The abundance, biomass and composition of pelagic ciliates in East African lakes of different salinity and trophy

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Abstract

Planktonic ciliates were studied in 17 tropical East African lakes of different salinity and trophic status. Oligotrichs (e.g., *Strombidium*, *Strobilidium* and *Halteria*) and scuticociliates (e.g., *Cyclidium*, *Pleuronema*, *Cristigera*), dominated the ciliate communities. Conductivity and trophic status were the most important environmental variables influencing the distribution of ciliate species in East African lakes. Herbivorous oligotrichs were important in oligotrophic and mesotrophic lakes, as they are in temperate and subtropical lakes, but their importance decreased with increasing chlorophyll *a* concentration and conductivity. On the other hand, the importance of scuticociliates (primarily bacterivores) increased with increasing chlorophyll *a* and conductivity.

Mean ciliate abundance ranged from 2 to 1,220 ciliates·mL^{-1} while the biomass range was from 1.9 to 1, 900 µg C·L^{-1} respectively from oligotrophic to eutrophic lakes. Abundance and biomass had positive relationships with phytoplankton biomass. The ciliate abundance and biomass were higher than those reported in temperate (Quebec) and subtropical (Florida) lakes of similar trophic status. However, regression models predicting abundance and biomass of ciliates from chlorophyll suggest that temperate (Quebec), subtropical (Florida) and tropical (East Africa) lakes have similar ciliate abundance and biomass per unit chlorophyll except some saline tropical lakes which have very high abundance and biomass of ciliates relative to chlorophyll.

Key words: Ciliated protozoa, high abundance and biomass, tropical lakes.

Introduction

Ciliates comprise a significant component of the abundance and biomass of freshwater plankton communities. Their densities may be between 1-30 ciliates/ml in oligotrophic and mesotrophic lakes but may be exceed 1000/ml in eutrophic lakes (Yasindi et al. 2002). Ciliates feed on bacteria, pico- and nanophytoplankton but they are prey for zooplankton and fish larvae (Porter et al. 1979). As such, ciliates form a link in the process of energy flow from the smallest plankton groups to the higher trophic levels. Some studies have found a significant relationship between the abundance and biomass of planktonic ciliates and lake trophic state as measured by chlorophyll *a* concentration (Beaver and Crisman, 1982). Ciliate species diversity and richness are also influenced by lake productivity whereby the most productive lakes have the highest diversity and richness. The type of food items also influences the distribution of ciliate species. Large oligotrichs (>30 µm), which graze on nanophytoplankton, dominate oligotrophic lakes while small ciliates (<30 µm) that graze on bacteria dominate eutrophic lakes in temperate and subtropical lakes (Beaver and Crisman, 1982). However, most studies of planktonic ciliates have mainly been confined to the temperate lakes with relatively few studies in subtropical and tropical waters. Previous studies of ciliates in tropical freshwater lakes have been confined to single lakes (Finlay *et al*. 1987; Taylor & Zinabu 1989; Yasindi 1995). Therefore, our knowledge of planktonic ciliates of tropical freshwaters in general and East African lakes in particular is still very poor. The goal of this study was to investigate the abundance, biomass, composition and the ecological role of ciliates in the food webs of tropical East African lakes of different salinity and trophic status and compare with previous studies intemperate lakes.

Materials and methods

Ciliate samples were taken from 17 lakes including Lakes Awassa, Abijata, Chamo, Langano and Zwai in Ethiopia and Lakes Baringo, Bogoria, Solai, Nakuru, Elmenteita, Naivasha, Oloidien, Sonachi, Simbi, Victoria, Malawi and Crescent lake in Kenya. 250-mL ciliate samples were collected in triplicate using a 4-L Van Dorn sampler at different depths, and immediately fixed in concentrated Bouin's fluid (5% v/v final concentration). In the laboratory, the water samples were concentrated to 50 ml by settling for 48 h. Subsamples of 0.5 to 5 mL (from eutrophic to oligotrophic lakes) were filtered onto gridded filters and stained by Quantitative Protargol Staining (QPS) technique of Montagnes & Lynn (1993). Ciliates were identified to genus or species level and enumerated. To determine ciliate biomass, ciliate dimensions were measured on a Summasketch III digitizing tablet and using microbiota software, which equates ciliates to standard geometric shapes such as cones, sphere and prolate spheroids (Roff & Hopcroft, 1986). The biovolume was then converted to biomass using a volume to carbon ratio of 0.14 pg C· µm^{-3} (Putt & Stoecker, 1989). Ciliates were counted either by scanning the whole stained filter when ciliate density was low or by counting ciliates in three randomly selected squares until 100 to 200 ciliates were counted. Species diversity was calculated based on Shannon diversity index using the MVSP (Kovac 1999). Ciliate size was expressed as equivalent spherical diameter (ESD) using the formula: ESD = 0.4775 Vol $^{1/3}$. Chlorophyll *a* concentration was measured and used as an indicator of trophic status. Bacteria were counted using the acridine-orange direct-count method of Hobbie *et al*. (1977). Physico-chemical factors such astemperature, pH, DO, alkalinity, conductivity and transparency were also measured.

