-temperature and Oxygen were measured with a digital Oxygenmeter (CO-411 model) Secchi depth was estimated with a standard Secchi disc of 20 cm diameter. pH was measured *in situ* with a portable digital pH meter. Chemical analysis for Nitrate, Phosphate, and Silica was carried out each month using standard spectrophotometric procedures, such as the Cadmium reduction, Phospho-molybdate and Molybdo-silicate methods.

Laboratory culture methods

Thermocyclops consimilis was raised in the laboratory for determination of the development times of the major life history stages as described in Bottrell *et al*. (1976), Vijverberg (1989) and Mavuti (1994). Culture bottles of 60 ml were used and *T. consimilis* was fed with 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 to culture media, zooplankton were filtered through 150 µm sieve so that the largest stages (adults) were retained on the sieve and the developmental stages passed into the filtrate. The sieve was gently immersed in filtered lake water to release the adults. Then, 15 ovigerous females were pipetted out individually into small test tubes with floating styroform on top and 45 µm mesh at the bottom, immersed in another larger flask containing filtered natural lake water, and incubated in a thermostatically controlled water bath at temperature 20 and 25.9°C close to the lake mean temperature (19.40 to 24.78°C) with a 12 hours photoperiod. Culture medium was replaced every 2 days and ovigerous females were continuously observed for hatching and such females were immediately removed after releasing their eggs. Developmental times of eggs to nauplii were observed twice a day (morning and night) and every two days for nauplii to copepodites and copepodties to adults. The culture was replenished with filtered lake water and mixed algal culture and the animals were given food in excess, because 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 eggs to nauplii for at least 120 eggs, from nauplii to copepodities for 70 nauplii and from copepodites to adults for at least 30 copepodites, and averages of these times are reported here.

Phytoplankton identification and biomass

Phytoplankton samples were examined with an inverted microscope and identification to genus or species level using taxonomic literature. Aliquots of preserved composite samples were used, after sedimentation, for the estimation of the relative abundance of the major algal groups with a Sedgwick-Rafter cell under an inverted microscope (Nikon) following the procedures

outlined in Hotzel and Croome (1999). Phytoplankton biomass was estimated as chlorophyll a concentration spectrophotometrically from water samples filtered through glass fibber filters (GF/C). Chlorophyll a was extracted from the phytoplankton concentrate with aqueous acetone (90%). The filters were manually ground with a glass rod to enhance extraction of pigments and centrifuged for 13 minutes. The concentration of Chlorophyll a was calculated according to Talling and Driver (1963) using absorbance measurements made at 665 and 750 nm.

Zooplankton identification and abundance estimation

Zooplankton species were identified using references of Koste (1978), Defaye (1988) and Fernando (2002). For subsampling, samples were poured into 210 ml beaker and stirred, and subsamples (*Ca,* 30 ml) were taken with a wide-mouth pipette and animals were counted in a small Petri-dish with equal transects on the bottom, under stereoscope microscope (magnification of 6-50x). Three transects were counted and further extrapolation was used to calculate the number of individuals/stages per cubic meter of lake water.

The major zooplankton groups (Rotifera, Cladocera and Copepoda) and immature copepods (nauplii and copepodites) were counted as separate groups and the final estimation of zooplankton abundance (individual m^{-3} of lake water) was computed for each month using the formula of Edmondson and Winberg (1971).

$$V = \pi r^2 d$$

where,

V is the volume of the water filtered (m^{-3}).
r is the radius of the net (m).
d is the length of the course of the net through the water (m).

Biomass and production of T. consimilis

The body length (L) of nauplii, copepodites and adults were measured from the top of the cephalothorax to the end of the abdomen with an ocular micrometer. All nauplii stages were measured separately (N1 – N5) and averages taken to calculate wet-weight and dry weight, and the length of copepodites of five different stages were also averaged. Weight-length regression equations determined for the same species in Lake Hawassa (Seyoum Mengistou and Fernando, 1991) was applied to obtain the wet-weight (WW) and dry-weight (DW) of nauplii, copepodites and adult copepods, although it is evident that L-W relationships change with temperature, food quality and availability, and genotype (Vijverberg, 1989).

$$WW = 10.227\ L^{2.249}$$
$$DW = 2.257\ L^{2.252}$$

Secondary production (*P*) of *T. consimilis* was calculated by the growth increment method (Winberg *et al.*, 1971; Downing, 1984 cited in Rigler and Downing, 1984), which takes into account biomass increment (ΔW), development time (*T*) and number of individuals (*N*) of each instar (subscripts: nauplii = n, copepodites = c and adults–eggs = e), using the following equation:

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

The adult mean weight was taken as the final value for copepodites, whereas W_e is the mean egg weight, ΔW_n is the weight change from last nauplii to first copepodite and ΔW_c is the weight change from first copepodite to adult. Biomass measurement of different stages of nauplii (I, II, III, IV and V) and copepodities (Copepodite I up to V) were carried out separately and their averages were used for production calculation. Naupliar and copepodite production estimates are somatic, while adult production is reproductive (eggs). The production: biomass (P:B) ratio (also called the biomass turnover rate) was also computed from the appropriate ratios. The biomass turnover times (B/P, days) were also estimated for some stages of *T. consimilis*. ANOVA statistics was performed to determine if changes in abundance between stations and months were statistically significant. The data are not shown here but are included in the discussion.

Biomass and production of the rotifer (B. calyciflorus)

Biomass of *B. calyciflorus* was estimated using an indirect technique of bio-volume calculation from body size measurements and application of approximate geometric formulae as in Ruttner-

kolisko (1977) and details are shown in Table 5. The geometric formula used for *B. calyciflorus* to calculate its volume was cylinder ignoring appendices (setae). The conversion factor from wet weight to dry weight was 26% according to Pauli (1989).

Secondary production of *B. calyciflorus* was calculated with the recruitment method based on the values for the finite birth rate, organism dry weight and egg developmental times (*cf.* Rodriguez and Tundisi, 2002).

$$P = P_x * W$$

where,
P = Production
P_x = recruitment of new individuals
W = Mean individual body dry weight

$$P_x = N_f * B$$

where,
N = number of females
B = finite birth rate (eggs/female/day)

$$B = E/D_e$$

where,
E = proportion of eggs per female
D_e = egg development time

D_e was calculated using the formula of Bottrell *et al.* (1976)

$$Ln\ De = ln\ a + b.ln\ t + c.\ (ln\ t)^2$$

where
a = 2.7547;
b = -0.2484;
c = -0.2408; t is lake temperature (^{0}C)

RESULTS AND DISCUSSION

Physico- chemical features

Higher Secchi depth readings were recorded in this study (0.37–0.60 m) whereas Brook Lemma *et al.* (2001) reported low value of 0.15–0.20 m. This suggests that the turbidity of Lake Kuriftu has increased during the last two decades and the disappearance of some large cladocerans in recent surveys may probably be associated with this. The report of Brook Lemma *et al.* (2001) included large *Daphnia sp.* with high clearance rates in Lake Kuriftu.

The surface water temperatures at the midlake station of Lake Kuriftu ranged from a minimum of 19.4 in September, 2008 to a maximum of 24.78°C in May. The vertical distribution of temperature and oxygen showed small differences between surface and deep waters at 5m, with no daytime thermal stratification., Occasionally, the depth profiles of dissolved oxygen showed oxygen maximum (5.97 mg/L, 78% O_2) in the upper layer of the water column and a minimum of 0.95 mg O_2 l^{-1} or 12% O_2 at 5m depth, which is most likely related to the demand for oxygen for oxidative decomposition of organic matter by heterotrophs. Continuous recycling of nutrients from bottom sediments was observed and primary production appeared to be light, rather than nutrient-limited in the shallow lake. Soluble reactive phosphate (PO_4-P) was low (8.64–37.00 µg/l). most likely because of rapid uptake by phytoplankton, as daily mixing and re-suspension was common in the lake. Nitrate (NO_3-N), concentration was low (32.60–44.60 µg/l). Silicate values ranged from 5.60 to 10.47 mg/l and the relatively low concentration of silica may be associated with its removal from solution by diatoms, which represent an important group of the phytoplankton community in Lake Kuriftu. Overall, Lake Kuriftu had low nutrient levels, which could limit primay production in such a shallow polymictic lake, and may partly account for the low secondary production of the lake.

Biological features

Species composition and chl a biomass of phytoplankton

A total of 44 species of phytoplankton belonging to 6 classes were identified in Lake Kuriftu in this study (Table 2), more than the 25 species identified by Zelalem Dessalegn (2007) in the same lake. Green algae had the highest species diversity, whereas blue-green algae were the most abundant and diatoms were the third major algal groups in terms of species richness and abundance. Dinoflagellates, cryptomonads and euglenoids were poorly represented. *Cylindrospermopsis curvispora* and *Microcystis aeruginosa* (blue-green algae) were the most important in terms of abundance and formed the most

conspicuous populations. The persistence and dominance of cyanobacteria in Lake Kuriftu is strongly associated with the high water temperature (19.40 to 24.78°C) and high turbulence and the highest cyanobacteria abundance was recorded in December (dry period).

