Limnologica 41 (2011) 30–36

Contents lists available at ScienceDirect

Limnologica

journal homepage: www.elsevier.de/limno

On the diet of Nile tilapia in two eutrophic tropical lakes containing toxin producing cyanobacteria

Ronald Semyalo [a,b,*], Thomas Rohrlack [c], Duncan Kayiira [d], Yusuf S. Kizito [b,1], Stephen Byarujali [d], George Nyakairu [e], Petter Larsson [a]

[a] Department of Biology, University of Bergen, Post Box 7803 N-5020 Bergen, Norway
[b] Department of Zoology, 7062 Makerere University, Kampala, Uganda
[c] Norwegian Institute of Water Research, Gaustadallèen 21, 0349 Oslo, Norway
[d] Department of Botany, 7062 Makerere University, Kampala, Uganda
[e] Department of Chemistry, 7062 Makerere University, Kampala, Uganda

ARTICLE INFO

Article history:
Received 25 July 2009
Received in revised form
11 March 2010
Accepted 14 April 2010

Keywords:
Nile tilapia
Diet
Microcystins
Cyanobacteria
Tropics
Uganda

ABSTRACT

Due to the production of toxins, cyanobacteria may adversely affect economically important fish such as Nile tilapia *Oreochromis niloticus* in tropical lakes. We studied the diet composition and factors affecting the diet of *Nile tilapia* in two tropical lakes where cyanotoxins were present. Particle-bound microcystins were present in all analysed water samples, ranging in concentration from 0.00012 to 1.11 and from 0.006 to 0.254 $\mu g\,L^{-1}$ in Murchison Bay in Lake Victoria and Lake Mburo, respectively. Detritus and phytoplankton were the main dietary components of the Nile tilapia, with phytoplankton contributing to over 30% by volume of stomach contents. The cyanobacteria *Microcystis* spp., which are also the most likely source of microcystins in the lakes, accounted for more than 80% of ingested phytoplankton. *Microcystis* spp. were also the most abundant cyanobacteria in both lakes ($>60\%$). We found no significant relationship between the contribution of phytoplankton in Nile tilapia diet and the concentration of microcystins in the water but we found a close association between water transparency and the contribution of insects to Nile tilapia diets in Murchison Bay. Our results further show that none of the other measured environmental variables was a good predictor of diet items in Nile tilapia. Adult Nile tilapia in our study lakes, rely heavily on filter feeding, particularly under conditions of low water transparency, trapping detritus and phytoplankton cells especially colonies. They can ingest more mobile prey like insects and insect larvae when the water transparency and visibility increases.

Introduction

Phytoplankton communities of eutrophic tropical lakes are often dominated by cyanobacteria that can form dense blooms (Gragnani et al., 1999), which, are often enhanced by nutrient runoff from human waste disposal and poor agricultural practices. Cyanobacterial blooms can cause a variety of problems in aquatic ecosystems, such as hypoxia and clogging of fish gills. Many cyanobacteria including the genera *Microcystis* and *Anabaena* also produce toxic bioactive compounds like the hepatotoxic microcystins and the neurotoxic anatoxin a, that are harmful to both humans (Carmichael, 2001) and fish (Malbrouck and Kestemont, 2006). In lakes with high concentrations of cyanobacteria, filter feeding zooplankton (Gragnani et al., 1999) and herbivorous fish, including Nile tilapia, silver carp, and bighead carp, may act as top–down controls of cyanobacteria, reducing algal populations by up to 93% of a cyanobacterial (*Microcystis* spp.) bloom (Kaihong et al., 2006).

The Nile tilapia (*Oreochromis niloticus*, L.) has been classified as a herbivorous filter-feeder in various studies (Moriarty et al., 1973). Studies on Nile tilapia in crater lakes (Bwanika et al., 2004) and *Oreochromis* spp. in Lake Victoria and Kyoga lake basins (Nagayi-Yawe et al., 2006) show that cyanobacteria can contribute over 51% of fish diets. Nile tilapia are able to assimilate up to 70–80% of ingested carbon from the cyanobacteria *Microcystis* spp., as compared to $<50\%$ for green algae (Moriarty and Moriarty, 1973). Several experimental studies have also reported higher filtration rates for cyanobacteria than green algae, probably on account of their larger particle size in the form of aggregates like colonies (Northcott et al., 1991; Turker et al., 2003).

For some fish however, there are doubts about their ability to utilise cyanobacteria (e.g. Kamujunke et al., 2002). Kamujunke

* Corresponding author at: Department of Biology, University of Bergen, Post box 7803, N-5020 Bergen, Norway. Tel.: +47 55 58 20 28, +47 90 29 26 12; fax: +47 55 58 96 67.
E-mail address: ronald.semyalo@bio.uib.no (R. Semyalo).
[1] Deceased.

0075-9511/$ - see front matter © 2010 Elsevier GmbH. All rights reserved.
doi:10.1016/j.limno.2010.04.002

et al. (2002) showed that cyanobacteria such as *Microcystis* spp. were a poor contributor to growth of juvenile roach (*Rutilus rutilus*) compared to *Aphanizomenon* spp. probably due to their poor digestibility. Cells of cyanobacteria with a mucous cover like *Microcystis* spp. can pass through fish guts undigested (Kamujunke et al., 2002). The main problem however, may be that cyanobacteria produce bioactive intracellular and extracellular compounds that may make them unattractive to grazers (Keshavanath et al., 1994) or even toxic for fish consuming them (Gupta and Guha, 2006). Various studies on lakes (Ochumba, 1990) and fish ponds (Jewel et al., 2003) have associated cyanobacteria blooms with massive fish deaths. However, incidents of mass fish mortalities are also often associated with indirect bloom effects such as increased ammonia concentration (Bury et al., 1995), oxygen depletion (Ochumba, 1990), and high pH (Wiegand and Pflugmacher, 2005), rather than cyanobacterial toxins.