We used the classification of lakes based on their ranges of conductivity by Talling & Talling (1965) to assign the lakes with conductivity < 600 µS·cm^{-1} to freshwater lakes, lakes with conductivity between 600 - 6000 µS·cm^{-1} as moderately saline lakes and saline lakes as lakes with conductivity > 6,000 µS·cm^{-1}.

Bivariate regression and multiple regression (Statsoft, Inc. 1995) were used to assess relationships between ciliate abundance and biomass with environmental factors.

According to chlorophyll range group 1 (or oligotrophic) comprised Malawi (< 5 mg.m^{-3}), group 2 (mesotrophic) had Naivasha, Oloidien, Victoria, Solai, Nakuru, Elmenteita, Sonachi, Simbi, and Bogoria (5-50 mg·m^{-3}), and Baringo, Abijata, Chamo, Awassa, Zwai, and Langano (> 50 mg·m^{-3}) formed Group 3 (eutrophic). We used the classification of lakes based on conductivityby Talling and Talling (1965) to assign the lakes with conductivity range of 207 - 350 µS·cm^{-1} to freshwater lakes (< 600 µS·cm^{-1}), lakes with 850 - 5,457 µS·cm^{-1} as moderately saline lakes (600 – 6,000 µS·cm^{-1}) and lakes between 11,824.5 –16,837 µS·cm^{-1} as saline (> 6,000 µS·cm^{-1}) lakes.

Table 1. Abundance, biomass and environmental variables measured. Abun = Abundance, Biom = biomass, Cond = conductivity, Temp = temperature, DO = dissolved oxygen, Alk = alkalinity, Chl *a* = Chlorophyll *a* and Bact = bacteria.

Lake	Abun	Biom	Cond	pH	Temp	DO	Alk	Chl *a*	Bact	Secchi	n
Baringo	5.6 ± 0.7	22 ± 19.6	912.0	8.2	25.2	9.3	233.3	43 ± 12	9.1	0.61	18
Bogoria	43.5 ± 8.2	220 ± 150	69792.0	9.4	26.9	12.9	14316.7	266 ± 8.9	66.7	0.13	6
Solai	21.7 ± 19	25 ± 22	5457.0	8.6	26.0	6.4	885.7	209 ± 11	42.9	0.07	6
Nakuru	32.4± 40.7	31± 68	16837.0	9.4	24.7	17.8	70.4	123 ±0.5	255.9	0.12	3
Elmenteita	640.3 ± 578	971 ± 763	15807.9	9.7	20.9	8.5	1973.6	123 ± 9.2	245.0	0.15	33
Sonachi	377.9 ± 70	1900 ± 1344	11824.5	9.5	21.3	8.8	1855.4	89 ± 6.9	40.5	0.16	63
Crescent	3.6 ±2.6	17 ± 11	294.4.0	7.7	20.0	3.9	24.6	32 ± 15	9.5	1.22	15
Naivasha	3.4 ± 0.4	17 ± 7	319.4	7.8	19.9	6.4	49.9	26 ± 1.9	8.2	1.07	75
Oloidien	6.9 ± 1.2	30 ± 12.6	2466.7	9.3	21.4	-	312.0	23.0	97.2	0.25	15
Simbi	2.9 ± 1.2	12 ± 8.5	21241.0	9.3	25.5	4.9	1860.1	82 ± 3	35.7	0.93	15
Victoria	12 ± 4.3	43 ± 13.2	207.0	6.4	26.2	6.7	-	31 ± 2.3	8.3	0.92	45
Malawi	2.2 ± 0.7	2.3 ± 0.7	256.1	-	24.9	7.3	-	1.5	2.9	20.00	66
Zwai	8.8 ± 0..2	42 ± 9	350 ± 5.8	8.5 ± 0.2	18 ± 0.1	-	4 ± 0.4	27.3	11.3	0.30	6
Langano	3.1 ± 0.9	22.7 ± 11	1580 ± 200	9.5 ± 0.1	24 ± 0.6	-	14 ± 0.4	13.4	7.0	0.23	12
Chamo	5.3 ± 44.7	11 ± 2.2	1320	8.9	-	-	12	44.2	16.7	0.65	3
Abijata	15.2 ± 13.8	60 ± 10.5	21500 ± 866	10 ± 0.1	24 ± 0.5	-	250 ± 32	11.6	43.8	0.65	3
Awassa	8.1 ± 1.9	8.9 ± 2.2	850 ± 288	8.3 ± 0.2	21 ± 0.4	-	9 ± 1.4	11.8	9.5	1.38	15