Phytoplankton biomass in Lake Kuriftu showed temporal and spatial variations during the study period (Fig. 2). The lowest chl a value was in August, 2008 and January, 2009 at both stations and associated with the rainy season and mid-dry season. There was an increase of phytoplankton biomass after the heavy rainy season (post-rainy) and the peak value was recorded in April at the end of the dry season. The low occurrence of phytoplankton biomass during the rainy months of July-August may be associated with heavy precipitation which results in high runoff that brings particulate materials into the lake with consequent reduction in light penetration. The occurrence of low phytoplankton biomass in lakes during periods of heavy rainfall is not unusual and has been reported even for the large Lake Victoria (Lung'Ayia *et al.,* 2000).

Table 2. List of the major species of phytoplankton identified from Lake Kuriftu during the study period

Phytoplankton group	Species name
Cyanophyceae	*Cylindrospermopsis africana* Kom. and Kaling
Cyanobacteria	*C. curvispora* M. Watanbe
(Blue-green algae)	*C. curvispora*
	Lyngbya circumcera
	Planktolyngebya tallingii Kom. and Kaling
	Planktolyngebya contorta (Lemm.) Anagn. And Kom.
	Microcystis aeruginosa Rab.
	Anabaena circinalis Rab.
	Anabaena nygaerdinom
	Psuedoanabaena sp.
Chlorophyceae	*Pediastrum simplex* Meyen
(Green algae)	*P. duplex* Meyen
	P. tetras
	Scenedesmus armatus Chod.
	S. acuminatus
	S. denticulatus
	S. dimorphus (Turp.)Kutz.
	S. quadricauda (Turp).Breb.
	S. bicudata
	Chlamydomonas reticula
	Coelestrum micropsporum
	C. acutum
	Phacotus lenticularis (Ehr.) Stein
	Monoraphidium minutum
	M. contoratum
	Pseodosphaerocystic lacustris
	P. angustus
	Tetraedron minimum
	T. muticum
	Tetrastrum netercanthium
Bacillariophyceae	*Thalassiosira sp.*
(Diatoms)	*Cymbella naviculiformis*
	C. gracilis Var Lunata
	Navicula cryptocephala Kutz.
	Nitzschia vermicularis (Kutz.)Grun.
	N. rostellate
	Synedra ulna
Dinophyceae	*Peridinium sp.*
(Dinoflagellates)	
Cryptophyceae	*Cryptomonas obovata* Skuja
(Cryptomonads)	*C. marssioni*
	C. orata
Euglenophyceae	*Phacus longicauda* (Ehr.) Duj.
(Euglenoids)	*P. tortus*
	Lepocincilis sp.

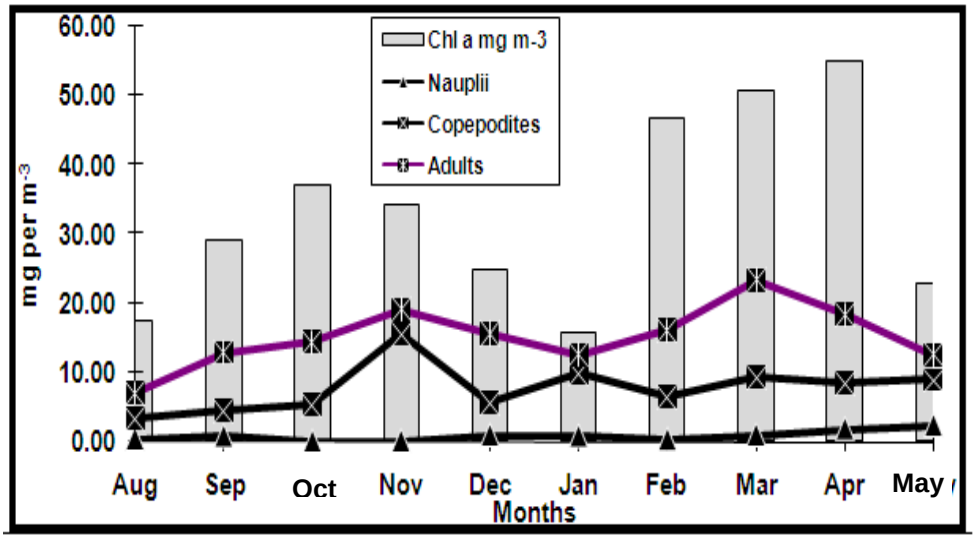

Fig. 2. Seasonal variation of biomass of nauplii, copepodites and adults of *T. consimilis* and phytoplankton biomass as chl a in Lake Kuriftu.