Upon ingestion and digestion of toxic cyanobacteria, cyanotoxins are released, and tend to accumulate in fish liver, muscles, and viscera (Mohamed et al., 2003, Chen et al., 2006). The effects of consumption of microcystins in fish are quite similar to those observed in mammals, i.e. the disruption of hepatocyte structure, apoptosis, liver necrosis, internal haemorrhage (Malbrouck and Kestemont, 2006), lowered growth rate (Bury et al., 1995), and reduced reproduction success (Baganz et al., 2004). Early life stages of fish are normally the most susceptible to the effects of cyanobacteria toxins (Malbrouck and Kestemont, 2006).

Ingestion of cyanobacterial cells is the most important route of cyanotoxin uptake by fish (Tencalla et al., 1994). Laboratory studies show that fish may minimise uptake of cyanotoxins by lowering their grazing rates on toxin containing cells (Keshavanath et al., 1994). There is no field evidence for this to our knowledge, especially in eutrophic topical lakes such as Lake Victoria where blooms often occur all year round (Haande, 2008). Studies on Nile tilapia in Lake Victoria indicate that owing to various ecological and environmental changes, including eutrophication, there can be a shift in fish diet into a more diverse diet (Njiru et al., 2004). Nonetheless, cyanobacteria are still a major constituent of the Nile tilapia diet in Lake Mburo and Lake Victoria (Bwanika et al., 2006), In light of recent reports on microcystins in these lakes (Sekadende et al., 2005; Okello et al., 2009; Semyalo et al., 2010), we may begin to observe an effect of these cyanotoxins on the contribution of phytoplankton to Nile tilapia diet.

We investigate the diet compositions and factors affecting the diet of Nile tilapia in two tropical eutrophic lakes where microcystins are present, Lake Victoria and Lake Mburo, Uganda. In these lakes the cyanobacterium *Microcystis aeruginosa* has been proposed as the most likely source of observed microcystins (Haande et al., 2007; Okello et al., in press). We also specifically sought to investigate the composition of phytoplankton (with special focus on cyanobacteria) in the fish diets.

Materials and methods

Our study was carried out in two Ugandan freshwater bodies; Lake Mburo and Murchison Bay, Lake Victoria between July 2004 and December 2005.

Study sites

Lake Mburo is a shallow lake with maximum depth of 4 m and an average depth of 2 m. The surface area is approximately 13 km^2. The lake is located between 00°30′–00°45′S and 45°00′–31°05′E at an average altitude of 1210 m within the protected Lake Mburo National Park in western Uganda. The park constitutes a major part of the lake's catchment. Besides wildlife, fishing, particularly of Nile tilapia, is an important economic activity in this lake. Lake Mburo has a large wildlife population, notably a large population of over 1000 individuals of the herbivore *Hippopotamus amphibius* that reside mainly in and around the lake. It is likely that the hippos release their waste into the lake. Studies on this lake have been largely restricted to wildlife communities around the lake and little work has been carried out on the phytoplankton, zooplankton, and fish communities due to its restricted access. The phytoplankton community structure of Lake Mburo indicates that cyanobacteria constitute ~90% of the phytoplankton community and that cyanobacteria of the genus *Microcystis* (~60%) and the genus *Anabaena* (~20%) make up > 80% of the cyanobacteria in the lake (Byarujali, 1995).

Lake Victoria is the world's largest tropical freshwater lake covering an area of 68,800 km^2 and supporting a population of over 30 million people in its catchment. In the last 50 years, the lake has undergone wide scale eutrophication, characterised by a loss of deep-water oxygen, dominance of bloom-forming cyanobacteria and losses in fish biodiversity (Verschuren et al., 2002). Cyanobacteria blooms are most prominent in areas close to shore, e.g. Winam Gulf (Ochumba and Kibaara, 1989), Mwanza Gulf (Sekadende et al., 2005), and Murchison Bay (Haande, 2008) .

Murchison Bay is only 8 km east of Kampala, the capital city of Uganda, and lies between latitude 00°15′N–00°18′N and longitude 32°33′E–32°41′E at an altitude of 1135 m. The bay covers an area of about 200 km^2 and is divided into two parts; the inner bay (18 km^2) and the outer bay separated by a narrows. Average depth of the inner bay is 3.2 m. The study site was located in the inner bay where the depth was approximately 3 m. Fishing and boat transport are the most prominent economic activities within this bay. Main fisheries include: Nile tilapia, Nile perch (*Lates niloticus*), and silver cyprinid (*Rastrineobola argentae*). Studies on the phytoplankton community structure of Murchison Bay indicate that cyanobacteria constitute ~60% of the phytoplankton community and that cyanobacteria of the genus *Microcystis* (31%) and the genus *Anabaena* (20%) make up > 50% of the cyanobacteria in the inner Murchison Bay (Haande, 2008).

Fish diet composition

To study the diet composition of *O. niloticus* in the two lakes, we collected fish samples using multimesh nylon gill nets, also known as Nordic survey nets (Appleberg et al. 1995) with 12 sections of 5.0, 6.25, 8.0, 10.0, 12.5, 15.5, 19.5, 24.0, 29.0, 35.0, 43.0, and 55.0 mm mesh, net depth 5 and 2.5 m length of each section. During each sampling the nets were set for a maximum period of 1 h, during which time they rapidly filled up. Pilot fishing trials were conducted for a three day period to determine fishing sites with the largest possible catch of Nile tilapia. We conducted the fishing once a month during the study period. We could not set fishing nets close to the shore in Lake Mburo because of hippopotami. Nets were therefore set in deeper waters where small sized fish (< 15 cm total length) were very scarce.

Captured fish were identified to species level (except halpochromines) and weighed. Nile tilapia were identified and weighed and total length was measured. The stomachs of samples of Nile tilapia were then removed and preserved in formalin. Stomach contents were analysed under a stereo microscope and phytoplankton identification and enumeration was carried out with the help of an inverted compound microscope. Estimation of stomach content composition was done using volumetric methods (Hynes, 1950).