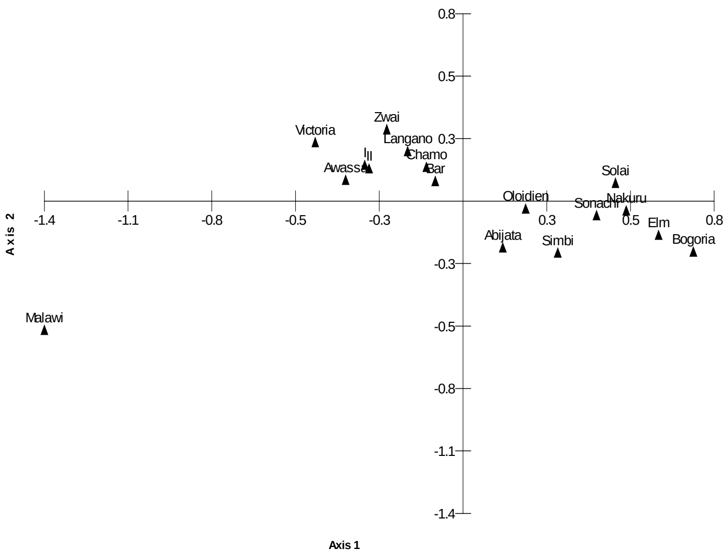

Figure 1. Principal components analysis diagram based on 6 environmental variables showing the distribution of the East African lakes on the first two principal components. The first axis is horizontal and the second is vertical. Bar = Baringo, Elm = Elmenteita, I = Crescent, II = Naivasha.

Table 2. The correlation matrix for ciliate biomass and environmental variables. Log_{10}-transformed means of all data for two years combined were used. Abbreviations as in Table 1. * = r is significant at 0.05 level of significance.

1	**2 Biomass**	Temp	pH	Cond	Alk	DO	Bact	Chl *a*	Secchi
Biomass	1.00	0.18	0.53*	0.59*	0.39	0.62*	0.74*	0.65*	-0.68*
Temp	0.18	1.00	-0.13	0.24	0.41	0.43	0.11	0.07	-0.07
PH	0.53*	-0.13	1.00	0.61*	0.56*	-0.06	0.62*	0.63*	-0.79*
Cond	0.59*	0.24	0.61*	1.00	0.79*	0.40	0.81*	0.64*	-0.59*
Alk	0.39	0.41	0.56*	0.79*	1.00	0.33	0.69*	0.63*	-0.59*
Do	0.62*	0.43	-0.06	0.40	0.33	1.00	0.43	0.56*	-0.26
Bact	0.74*	0.11	0.62*	0.81*	0.69*	0.43	1.00	0.75*	-0.71*
Chl *a*	0.65*	0.07	0.63*	0.64*	0.63*	0.56*	0.75*	1.00	-0.82*
Secchi	-0.68*	-0.07	-0.79*	-0.59*	-0.59*	-0.26	-0.71*	-0.82*	1.00