Composition and seasonal abundance of zooplankton groups

A total of nine species of zooplankton were identified in Lake Kuriftu. In terms of abundance, the dominant species was *Thermocyclops consimilis* (71%) followed by *Brachionus calyciforus* (12.0%) and the cladoceran *Ceriodaphnia* (11.8%). Other rotifers such as P*olyathra, Asplanchna, Filinia*, and *Keratella* species and cladocerans such as *Diaphanosoma* and *Moina* species were present in low numbers (< 1%). More than 78% of the cladoceran community was composed of *Ceriodaphnia* species while *Diaphanosoma* and *Moina* were rare. *Daphnia*, which was reported by Brook Lemma *et al.* (2001) was not found in this study. The reason for the disappearance of *Daphnia* needs more elaborate research than was done in this study. This study did not consider cladoceran production, although *Ceriodaphnia* was almost equally abundant as *B. calyciflorus* in the lake.

Total zooplankton densities were usually low during the heavy rainy months, following a decrease of nutrients resulting from the dilution of superficial water (Rodriguez and Tundisi, 2002), low algal production and increased turbidity, rather than predation factors. Rotifers dominated during the long dry season (December – March) when other zooplankters were low and water temperatures were consistently higher than 20°C. Minimum value for rotifers was recorded during the post-rainy month in August (6.9 $x10^2/m^3$) and more than 84% of the rotifer community was composed of *Brachionus* species.

Duration of development of T. consimilis

The rate of embryonic development of *T. consimilis* under laboratory conditions showed decrease with temperature (Table 3), as supported by Amarasinghe *et al*. (1997), who concluded that the duration of embryonic development in planktonic freshwater copepods is primarily a function of temperature. The Lake Kuriftu species showed relatively shorter development time than similar species studied by other workers. *T. consimilis* took an average of 16.05 days to complete a generation time at 25.6°C and a relatively longer development time at 20°C completing a generation in 21.4 days.

Table 3. Developmental time (days) of different stages of *T. consimilis* in Lake Kuriftu (Results are means of several observations at two temperatures).

Stages	20°C	25.9°C
Egg to nauplii (stage IV)	2.1	1.75
Nauplii to copepodites (stage IV)	5.5	4.20
Copepodities to adult	13.2	10.10
Egg to adult	21.4	16.05

Post-embryonic naupliar duration appeared to be relatively independent of food concentrations, as food supply largely influenced copepodite development times in freshwater copepods (Hart, 1990). However as the experiment in the study was under non-limiting food levels, postembryonic development times were highly influenced by temperature rather than by food levels.

Biomass estimates of stages of T. consimilis

The mean dry weight of egg, nauplius, copepodite, adult male and adult female were 0.0046, 0.082, 0.58, 1.18, and 1.29 µg, respectively. These data were used to calculate the biomass of all stages for *T. consimilis* during each month (Fig. 3). The sum of mean biomass of all stages was 23.79 mg DW m^{-3}. Higher mean biomass value was recorded in November and March (post and pre-rainy season), and minimum biomass values for all stages were recorded in August (rainy season). Generally, adults of *T. consimilis* had the highest biomass with maximum value in March (max. 23.27 mg DW m^{-3}) and minimum value in August (min. 7.00 mg DW m^{-3}).. Nauplii had the lowest biomass with average value of 0.83 mg DW m^{-3} and copepodites had an average biomass of 7.76 mg DW m^{-3}. In general the highest biomass of *T. consimilis* coincided with the post-rainy months of October-November and the lowest biomass was recorded during heavy rainfall month of August.

When the mean biomass of *T. consimilis* is compared with similar cyclopoids in tropical and sub-tropical lakes,, it is observed to be low in general (Table 4). The literature data on biomass of tropical and subtropical copepods show wide-ranging values, as a result of wide variation in food and temperature between the lakes (Table 4). The trophic status of the lakes appears to be partly associated with variations in cyclopoid biomass. For instance, the mean annual biomass of *T. consimilis* in Lake Kuriftu was 23.79 mg DW m^{-3}, which is lower than values recorded in productive equatorial lakes i.e., Lakes George, Chad and Naivasha, but much higher than the value recorded in meso-oligotrophic Lake Tana in Ethiopia. Lake size and food quality also play some role because biomass of *T. consimilis* in Lake Kurifu is lower when compared with a similar cyclopoid in Lake Hawassa, which is more than 100 X larger in size and dominated by chlorophyceae, while Lake Kuriftu is dominated by Cyanobacteria. Moreover, the seasonal peak in cyclopoid biomass in Lake Hawassa was during the rainy months and in Lake Kuriftu, during the post-rainy months, mainly associated with green algal food in Lake Hawassa and decomposed cyanophyte detrital food in Lake Kuriftu and Lake Tana. It was further noted that the size of *T. consimilis* in Lake Kuriftu is small compared with the same species in other lakes (*e.g.*, Lakes Tana, Hawassa, Hora) and this may reflect poor and unfavourable food conditions in Lake Kuriftu. However, further studies have to be done on qualitative assessment of detrital and live food for zooplankton production in shallow and deep lakes in order to verify/refute this suggestion.