Physico-chemical and biological environment

During the fish sampling, physico-chemical water measurements were taken at 1 m depth intervals. We measured water temperature, dissolved oxygen, using a hand held dissolved oxygen meter (YSI 85, Yellow Spring Instruments), and water transparency using a black and white Secchi disc with a diameter of 20 cm. We filtered 100 ml of surface water through GFC filters that were wrapped in aluminium foil and kept in an ice box for 24 h before chlorophyll analysis. Chlorophyll *a* was extracted using methanol and measurements made using a spectrophotometer, following basic methods (Lorenzen, 1967). Integrated water samples (100 cm^3) were filtered through a GFC filter for measurement of particle bound microcystin concentration at each site. Filters were wrapped in aluminium foil and placed in an ice box, then transported to the laboratory and stored in a freezer. In the laboratory, filters were placed into a reaction tube and the extraction agent (75% methanol and 25% distilled water) added and shaken vigorously at room temperature for 30 min. The resulting extract was then decanted into an evaporation flask. The extracts were centrifuged at 500*g* to remove any particles. The extract was then kept at −18 °C prior to analysis. Analysis of all samples for microcystins was done using liquid chromatography coupled with mass spectroscopy. Microcystins LR, YR, and RR in phytoplankton extracts were quantified in positive ESI mode and single-ion monitoring using the ions 995.5, 1045.5 $[M+H]^+$, and 519.8 $[M+2H]^{2+}$. The resulting measurements were presented as a total of all microcystins.

Water samples for phytoplankton were collected using a one litre horizontal Van Dorn water sampler for identification and quantification of the different cyanobacteria groups in the study area. 100 ml of the collected water sample were stored in opaque glass bottles; 5 ml of Lugol's iodine was added to preserve the algal cells. Identification of algae groups was carried out to genus level. Enumeration of algal cells was done by inverted microscope method (Lund et al., 1958) using a Sedgwick rafter cell.

Statistical analysis

Diet composition of Nile tilapia was estimated as stomach content to the nearest ml and converted to percent by volume (Hynes 1950). Cells of each phytoplankton genus in each subsample of stomach contents were enumerated to obtain percent number (%*N*). The percent frequency of occurrence for each group in the samples (%FO) (Magalhaes et al., 2003) was obtained as well as the percent volume (%*V*) calculated from known species biovolume estimates (Hillebrand et al., 1999). A comparison between major food items for fish in the two lakes was done by Spearman rank correlation. The electivity index, log *Q* (Jacobs, 1974), was used to measure selection for cyanobacteria:

$$Q = \frac{r(1-p)}{p(1-r)}$$

where *r* is the fraction of an algae group in the stomach and *p* is the fraction of that group in the lake plankton and log *Q* varies symmetrically from $-\infty$ to 0 for negative selection, from 0 to $+\infty$ for positive selection. We used forward-stepwise multiple linear regression analysis using the statistical package R (R Development Core Team, 2008) to test relationships between measured environmental variables (water transparency, dissolved oxygen, surface temperature, chlorophyll *a* and microcystin concentration) and Nile tilapia diet composition. Pearson's moment correlation and Wilcoxon rank sum test were used for various comparisons among and between environmental variables and diet items.

Results

Catch statistics

O. niloticus made up 18.6% ($n=45$) and 25.7% ($n=34$) of total biomass caught in Murchison Bay and Lake Mburo, respectively. Other major fish species caught in Lake Mburo included *O. esculentus* (61.7%), Haplochromines (10.1%), *O. variabilis* (6.6%), *O. leucostictus* (2%), and *R. argentae* (1%). Major fish species caught in Murchison Bay included *L. niloticus* (31.85%), Haplochromines (19.9%), *Bryocynus* sp. (11.5%), *R. argentae* (7.8%), and *Tilapia zilli* (3.3%). In both study areas, despite their low contribution to total biomass of fish caught, small fishes like the haplochromine cichlids, *Bryocynus* spp., and *R. argentae* were the most abundant by number in the catches. Catches of other *Oreochromis* spp. were too low, particularly in Murchison Bay, to be used in this study.

General diet

Detritus and phytoplankton were the most abundant diet items in the stomachs of Nile tilapia, constituting 77% in Lake Mburo and 83% in Murchison Bay (Fig. 1). Other dietary items identified included insects (Chironomidae only), zooplankton, fish scales, stones, and fish eggs. The relative importance of all food items by percent volume contribution was highly correlated between the two lakes (Spearman Rank correlation $r_s=0.986$).

Observations on all fish stomachs analysed show that juvenile Nile tilapia (TL < 200 mm) consumed a significantly larger percentage of detritus than adult Nile tilapia (TL > 200 mm) ($W=131$, $p<0.05$) and a lower percentage volume of zooplankton ($W=287$, $p<0.05$), but do not show any significant differences in amount of phytoplankton, insects, and other items in their diet ($p>0.05$). Detritus was the most abundant food item in stomachs of juvenile fish followed by phytoplankton, insects, and zooplankton whereas adults tended to ingest comparable amounts of detritus, phytoplankton, and insects (Fig. 2).

Stepwise multiple linear regression analysis of environmental variables (water transparency, dissolved oxygen, surface temperature, chlorophyll *a*, and microcystin concentration) as predictor variables and dietary items (detritus, phytoplankton,

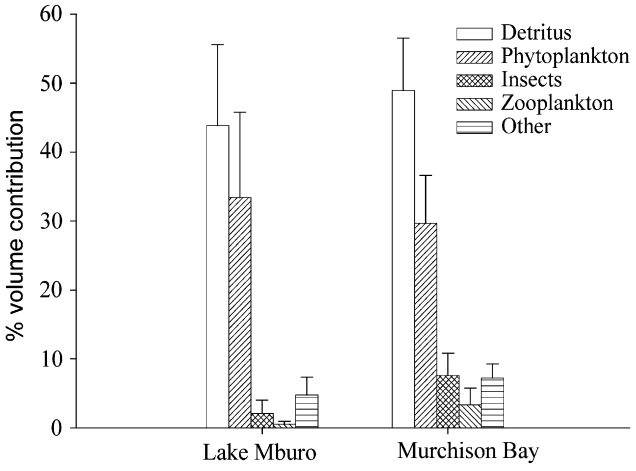

Fig. 1. Percent volume contribution (+S.E.) of major food items to diets of fish in Lake Mburo ($n=22$) and Murchison Bay, Lake Victoria ($n=44$).

insects, zooplankton, and others) as dependant variables showed water transparency had a positive association ($R^2=0.8$, $F=56.2$, $p<0.001$) with insects in the diets of fish obtained from the Murchison Bay.