Results

Principal Component Analysis (PCA) of environmental variables divided the lakes into oligotrophic, mesotrophic and eutrophic lakes (Figure 1). 49 ciliate genera were identified from the 17 lakes. Small ciliates (< 30 µm ESD), mainly *Strobilidium*, *Strombidium*, and *Halteria* (Oligotrichida), and *Cyclidiun*, *Cristigera*, and *Pleuronema* (Scuticociliatida) dominated abundance. Other abundant ciliates belonged to Cyrtophorida, Peniculida, Heterotrichida, Prostomatida, Hypotrichida, and Haptorida. Shannon-Weaver species diversity had a negative and significant relationship with chlorophyll *a* concentration ($r = -0.53$, $P < 0.05$). The ciliate abundance and biomass, as well as the environmental variables measured are summarized in table 1 while table 2 shows the correlations of environmental variables with ciliate biomass and with each other. Mean ciliate abundance ranged from 1.8 ciliates$\cdot$mL^{-1} in Lake Malawi to 1,220 ciliates$\cdot$mL^{-1} in Lake Elmenteita during the two years of study. Mean ciliate biomass ranged from 1.9 µg C$\cdot$L^{-1} in Lake Malawi to 1,900 µg C$\cdot$L^{-1} in Lake Sonachi. Ciliate abundance and biomass were positively related to chlorophyll *a* concentration (Figure 2) and to conductivity (Figure 3). Ciliates in Oligotrichida and Scuticociliatida were the most abundant in East African lakes. However, the relative importance of Oligotrichida was greatest in Lake Malawi (< 5 mg.m^{-3} chl.), where they contributed 93.1% of total ciliate abundance and decreased with increasing chlorophyll, contributing 5.2% in lakes with > 50 mg.m^{-3} chlorophyll. The importance of scuticociliates increased with increasing chlorophyll accounting for 0.7% in Lake Malawi and 80.2% in lakes with > 50 mg.m^{-3} chlorophyll (Table 3). The dominance of Oligotrichida and Scuticociliatida along the conductivity gradient was similar to the trend observed along the chlorophyll gradient. The mean size of ciliates ranged from 10.3 ±0.2 µm to 193 ±35 µm (ESD) among lakes. Ciliate biovolume ranged from 10^2 to 10^6 µm^3.

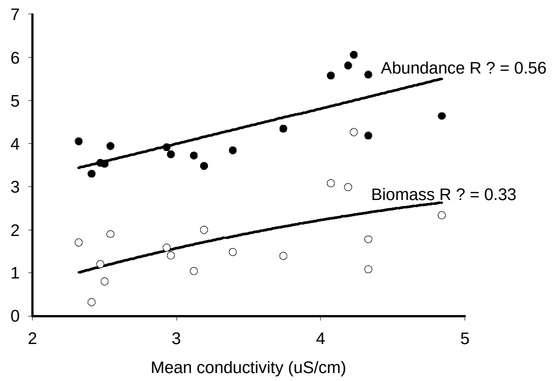

Figure 2. The relationship between mean $\log_{10}$ ciliate abundance and biomass with mean $\log_{10}$ chlorophyll *a* concentration in East African lakes. Both abundance and conductivity were $\log_{10}$-transformed.

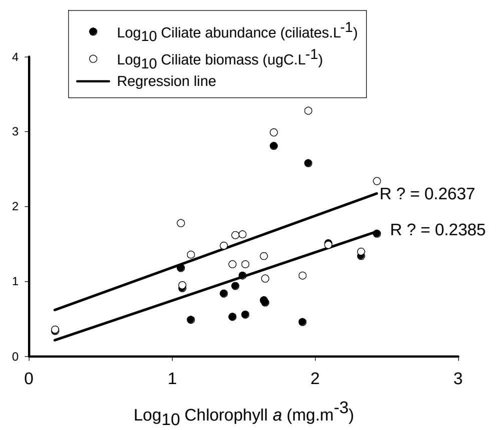

Figure 3. The relationship between mean ciliate abundance and biomas with mean conductivity in East African lakes. Both abundance and conductivity were $\log_{10}$-transformed.

Discussion

The dominant abundance of Scuticociliates and Oligotrichs in tropical (East Africa) lakes contrasts to sub-tropical (Florida) lakes where Oligotrichida, Scuticociliatida and Haptorida co-dominated (Beaver & Crisman 1982). Scuticociliates, especially *Cyclidium,* were the most abundant ciliates in most lakes and increased with increasing trophy as in subtropical and temperate lakes (Beaver & Crisman 1982). The weak negative relationship between ciliate diversity and trophy in East African lakes contradicts the positive relationship in subtropical lakes (Beaver & Crisman 1989b), and may be due to high salinity and probably the large blue-green algae that dominate saline, eutrophic tropical lakes and low diversity of edible algae. Beaver & Crisman (1989) attributed low species diversity of ciliates in oligotrophic lakes to reduced phytoplankton abundance and diversity.

