Food web structure and mercury transfer in two contrasting Ugandan highland crater lakes (East Africa)

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Abstract

Volcanic crater lakes scattered throughout western Uganda are important local sources of water and fish. Two representative but contrasting crater lakes near the Kibale National Park were sampled in 2000; the hyper-eutrophic Lake Saka, which is highly affected by agricultural practices, and the mesotrophic Lake Nkuruba that is still surrounded by intact forest. The food web structures in these two lakes were assessed using stable nitrogen (δ^{15}N) and carbon (δ^{13}C) isotope analyses, and the mercury (THg) transfer patterns were quantified. The δ^{15}N results indicate that food webs in both lakes are abbreviated, with only one to two trophic levels from primary consumers. The Lake Saka biota had distinctively enriched δ^{13}C values compared with those in Lake Nkuruba, which may be due to ^{12}C-limited phytoplankton blooms in this lake. In Lake Nkuruba, two introduced tilapiine species and the introduced guppy *Poecilia reticulata* fed predominantly upon invertebrates and decomposed terrestrial plant material. In Lake Saka, the introduced Nile perch *Lates niloticus* appeared to occupy the top trophic position, but stable isotope values of the endemic haplochromine cichlids exclude those as Nile perch prey items. THg was found to biomagnify through the food web, reaching highest concentrations in *P. reticulata* in Nkuruba, which tended to be higher than for *L. niloticus* in Saka, suggesting increased bioavailability of THg in Nkuruba. Maximum THg concentrations in fish never approached WHO recommended guidelines (200 ng g^{-1}) designed to protect at-risk groups.

Key words: haplochromine cichlids, mercury, Nile perch, stable nitrogen and carbon isotopes, tilapia

Résumé

Les lacs de cratère éparpillés dans tout l'Ouest ougandais sont d'importantes sources locales d'eau et de poissons. En 2000, on a échantillonné deux lacs de cratères représentatifs quoique différents situés près du Parc National de Kibale: le lac Saka, hyper-eutrophique, qui subit fortement l'impact de pratiques agricoles et le lac Nkuruba, mésotrophique, qui est encore entouré de forêt intacte. Les structures du réseau trophique de ces deux lacs ont été évaluées au moyen d'analyses des isotopes stables d'azote (δ^{15}N) et de carbone (δ^{13}C), et les patterns de transfert du mercure (THg) ont été quantifiés. Les résultats δ^{15}N indiquent que les réseaux trophiques des deux lacs sont raccourcis, avec seulement un à deux niveaux trophiques à partir des consommateurs primaires. Le biote du lac Saka a des valeurs de δ^{13}C distinctement enrichies en comparaison de celles du lac Nkuruba, ce qui est peut-être dû à la floraison limitée par le ^{12}C du phytoplancton dans ce lac. Dans le lac Nkuruba, deux espèces de tilapias introduites et le guppy introduit *Poecila reticulata* se nourrissent principalement d'invertébrés et de matière végétale terrestre décomposée. Dans le lac Saka, la perche du Nil *Lates niloticus*, introduite, semble occuper la position trophique la plus haute, mais les valeurs des isotopes stables des cichlidés haplochromines endémiques excluent qu'ils soient la proie des perches du Nil. On a découvert que le THg était bio-magnifié dans le réseau alimentaire, atteignant les plus fortes concentrations chez *P. reticulata* à Nkuruba, qui tend à être plus élevé que chez *L. niloticus* à Saka, ce qui suggère une bio-disponibilité accrue du THg à Nkuruba. Les concentrations maximales de Thg dans les poissons n'ont jamais approché les valeurs recommandées par les directives de l'OMS (200 ng G^{-1}), fixées pour protéger les groupes à risques.

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Introduction

Volcanic crater lakes are common throughout the foothills of the Rwenzori Mountains in the Kibale and Kigezi districts of south-western Uganda, and have been the focus of numerous limnological studies (Beadle, 1966, 1981; Melack, 1978; Kizito *et al.*, 1993; Chapman *et al.*, 1998). These crater lakes serve as an important source of water and fish to people in the region. The lakes and their faunas are increasingly threatened by human activities, including deforestation for fuel wood (The Republic of Uganda, 1997) and agricultural runoff (Chapman *et al.*, 1998; Crisman *et al.*, 2001). There are, however, national parks and conservation areas throughout the region preserving portions of the tropical highland rain forest ecosystem. Within this mix of highly impacted and conserved regions, these crater lakes provide natural microcosms for examining a diverse range of East African environmental issues.