Phytoplankton in diet

Quantitative analysis of the phytoplankton found in the stomachs of Nile tilapia (Table 2) revealed that the group Cyanophyceae was the most dominant phytoplankton by volume in the stomachs of fish captured in Lake Mburo (92%) and Murchison Bay (98%). Chlorophyceae contributed 7% by biovolume in fish from Lake Mburo, and less than 1% in Murchison Bay fish. Bacillariophycea, Chrysophyceae, and Gamophyceae each made up less than 1% biovolume in fish from both lakes (Table 2). Among the Cyanophyceae, the genus *Microcystis* was the most prominent contributing >80% of ingested cyanobacteria in fish stomachs from Lake Mburo and Murchison Bay.

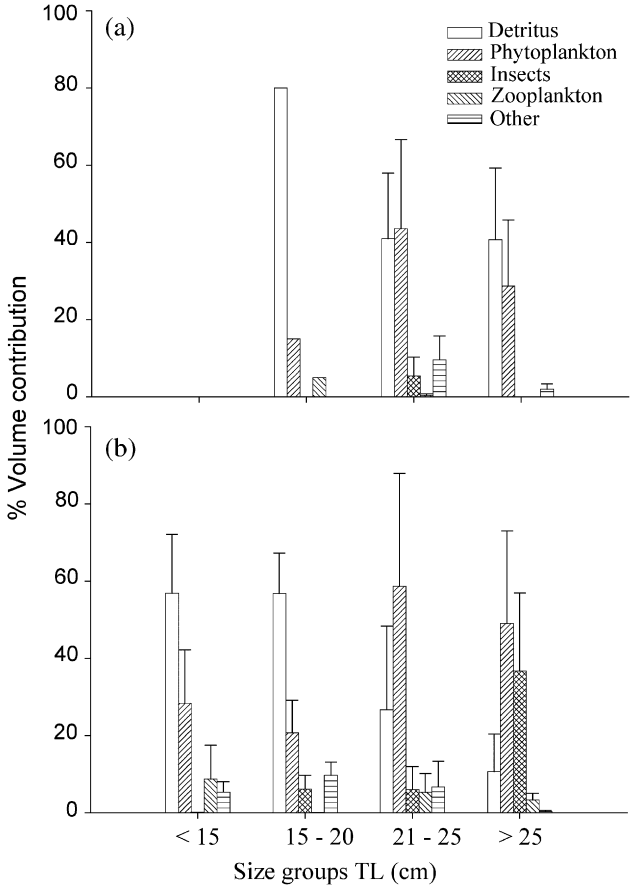

Fig. 2. Dietary contribution by percent volume contribution of food items (+S.E.) in *Nile tilapia* across three size classes in: (a) Lake Mburo 15–20 ($n=2$), 20–25 ($n=9$), >25 ($n=11$); (b) four size classes 9–14 ($n=7$), 15–20 ($n=27$), 20–25 ($n=4$), >25 ($n=6$) in Murchison Bay, Lake Victoria.

Environmental variables

Although we observed monthly differences in all measured environmental variables we did not find any statistically significant seasonal differences ($p>0.05$) in either study area (Table 1).

Analysis of the phytoplankton community composition in lakes showed that Cyanophyceae were the most abundant group by biomass (Fig. 3) and that *Microcystis* spp. (62% and 76%) were the most abundant group of Cyanophyceae in Lake Mburo and Murchison Bay, followed by *Anabaena* spp. (24% and 20%) and *Aphanocapsa* spp. (12% and 3%). There was a close correlation between composition of Cyanophyceae in lakes and composition of ingested Cyanophyceae (Pearson's $r=0.6457$, $p<0.001$). Our results show that there was a high selection for the phytoplankton group *Microcystis* ($\log Q>3.0$, Table 3) as compared to other major groups of ingested Cyanophyceae.

Microcystins (RR, LR and YR) were present in both lakes during all seasons of sampling (Table 1). In Lake Mburo, the highest value of microcystin concentration (0.254 $\mu g\,L^{-1}$) was recorded in July and the lowest (0.006 $\mu g\,L^{-1}$) in September. In Murchison Bay, the highest value of microcystin concentration (1.11 $\mu g\,L^{-1}$) was recorded in December and the lowest (0.00012 $\mu g\,L^{-1}$) in April. In both study areas the highest mean levels of microcystins were recorded during the second wet season (September–December) and the lowest mean measurements during the first wet season (March–May) (Table 1).

In Lake Mburo, mean seasonal water temperature measurements showed peaks during the wet seasons of March–May and September–December (Table 1). Water temperatures varied by up to 2° during the time of study, with higher temperatures (>25 °C) recorded during February (dry season), May, and October (wet season) and lower temperatures (<24 °C) in January and July (dry season). Differences of less than 1 °C between the different depths on days of sampling suggested a well mixed water environment throughout the year. As shown in Table 1, mean seasonal water temperatures in Murchison Bay varied between 25 and 30 °C. The lowest mean temperatures were recorded in June–August and

Table 1
Mean values of dissolved oxygen, water transparency (Secchi), surface temperature (°C), surface chlorophyll *a* and microcystins concentration for Lake Mburo, Murchison Bay, and Lake Victoria, respectively, measured during the different seasons from July 2004–December 2005 (na=not available).