Table 3. The contribution to total ciliate abundance of ciliate orders in East African lakes of different chlorophyll *a* concentration.

Ciliate orders	Chlorophyll *a* concentration (mg·m^{-3})		
	< 5	5 - 50	> 50
Armophorida	0.00	0.03	0.07
Cyrtophorida	0.00	0.88	3.36
Haptorida	0.50	3.30	0.99
Hetereotrichida	0.67	3.24	1.30
Hypotrichida	0.00	0.73	1.42
Oligotrichida	93.14	42.61	5.24
Peniculida	0.00	1.96	2.93
Peritrichida	0.00	14.52	1.15
Pleurostomatida	0.00	0.13	1.46
Prostomatida	0.50	3.18	1.77
Scuticociliatida	0.67	14.58	80.15
Stichotricha	0.00	1.14	0.01
Suctoria	0.00	0.19	0.12
Tintinnida	0.00	7.07	0.00
Others	4.52	6.46	0.04

High salinity reduces the number of species that can live in lakes (Williams *et al*. 1990). The ciliate biovolume ranged from 10^2 to 10^6 µm^3 but majority of ciliates were from 10^3 to 10^4 µm^3, similar to most ciliates in temperate lakes (Müller 1989). The ciliate abundance range of 2 to 1,220 ciliates·mL^{-1} in East African lakes is larger than reported for temperate of 3.3 cells·mL^{-1} to 21.6 cells·mL^{-1} (Pace 1986) and subtropical lakes of 10.8 to 155.5 ciliates·mL^{-1} (Beaver & Crisman 1982). Similarly, the biomass range of 1.9 to 1,900 µg C·L^{-1} is also higher than observed in both temperate and subtropical lakes of 12.3 to 56.3 µg C·L^{-1} (Pace 1986) and 9.3 µg C·L^{-1} to 126 µg C·L^{-1} (Beaver & Crisman 1982), respectively. Both ciliate abundance and biomass increase with increasing trophy in lakes of the three zones and from temperate to tropical lakes. Although not all oligotrophic lakes in East Africa have higher abundance and biomass than lakes in the temperate and subtropical zones, tropical lakes generally have higher ciliate abundance and biomass, a phenomenon attributed to higher chlorophyll concentration in tropical lakes. When regression models predicting abundance and biomass of ciliates from chlorophyll were compared for our East African lakes and temperate lakes, the slopes were not significantly different (ANOVA interaction, P > 0.05). These results suggest that temperate, subtropical and tropical lakes have similar ciliate abundance and biomass per unit chlorophyll. However, some tropical lakes have very high abundance and biomass of ciliates relative to chlorophyll probably due to high salinity. Eutrophic, saline lakes such as Elmenteita, Sonachi and Bogoria supported a higher abundance of ciliates probably due to high phytoplankton biomass and bacterial abundance (> 10^7 bacteria·ml^{-1}) (e.g., Finlay *et al*. 1987). Since chlorophyll is significantly higher in East Africa lakes than in subtropical and temperate lakes (ANOVA, $P < 0.05$), it appears that ciliate cell sizes become smaller with increase in chlorophyll, probably as a response to increasing availability of bacterial food which also increases with chlorophyll. Thus, the majority of ciliates in East African lakes are mainly bacterivorous and herbivorous. These two trophic groups account for 75% of ciliate population production (Yasindi, 2001). According to Yasindi (2001) most of this ciliate production in East African lakes is consumed by zooplankton, which are, in turn, consumed by fish (Beadle, 1981; Mwebaza-Ndawula, 1994).

It is clear from this study that both ciliate abundance and biomass increase with increasing trophy in lakes of the three zones and from temperate to tropical lakes. Also East African lakes have higher ciliate abundance and biomass than subtropical and temperate lakes mainly due to higher chlorophyll but the high abundance of bacteria is also important. Like in temperate and subtropical lakes, herbivorous ciliates dominate oligotrophic lakes while small bacterivorous ciliates dominate eutrophic lakes.

Therefore, ciliates form an important linkage through which production from the microbial loop may be transferred to the classic food chains in East African lakes as in temperate waters**.**

Acknowledgements

This research was supported by a Rockefeller African Dissertation Internship Award (ADIA) RF 96022 # 785, and a Commonwealth Scholarship (to A.W.Y.) and the National Science and Engineering Research Council Grant (to W.D.T.).

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