Table 4. Comparison of production rates of Cyclopoids from some tropical African lakes. (Biomass in mg DW m^{-3}, mean daily production in mg DW m^{-3} d^{-1}; total annual production as mg DW m^{-3} yr^{-1} , daily P:B ratio (d^{-1}) and annual P:B ratio (yr^{-1})).

Species	Lake Temp (^{0}c)	B	Daily Prod.	Ann. Prod.	DailyP:B	Ann. P:B	Country and Lake	Reference
Mesocyclops aequatorialis	23/24	-	-	-	0.18	14.3	Ethiopia Hawassa	Seyoum Mengistou and Fernando (1991)
Thermocyclops consimilis	23/24	95	6.9	535.2	0.044	14.6	Ethiopia Hawassa	Seyoum Mengistou and Fernando, (1991)
Thermcyclops oblongatus	22	120	11	4022	0.09	73.5	Kenya Naivasha	Mavuti (1994)
Thermocyclops hyalinus	25	248	18.6	7154	0.08	28.8	Uganda George	Burgis (1974)
Thermocyclops neglectus	26	56.4	9.6	3580	0.17	63.5	Chad Chad	Leveque and Saint Jean (1983)
Mesocyclops aequatorialis	-	-	3.2–7.0*	-	-	-	Malawi Malawi	Irvine &andWaya (1999)
M. aequatorialis	21/22	6.18	0.43	157	0.07	25.4	Ethiopia Tana	Ayalew Wondie and Seyoum Mengistou (2006)
Thermocyclops ethiopiensis	21/22	7.33	0.42	156	0.06	21.3	Ethiopia Tana	Ayalew Wondie and Seyoum Mengistou (2006)
Thermocyclops consimilis	22.45	23.8	0.78	311.27	0.033	13.10	Ethiopia Kuriftu	Present study

Secondary production rates and P:B ratio of T. consimilis

Figure 3 shows the seasonal variations in the % contribution of the life stages of *T. consimilis* to total secondary production. The highest contribution was by copepodites (71%). Similar result of high contribution by copepodites was documented in Lakes Hawassa (Ethiopia) and George (Uganda) whereas more than 50% of the total zooplankton production was by nauplii in Lakes Naivasha (Kenya) and Tana (Ethiopia). It is hard to generalize about the causes of such differences, but food quality seems to be an important factor. On account of small size, nauplii require picoplanctonic food whereas particulate carbon (live and detrital algae) may be preferred by the larger copepodites.

The contribution of adult (eggs) to total production was very low in all African lakes, and in all months in Lake Kuriftu. However, this species did not show period with zero egg production, and reproduction was continuous. Maximum egg production was recorded in January (max. 0.135 mg m^{-3} day^{-1}) and was associated with food as temperature was lowest (20.3°C) during this month. Minimum egg production of *T. consimilis* was recorded during the rainy season (August,) and in the dry season (February), both due to food and temperature constraints (Fig. 3). In general, in Lake Kuriftu, daily secondary production was low for all stages during the major rainy season (July - August) due to high turbidity, low food quality and low water temperature.

Areal daily production rates (mg DW m^{-2} d^{-1}) of cyclopoids from different tropical African lakes are given in Table 4. The lowest daily secondary production is for Lake Kuriftu (2.34 mg DW$m^{-2}d^{-1}$) and the highest for hypereutrophic equatorial Lake George (44 mg DW.m^{-2}.d^{-1}). Annual mean production (calculated as geometric mean for the 10 months) rate for all stages in Lake Kuriftu was 311.27 mg DW m^{-3} yr^{-1} (ranging from 118.12 to 434.92 mg DW m^{-3} yr^{-1}). *T. consimilis* in Lake Kuriftu had higher annual production than T. *ethiopiensis* and *Mesocyclops aequatorialis* in Lake Tana, despite better food quality of detritus in Lake Tana (Ayalew Wondie and Seyoum Mengistou, 2006). However, *T. consimilis* in Lake Hawassa was 1.7-fold more productive than in Lake Kuriftu, probably because of high secondary production rates during the rainy months which were associated with high algal production.