Environmental variable	*n*	Dry season (January–February)	Wet season (March–May)	Dry season (June–August)	Wet season (September–December)
Lake Mburo					
DO ($mg\,L^{-1}$)	54	7.6	9.7	9.4	5.6
Secchi (M)	18	0.36	0.32	0.32	0.34
Chlorophyll *a* ($\mu g\,L^{-1}$)	11	66.73	58.09	65.12	67.55
Surface temp (°C)		25.30	25.33	24.45	25.12
MCs concentration in water ($\mu g\,L^{-1}$)	17	0.064	0.110	0.195 (Jun-na)	0.225
Murchison Bay					
DO ($mg\,L^{-1}$, % saturation)	72	6.8	7.4	5.4	5.4
Secchi (M)	18	0.36	0.82	0.62	0.55
Chlorophyll *a* ($\mu g\,L^{-1}$)	17	43.05	35.97	43.80	38.00
Surface temp (°C)		28.75	26.87	25.33	30.03
MCs concentration in water ($\mu g\,L^{-1}$)	16	0.400	0.197 (May-na)	0.224	0.682

Table 2
An analysis of the different phytoplankton groups identified in the stomachs of fish captured in Lake Mburo (n=22) and Murchison Bay, Lake Victoria (n=44), giving percentage in volume (V=total biovolume), number (N=number of cells) and frequency of occurrence (FO=number of fish with item in stomach).

Genus	Lake Mburo			Murchison Bay		
	%V	%N	%FO	%V	%N	%FO
Chrysophyceae						
Chrysococcus spp.	0.01	0.01	6	0	0	0
Chrysocapsa spp.	0.01	0.2	12	0.01	0.02	3
Cyanophyceae						
Planktolyngbya spp.	0.1	1	71	0.02	0.3	58
Aphanocapsa spp.	2	7	53	0.03	0.2	13
Cylindrospermopsis	0.03	0.4	24	0	0	0
Microcystis	82	67	88	87	67	97
Chroococus	0.5	1	47	0.02	0.07	6
Merismopidia	0.1	4	59	0.37	10	68
Anabaena	2.5	5	47	8	15	65
Coelosphaerium	0.4	2	18	0.1	0.4	6
Aphanizomenon	0.004	0.01	6	0	0	0
Gomphosphaeria	5.196	4	6	3	2	3
Phormidium	0.01	0.01	6	0	0	0
Anabaenopsis	0.01	0.04	6	0	0	0
Spirulina	0.01	0.1	24	0.06	0.8	13
Anacystis	0.02	2	6	0	0	0
Plectonema	0	0	0	0.01	0.01	3
Limnothrix	0	0	0	0.02	0.01	3
Oscillatoria	0	0	0	0.01	0.05	10
Wothrix	0	0	0	0	0.4	16
Chlorophyceae						
Scenedesmus	0.01	2	76	0.12	1	29
Sphaerocystis	0.1	2	29	0.4	1	6
Pediastrum	6	0.04	18	0.05	0.03	23
Selenastrum	0.01	0.02	6	0	0	0
Oocystis	0.01	0.1	6	0	0	0
Spirogyra	0.2	0.1	6	0	0	0
Volvox	1	0.02	6	0	0	0
Coelastrum	0	0	0	0.01	0.01	13
Tetraedron	0	0	0	0.01	0.01	3
Ankistrodesmus	0	0	0	0.02	0.5	32
Oedogonium	0	0	0	0.02	0.05	3
Ulothrix	0	0	0	0.1	0.1	23
Bacillariophyceae						
Melosira	0.02	0.4	29	0.1	0.1	29
Flagillaria	0	0	0	0.02	0.1	6
Navicula	0	0	0	0.4	1	35
Nitzschia	0.01	0.05	12	0.07	0.7	61
Diatoma	0	0	0	0.01	0.03	10
Tabellaria	0	0	0	0.01	0.03	10
Gamophyceae						
Netrium	0	0	0	0.7	0.01	3
Zygnema	0.05	0.06	6	0.01	0.01	3
Closterium	0	0	0	0.01	0.01	3
Staurastrum	0	0	0	0.01	0.01	6

the highest in September–December. The water column in the shallow part of the bay was mostly fully mixed throughout the year.

Mean levels of dissolved oxygen saturation in Lake Mburo varied from 59% to 103% (Table 1). Only in December did the percent saturation drop below 60%. In Murchison Bay, mean levels of dissolved oxygen saturation varied from 58% to 78% saturation in February (Table 1). For most of the year, DO saturation was above 60% at all depths, with exception of June–August when near anoxic conditions (<2 mg L^{-1}, <20% saturation) were recorded 1 m from the bottom of the water column.

The water transparency of Lake Mburo was low with secchi depth measurements of <0.5 m (Table 1). In Murchison Bay, water transparency was also low with a secchi depth ranging from 0.3 to 0.9 m (Table 1). The highest levels of chlorophyll *a*

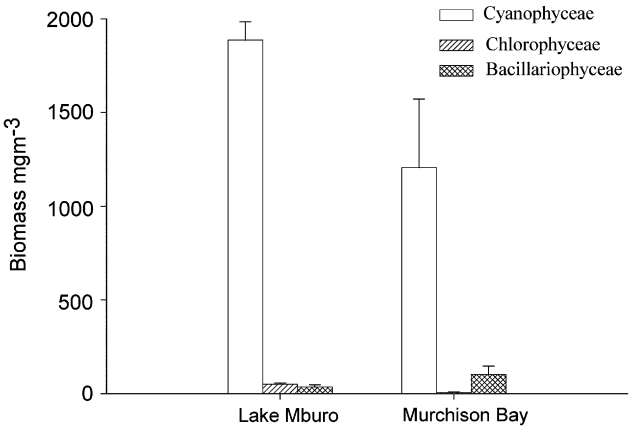

Fig. 3. Mean biomass estimates (+S.E.) of dominant phytoplankton groups in Lake Mburo (n=18) and Murchison Bay, Lake Victoria (n=18) from monthly measurements (July 2004–December 2005).

Table 3
Selectivity index log *Q* of the major groups of cyanobacteria found in the diets of Nile tilapia fish in Lake Mburo (n=22) and Murchison Bay, Lake Victoria (n=44). N/A=not available.

Genus	Selectivity index (log *Q*)					
	Lake Mburo			***Murchison Bay***		
	Min	***Mean***	***Max***	***Min***	***Mean***	***Max***
Microcystis	3.56	3.92	3.99	2.99	3.87	3.99
Anabaena	−1.26	0.93	3.06	−1.22	1.75	3.64
Aphanocapsa	2.06	2.14	2.21	N/A	N/A	N/A
Other cyanobacteria	−0.39	0.89	3.48	−0.22	−0.11	0.00

(98.2 μg L^{-1}) in Lake Mburo were recorded during the second wet season in September and the lowest (44.7 μg L^{-1}) in the first wet season in May. We also observed high amounts of suspended material (silt). The highest level of chlorophyll *a* (51.8 μg L^{-1}) and the lowest levels (37.6 μg L^{-1}) in Murchison Bay were recorded during the second wet season in the months of September and November, respectively. We also observed high amounts of suspended material (silt) in the water.

Discussion

Phytoplankton and detritus are the main dietary items found in the stomachs of Nile tilapia from both Lake Mburo and Murchison Bay. The presence of detritus, insects, zooplankton, and other diet items like fish eggs, provides evidence for a generalist/omnivorous feeding strategy for the Nile tilapia in the study lakes. It is also likely that the high proportions of detritus compared to other food items in the diet including phytoplankton was a consequence of Nile tilapia foraging close to the sediment (Balirwa, 1992). In general, phytoplankton contributed up to a third of the total food items ingested, and was consumed mostly by the adult Nile tilapia (>20 cm TL), which have a better ability to ingest and digest large and tough phytoplankton cells (Lu et al., 2004). Nile tilapia consumed phytoplankton from at least five different groups: Cyanophyceae contributed the largest percentage ingested (Table 2).

The contribution of phytoplankton to the diet of Nile tilapia (~30%) was comparable to previously observed results for Lake Mburo (43%) but not for Lake Victoria (6%) (Bwanika et al., 2006). Bwanika et al. (2006) attributed the difference in phytoplankton contribution to diet between the two lakes to a cascading effect of

the piscivorous Nile perch: Nile tilapia in lakes without Nile perch were found to have a less omnivorous diet than lakes with Nile perch. Although Nile perch is present in Murchison Bay, the amount of phytoplankton in adult Nile tilapia diet in our study was not different from those in Lake Mburo, where Nile perch is absent. However, Bwanika et al. (2006) also suggest that environmental conditions that lower visibility, such as low water transparency, may provide refugia for fish from Nile perch predation, which would increase the competition for other food resources with other fish species, thereby restricting the Nile tilapia to a more herbivorous diet. We believe our findings are consistent with this assumption, especially in Murchison Bay, where we also observed a significant relationship ($p < 0.001$) between water transparency and amount of insects in Nile tilapia diet. In addition to a reduction in competitors due to Nile perch predation, an increase in water transparency may allow fish to engage in active pursuit to include a variety of animal and plant materials in their diet (Moriarty et al., 1973).

The sampling sites used in this study were shallow (< 5 m) and located in open water away from the littoral zone. The water column in both study areas was well mixed with a low water transparency, as a result of high phytoplankton biomass (Kayiira, 2007; Haande, 2008) and high quantity of suspended silt. These conditions may also explain the high abundance of phytoplankton and detritus and the total lack of food items associated with littoral-like plant material (Bwanika et al., 2006) in fish diets. Water transparency was the only environmental variable that was closely associated with diet items for the Nile tilapia. Although we observed variation in other environmental variables both between and within seasons they were not statistically significant (Table 1). The absence of strong seasonal patterns is common in tropical lakes, and biological processes seem more relevant than physical and chemical processes in controlling food web dynamics.

The composition of the cyanobacteria in Nile tilapia diet was dominated by *Microcystis* spp., which is a likely source of known microcystins in these lakes. Nonetheless, we were unable to establish a relationship between microcystin concentrations and the amount of phytoplankton in Nile tilapia diets ($p > 0.05$). We did not find any evidence for avoidance of *Microcystis* spp. in relation to the presence of microcystins in the lake. Instead, we found that the proportion of *Microcystis* spp. in fish stomachs ($> 80\%$) was higher than its proportion in the phytoplankton community (62–76%) suggesting that it is selected for (Table 3) by some kind of mechanism in the feeding strategy of the Nile tilapia. One explanation for this could be that *Microcystis* spp. tend to form large colonies that are more efficiently ingested by a filter-feeding fish like Nile tilapia than single cells (Turker et al., 2003), especially by the adults. This would explain why *Microcystis* and *Anabaena* are the most dominant phytoplankton ingested by the Nile tilapia in several Ugandan lakes (Bwanika et al., 2006).

Although only a few studies have been conducted on the microcystin production potential of cyanobacterial communities of Lake Mburo (Okello et al., in press), Murchison Bay (Haande et al., 2007), and other inland waters of Lake Victoria (Krienitz et al., 2002; Sekadende et al., 2005), they report microcystins in the water at levels comparable to our findings, suggesting that the cyanobacterium *M. aeruginosa* is the most probable source for these bioactive compounds. Previous work on carbon assimilation of algae (Moriarty and Moriarty, 1973) shows that Nile tilapia are able to digest and assimilate carbon from cyanobacteria of the genus *Microcystis* and *Anabaena*. Thus, an increase in toxin-producing cyanobacteria within the water would result in an increase in the uptake microcystins over the gastrointestinal tract (Tencalla et al., 1994). Several field studies with Nile tilapia have shown that ingested microcystins can be assimilated, ending up in fish tissue (Magalhaes et al., 2003; Mohamed et al., 2003; Deblois et al., 2008).