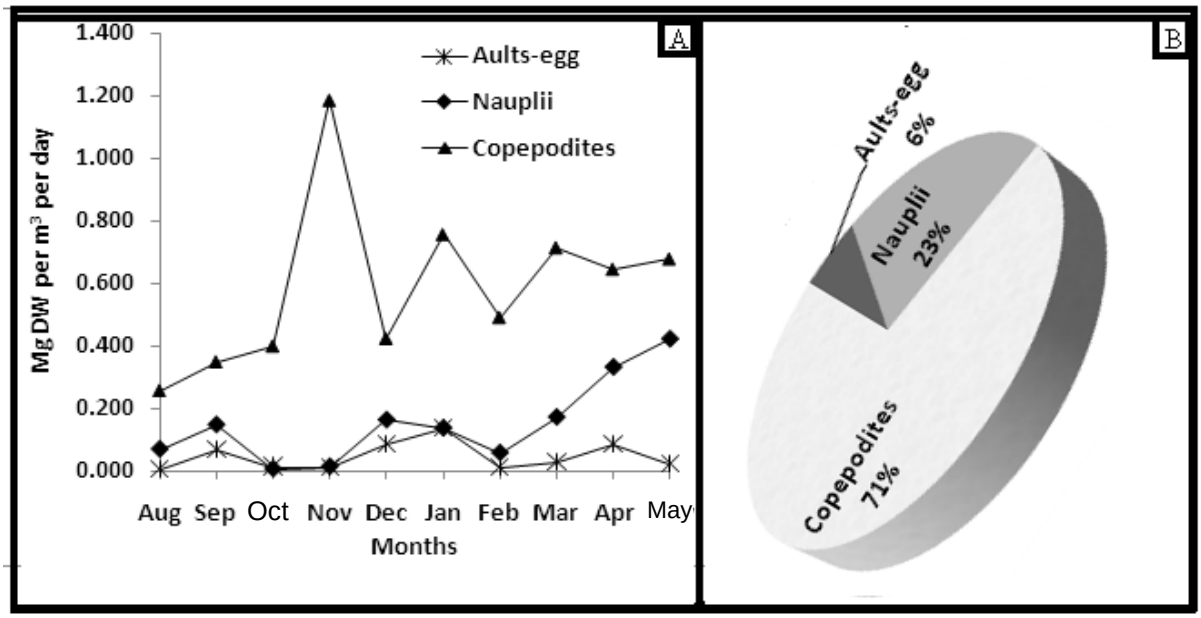

Fig. 3. Seasonal variation in production rates (mg DW m^{-3}) (A) and percentage contribution (B) of nauplii, copepodites and adults-eggs of *T. consimilis* in Lake Kuriftu.

The mean daily P:B ratio for *T. consimilis* in Lake Kuriftu was 0.033. Eggs had the highest daily P:B ratio and copepodites the lowest which was also seasonally stable for this species. The turnover time (days) of biomass (B:P) was 5.5 for naulpii, 13.2 for copepodites and 2.2 for eggs, giving a generation time of 20.9 days, which is in close agreement with the life span of 21.4 days obtained from the culture experiments (Table 3). The annual P:B ratio for this species during the study period was 13.10, which was comparable to results obtained for cyclopids from other Ethiopian lakes (Table 4) but much lower when compared to similar cyclopoids from other tropical African lakes. Overall, the low annual biomass turnover rate in Lake Kuriftu (13.1 yr^{-1}) is a reflection of the poor food quality and low secondary productivity in this shallow polymictic lake. Further, it was noted in this study that nutrients and chl a levels were quite low in Lake Kuriftu and coupled with the increased turbity in the lake, result in low primary production. This is particularly observed during the rainy months where both primary and secondary productions were low. During the dry season, rotifer production attains high values because of high chl a biomass and temperature.

Cyclopoid production increases during the post-rainy months (October - November) because of high chl a levels (next to dry season) which was supplemented with decomposed detrital food as a result of the small rain (40 mm) recorded in November, 2008. Apparently, the low quality of this type of food limited secondary production when compared to the large shallow Lake Tana, where cyclopoid production was highest during the same post-rainy season and was supported by decomposed detrital (cyanophyte) particles enhanced by sediment resuspension and mixing by wind (*cf*. Nanzanto and Yasuno, 1985, Ayalew Wondie and Seyoum Mengistou, 2006).

It appears that there is some difference in the quality of detrital food sources between the two shallow lakes of different sizes. It is generally accepted that phytoplankton dominated by colonial and filamentous cyanobacteria are inedible and less nutritious (de Bernardi and Guissani, 1990); however, it has also been shown that when decomposed, cell exudates and bacterial growth on such food can provide adequate nutrition for zooplankton growth. For example, Uye *et al*., (2000) reported that even in winter in the Ise Bay of Central, Japan, 64% of the primary production was transformed to detrital

or dissolved forms via cell exudation and degradation and provided high nutrition for zooplankton. Wetzel (2001) maintains that detritus, although of poor nutritional quality and low assimilation rate, when combined with bacteria, can form the major energy source for much of the year for macrozooplankton. In some cases, detrital assimilation by large cladocerans has been documented to be > 50%, although the assimilation efficiency on detritus is quite low (10%) when compared with that of algae or bacteria (50–79%) (Wetzel, 2001). Nanazato and Yasuno (1985) have shown that decomposed *Microcystis* and bacteria may be the main food for small cladocerans in summer in Lake Kasumigaura, Japan, and they attributed the high decomposition to the high lake temperature in summer.

Rotifer biomass and production rates

Rotifer embryonic developmental time

Embryonic development time (De) of *B. calyciflorus* varied between 0.55 and 0.84 days with mean value of 0.66 days. De were highly correlated with lake temperature (see Table 6), as in other studies. Okano (1994) obtained De values for *Branchionus falcatus, Filinia longiseta* and *Keratella cochlearis* at 0.83 days, when mean water temperature was 20.4°C. The embryonic development time for *F. pejleri* and *Keratella americana* with mean lake temperature of 20.9°C was 19 hours (Rodriguez and Tundisi, 2002).

Individual and population biomass of B. calyciflorus

B. calyciflorus had a mean dry weight of 0.11µg ind^{-1} in Lake Kuriftu (Table 5). This is slightly higher that data reported for similar tropical rotifers. For example, Rodriguez and Tundisi (2002) obtained the dry mass of *Filinia pejlerii* and *Keratella americana* at 0.02 µg DW ind^{-1}. Tundisi *et al*. (2006) calculated the dry mass of the same species as 0.23 µg DW ind^{-1} and for *Brachionus mirus tpicus* and *B. havanaensis havanaensis*, it was 0.01 and 0.02 µg DW ind^{-1}, respectively.

Table 5. Geometric formulae used for calculation of the body volume, dimensions measured (in µm), calculated biovolume (in µm^3), conversion factor for transforming wet weight to dry weight, and dry weight biomass (in µg DW m^{-3} ind^{-1}) for *B. calyciflorus* in Lake Kuriftu.

Species	Geometric formulae used	Measurements for formulae	Dimensions	Biovolume	Factor	Biomass
Brachionus calyciflorus	Cylinder $=\prod r^2h$	a=h b = 2r	a=155 b = 60	438030	26%	0.11

Body

a = length
b = width

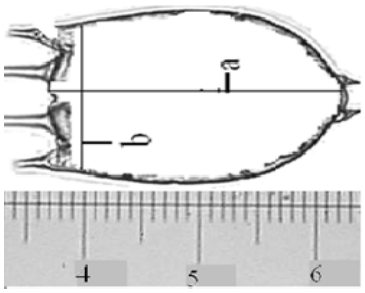

Table 6. Monthly data for *B. calyciflorus* in Lake Kuriftu during the study period - lake temperature (T), number of females (N_f), number of eggs (m^{-3}), total biomass (µg DW m^{-3}), egg developmental time (De, days), finite birth rate (B; eggs/female/day), recruitment of new individuals (P_N) ($m^{-3}d^{-1}$) and daily production (µg DW m^{-3} d^{-1}).

Months	T(°C)	(N_f) in m^{-3}	Eggs in m^{-3}	Biomass	De	B	P_N	P
August	22.30	335.40	123.85	36.89	0.66	0.56	187.46	20.62
September	19.40	1271.55	0.00	139.87	0.84	0.00	0.00	0.00
October	24.50	1012.55	842.18	111.38	0.56	1.49	1512.29	166.35
November	24.50	1644.70	0.00	180.92	0.56	0.00	0.00	0.00
December	20.80	13937.85	4384.29	1533.16	0.75	0.42	5864.17	645.06
January	20.30	12918.45	2724.70	1421.03	0.78	0.27	3492.28	384.15
February	22.00	6543.90	148.62	719.83	0.68	0.03	219.56	24.15
March	22.10	4339.35	1585.28	477.33	0.67	0.54	2361.06	259.72
April	23.80	11522.65	767.87	1267.49	0.59	0.11	1307.52	143.83
May	24.78	3715.50	792.64	408.71	0.55	0.39	1453.45	159.88
Mean	22.45	5724.19	1136.94	629.66	0.66	0.38	1639.78	180.38