The Nile tilapia plays an important role as a primary consumer in the aquatic food chain of these lakes (Balirwa, 1992; Bwanika et al., 2006) and it is an important source of protein to higher predators like humans and birds of prey. The presence of harmful bioactive compounds from cyanobacteria such as microcystins in their tissues increases the chances of microcystin accumulation and transfer higher up in the food chain, which may result in a decline of the Nile tilapia fishery and fatalities especially for avian life. Studies are required to ascertain the level of microcystins in Nile tilapia tissue from these lakes and an assessment of the potential health risk faced by humans living off this fishery. The presence of microcystins in the water in our study lakes, on some occasions with levels $> 1.0\ \mu g\ L^{-1}$ is also a great health risk for humans consuming this water in its raw form (Carmichael, 2001) and should be addressed through continuous monitoring and water treatment.

Acknowledgements

We would like to thank Noeline Ndagire for her assistance with field work and analysis of fish stomach samples. We thank Madina Namyalo for assistance with field work. We thank Justin James Meager, Jon Egil Skjæraasen, Winfred Lampert and two anonymous reviewers for their comments to the manuscript. This study was supported by a grant from the Norwegian Agency for Development Cooperation (NORAD) under the Ecological and socio-economic implications of harmful algal blooms (HABs) in Ugandan lakes (project number UGA-2027).

References

Appleberg, M., Hesthagen, B.H.M., Kleiven, T., Kurkilahti, E., Raitaniemi, M., Rask, M., 1995. Development and intercalibration of methods in Nordic freshwater fish monitoring. Water Air Soil Pollut. 85, 401–406.

Baganz, D., Staaks, G., Pflugmacher, S., Steinberg, C.E.W., 2004. A comparative study on the microcystin induced behavioural changes of two fish species, *Danio rerio* and *Leucaspius delineatus*. Environ. Toxicol. 19, 564–570.

Balirwa, J.S., 1992. The evolution of the fishery of *Oreochromis niloticus* (Pisces, Cichlidae) in Lake Victoria. Hydrobiologia 232, 85–89.

Bury, N.R., Eddy, F.B., Codd, G.A., 1995. The effects of the cyanobacterium *Microcystis aeruginosa*, the cyanobacterial hepatotoxin microcystin-Lr, and ammonia on growth-rate and ionic regulation of brown trout. J. Fish Biol. 46, 1042–1054.

Bwanika, G.N., Chapman, L.J., Kizito, Y., Balirwa, J., 2006. Cascading effects of introduced Nile Perch (*Lates niloticus*) on the foraging ecology of Nile tilapia (*Oreochromis niloticus*). Ecol. Freshwater Fish 15, 470–481.

Bwanika, G.N., Makanga, B., Kizito, Y., Chapman, L.J., Balirwa, J., 2004. Observations on the biology of Nile tilapia, *Oreochromis niloticus* L., in two Ugandan crater lakes. Afr. J. Ecol. 42, 93–101.

Byarujali, S.M., 1995. Phytoplankton production in L. Mburo – Western Uganda. In: Proceedings of the First Conference on Ecology and Sustainable Natural Resource Management for Development, Mweya, Queen Elizabeth National Park, Uganda. pp. 284–290.

Carmichael, W.W., 2001. Health effects of toxin-producing cyanobacteria: "The CyanoHABs". Hum. Ecol. Risk Assess. 7, 1393–1407.

Chen, J., Xie, P., Zhang, D.W., Ke, Z.X., Yang, H., 2006. In situ studies on the bioaccumulation of microcystins in the phytoplanktivorous silver carp (*Hypophthalmichthys molitrix*) stocked in Lake Taihu with dense toxic Microcystis blooms. Aquaculture 261, 1026–1038.

Deblois, C.P., Aranda-Rodriguez, R., Giani, A., Bird, D.F., 2008. Microcystin accumulation in liver and muscle of tilapia in two large Brazilian hydroelectric reservoirs. Toxicon 51, 435–448.

Gragnani, A., Scheffer, M., Rinaldi, S., 1999. Top–down control of cyanobacteria: a theoretical analysis. Am. Nat. 153, 59–72.

Gupta, U.S., Guha, S., 2006. Microcystin toxicity in a freshwater fish, *Heteropneustes fossilis* (Bloch). Curr. Sci. 91, 1261–1271.

Haande, S., 2008. On the ecology, toxicology, and phylogeny of cyanobacteria in Murchison Bay of Lake Victoria, Uganda. Ph.D Thesis, University of Bergen, Bergen.

Haande, S., Ballot, A., Rohrlack, T., Fastner, J., Wiedner, C., Edvardsen, B., 2007. Diversity of *Microcystis aeruginosa* isolates (Chroococcales, Cyanobacteria) from East-African water bodies. Arch. Microbiol. 188, 15–25.

Hillebrand, H., Durselen, C.D., Kirschtel, D., Pollingher, U., Zohary, T., 1999. Biovolume calculation for pelagic and benthic microalgae. J. Phycol. 35, 403–424.

Hynes, H.B.N., 1950. The food of freshwater sticklebacks (*Gasterosteus aculeatus* and *Pygosteus pungitius*) with a review of methods used in studies of the food of fishes. J. Anim. Ecol. 19, 36–58.
Jacobs, J., 1974. Quantitative measurement of food selection: a modification of the forage ratio and Ivlev's electivity index. Oecologia 14, 413–417.
Jewel, M.A.S., Affan, M.A., Khan, S., 2003. Fish mortality due to cyanobacterial bloom in an aquaculture pond in Bangladesh. Pak. J. Biol. Sci. 6 (12), 1046–1050.
Kaihong, L., Chunhua, J., Shuanglin, D., Binhe, G., Bowen, S.H., 2006. Feeding and control of blue-green algal blooms by tilapia (*Oreochromis niloticus*). Hydrobiologia 568, 111–120.
Kamujunke, N., Schmidt, K., Pflugmacher, S., Mehner, T., 2002. Consumption of cyanobacteria by roach (*Rutilus rutilus*) useful or harmful to the fish? Freshwater Biol. 47 243–250.
Kayiira, D., 2007. Algal community of Lake Mburo and Murchison Bay, Lake Victoria. Masters Thesis, Makerere University, Kampala.
Keshavanath, P., Beveridge, M.C.M., Baird, D.J., Lawton, L.A., Nimmo, A., Codd, G.A., 1994. The functional grazing response of a phytoplanktivorous Fish *Oreochromis niloticus* to mixtures of toxic and nontoxic strains of the cyanobacterium *Microcystis aeruginosa*. J. Fish Biol. 45, 123–129.
Krienitz, L., Ballot, A., Wiegand, C., Kotut, K., Codd, G.A., Pflugmacher, S., 2002. Cyanotoxin-producing bloom of *Anabaena flos-aquae, Anabaena discoidea* and *Microcystis aeruginosa* (cyanobacteria) in Nyanza Gulf of Lake Victoria, Kenya. J. Appl. Bot. – Angew. Bot. 76, 179–183.
Lorenzen, C.J., 1967. Determination of chlorophyll and pheopigments: spectrophotometric equations. Limnol. Oceanogr. 12, 343–346.
Lu, J., Takeuchi, T., Satoh, H., 2004. Ingestion and assimilation of three species of freshwater algae by larval tilapia *Oreochromis niloticus*. Aquaculture 238, 437–449.
Lund, J.W.G., Kipling, C., Le Cren, E.D., 1958. The inverted microscope method of estimating algal numbers and the statistical basis of estimations by counting. Hydrobiologia 11, 143–170.
Magalhaes, V.F., Marinho, M.M., Domingos, P., Oliveira, A.C., Costa, S.M., Azevedo, L.O., Azevedo, S., 2003. Microcystins (cyanobacteria hepatotoxins) bioaccumulation in fish and crustaceans from Sepetiba Bay (Brasil, RJ). Toxicon 42, 289–295.
Malbrouck, C., Kestemont, P., 2006. Effects of microcystins on fish. Environ. Toxicol. Chem. 25, 72–86.
Mohamed, Z.A., Carmichael, W.W., Hussein, A.A., 2003. Estimation of microcystins in the freshwater fish *Oreochromis niloticus* in an Egyptian fish farm containing a Microcystis bloom. Environ. Toxicol. 18, 137–141.
Moriarty, D.J.W., Darlington, P.E.C.J., Dunn, I.G., Moriarty, M.C., Tevlin, M.P., 1973. Feeding and grazing in lake george, Uganda. Proc. Roy. Soc. London 184, 299–319.
Moriarty, D.J.W., Moriarty, C.M., 1973. The assimilation of carbon from phytoplankton by two herbivourous fishes: *Tilapia nilotica* and *Haplochromis nigripinnis*. J. Zool. 171, 41–55.
Nagayi-Yawe, K.J., Ogutu-Ohwayo, R., Kizito, Y.S., Balirwa, J.S., 2006. Population characteristics of *Oreochromis esculentus* in the Victoria and Kyoga lake basins. Implications for conservation and improvement of the stocks: Afr. J. Ecol. 44, 423–430.
Njiru, M., Okeyo-Owuor, J.B., Muchiri, M., Cowx, I.G., 2004. Shifts in the food of Nile tilapia, *Oreochromis niloticus* (L.) in Lake Victoria, Kenya. Afr. J. Ecol. 42, 163–170.
Northcott, M.E., Beveridge, M.C.M., Ross, L.G., 1991. A laboratory investigation of the filtration and ingestion rates of the tilapia, *Oreochromis niloticus*, Feeding on 2 species of blue-green-algae. Environ. Biol. Fishes 31, 75–85.
Ochumba, P.B.O., 1990. Massive fish kills within the Nyanza Gulf of lake Victoria, Kenya. Hydrobiologia 208, 93–99.
Ochumba, P.B.O., Kibaara, D.I., 1989. Observations on blue-green algal blooms in the open waters of Lake Victoria, Kenya. Afr. J. Ecol. 27, 23–34.
Okello, W., Portmann, C., Erhard, M., Gademann, K., Kurmayer, R., 2009. Occurrence of microcystin-producing cyanobacteria in Ugandan freshwater habitats. Environ. Toxicol. in press, doi:10.1002/tox.20522.
R Development Core Team, 2008. R. A Language and Environment for Statistical Computing. R Foundation for Statistical Computing, Vienna, Austria.
Sekadende, B.C., Lyimo, T.J., Kurmayer, R., 2005. Microcystin production by cyanobacteria in the Mwanza Gulf (Lake Victoria, Tanzania). Hydrobiologia 543, 299–304.
Semyalo, R., Rohrlack, T., Naggawa, C., Nyakairu, G.W., 2010. Microcystin concentrations in Nile tilapia (*Oreochromis niloticus*) caught from Murchison Bay, Lake Victoria and Lake Mburo: Uganda. Hydrobiologia 638, 235–244.
Tencalla, F.G., Dietrich, D.R., Schlatter, C., 1994. Toxicity of *Microcystis aeruginosa* peptide toxin to yearling rainbow-trout (*Oncorhynchus-Mykiss*). Aquat. Toxicol. 30, 215–224.
Turker, H., Eversole, A.G., Brune, D.E., 2003. Filtration of green algae and cyanobacteria by Nile tilapia, *Oreochromis niloticus*, in the partitioned aquaculture system. Aquaculture 215, 93–101.
Verschuren, D., Johnson, T.C., Kling, H.J., Edgington, D.N., Leavitt, P.R., Brown, E.T., Talbot, M.R., Hecky, R.E., 2002. History and timing of human impact on Lake Victoria, East Africa. Proc. Roy. Soc. London Ser. B – Biol. Sci. 269, 289–294.
Wiegand, C., Pflugmacher, S., 2005. Ecotoxicological effects of selected cyanobacterial secondary metabolites a short review. Toxicol. Appl. Pharmacol. 203, 201–218.