Differences between monthly biomass values of *B. calyciflorus* (Table 6) were significant (ANOVA, $P < 0.05$). The average dry biomass of *B. calyciflorus* in this study was 629.66 µg DW m^{-3} with a maximum value of 1533.16µg DW m^{-3} in December (Dry) and minimum value 36.89 µg DW m^{-3} in August (Rainy). The biomass of *B. calyciflorus* in Lake Kuriftu was comparable with the biomass of the same species (75.66 µg DW m^{-3}) but higher than *Brachionus mirus typicus* (57.55 µg DW m^{-3}) and *B. havanaensis havanaensis* (65.55 µg DW m^{-3}) in Lake São Paulo, Brazil (Tundisi *et al.*, 2006). In April, when chl a was highest (49.1 mg/m3), the biomass of *B. calyciflorus* was low, suggesting that the species composition of algal food, rather than its biomass, was the major cause of high rotifer production rates during the dry months (December – March).

Production rates and P:B ratio of B. calyciflorus

The mean daily production of *B. calyciflorus* during this study period was 180.38 µg DW $m^{-3}d^{-1}$ with a maximum value of 645.06 µg DW$m^{-3}d^{-1}$ in December (dry) and a minimum value of 0.00µg DW$m^{-3}d^{-1}$ during the rainy and post-rainy months of September and November (Table 6). Persistent high secondary production rates were recorded from December to March (dry months) for *B. calyciforus* in Lake Kuriftu.

When compared to other rotifers, mean daily production of *B. calyciflorus* was lower than daily production of *Filinia pejleri* (48.37 mg DW m^{-3} d^{-1}) and *Keratella americana* (91.09 mg DW m^{-3} d^{-1}) in a Brazilian reservoir (Rodriguez and Tundisi, 2002), even with all limitations of sampling and culture observation noted earlier. In small eutrophic lakes, rotifer production could be expected to be high because of the high food threshold level of rotifers (Wetzel, 2001); however, in Lake Kuriftu, rotifer production appears to be constrained by the low nutrient and algal biomass for most of the year. Nevertheless, during the dry months, rotifer production attained high values.

B. *calyciflorus* had a mean daily P:B ratio of 0.29 and an annual P:B ratio of 104.6 (Table 6). Almost a third of its biomass was replaced daily on the average. Thus, although *B. calyciflorus* contributed less biomass because of its small size when compared to cyclopoids; it contributed high annual biomass turnover rate of 104.6 providing food source in the food web of the lake. It is evident that secondary production and biomass turnover rates were well segregated temporally in Lake Kuriftu. Rotifers had the highest production and biomass turnover rates during the dry season (December and January) whereas *T. consimilis* had the highest production during post-rainy and pre-rainy months. Therefore these two zooplankton taxa can provide food to planktivores at different times of the year.

CONCLUSION

The level of secondary production by the dominant cyclopoid and rotifer species in the shallow polymictic Lake Kuriftu was found to be low when compared with values reported from other tropical lakes and similar zooplankton species. The low rotifer production values reported here is partly because of underestimation of its abundance as a result of the wide mesh (64 μm) of the net used, and the long monthly sampling and culture observation intervals used. Rotifer production rates were highest during the dry months (December – March), associated with high temperature and chl a biomass. The highest chl a was recorded in April (end of dry season and beginning of small rains) which suggests that the composition rather than the biomass of phytoplankton during the dry season is critical for rotifer secondary production. Highest production rates for the cyclopoid *T. consimilis* were recorded during the post-rainy months (October-November) when chl a biomass was also high. There was unusual rain (40 mm) in November 2008 after a dry spell in October 2008 (~ 5 mm). Therefore, it is suggested that decomposed detrital particles could be a supplementary source of nutrition for cyclopoid production in November after a one month time lag from the highest peak of algal biomass in October. The low quality of this detrital food in this small lake partly accounts for the low secondary production of *T. consimilis*. Secondary production in general was lowest during the rainy months of July-September when algal biomass was also the lowest in this shallow polymictic lake. The high biomass turnover rate of the rotifer (104.6 yr^{-1}) and high seasonal cyclopoid production were temporally segregated and provide food for planktivores at different times during the year. Overall, this study determined that the low secondary production rates in this shallow lake were mainly due to low nutrients and algal biomass, low temperature and low quality of decomposed detrital particles. This finding is also supported by the observed low fish production of Lake Kuriftu.

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