Contaminant concentrations and distribution in those crater lakes have not been studied, particularly the potent human neurotoxicant methylmercury (MeHg), which normally constitutes at least 90% of the total mercury (THg) burden in fish (Bloom, 1992). As MeHg biomagnifies through food webs, concentrations in top predator fish can be three orders of magnitude higher than those in the ambient water (Meili, 1997). As such, it is important to determine THg concentrations in fish from regions where human reliance on fish protein is high. Because biomagnification of MeHg to high concentrations in top predators in aquatic ecosystems is influenced by food web structure and length (Cabana *et al.*, 1994), we analysed stable nitrogen (δ^{15}N) and carbon (δ^{13}C) isotopes in fish and their food. Analyses of δ^{15}N and δ^{13}C are now a standard technique in food web studies, and have been successfully applied to aquatic ecosystem research globally. Typically, δ^{15}N values have been used to characterize relative trophic position while δ^{13}C values have been used to determine the sources and flow of carbon in a food web (Cabana & Rasmussen, 1994; Hecky & Hesslein, 1995).

We present the first data on food web structure and THg from highland tropical crater lakes in Uganda. Lake Nkuruba is located in a locally developed conservation area that maintains a rain forest ecosystem within its rim (Chapman *et al.*, 1998). Lake Saka has been severely affected by extensive agriculture which has led to severe eutrophication of the lake over the past half century (Crisman *et al.*, 2001).

Methods

In Lake Nkuruba (Table 1; Fig. 1), all three fish species, *Tilapia zillii* (Gervais 1874), *Oreochromis leucostictus* (Trewavas 1933), and the guppy *Poecilia reticulata* (Peters 1859) were introduced, likely by missionaries at some unknown date (Chapman *et al.*, 1998). This lake is anoxic below 9–15 m. There are no aquatic macrophytes, but tropical rain forest trees closely surround the lake, with dense depositions of tree litter within the lake. Chlorophyll is fairly low (4–12 mg l^{-1}; Table 1), and total phosphorous measured in 1990–1992 ranged from 38 to 43 μg l^{-1}, while nitrate was not detected (Kizito *et al.*, 1993), and secchi depths ranged from 1.5 to 5 m, making this lake mesotrophic. The crater rim around Lake Nkuruba is high, extending to 45 m, which blocks direct light to the lake for much of the day.

Lake Saka (Table 1; Fig. 1), 17 km from Lake Nkuruba, was stocked with Nile perch *Lates niloticus* (Linnaeus 1758) in the early 1970s and with Nile tilapia *O. niloticus niloticus* (Linnaeus 1758) at some unknown date. Fishermen exploit the lake and sell the *L. niloticus* in nearby Fort Portal, although *L. niloticus* and *O. niloticus* have been increasingly difficult to catch, suggesting severe stock depletion. The lake harbours a flock of haplochromine cichlids, with at least two potentially endemic species and one widespread species *Astatoreochromis alluaudi* (Pellegrin 1904), as well as a small number of other indigenous fishes such as *Barbus neumaeyari* (Fischer 1884). Lake Saka

Table 1 Selected water quality parameters for lakes Saka and Nkuruba. Superscripts indicate source of data

Parameter	Lake Saka	Lake Nkuruba
Latitude/longitude	0°40′N, 30°15′E	0°32′N, 30°19′E
Elevation (m)	1520	1519
Surface area (ha)	15[a]	3[b]
Maximum depth	12[a]	38[b]
Chlorophyll *a* (μg l^{-1})	134[b]	4–12[b]
Surface dissolved oxygen (mg l^{-1})	6–15[c]	4–8[b]
Secchi depth (m)	0.3–0.7[c]	1.5–5[b]
Surface pH	7.7[c]	8.2[b]
Surface conductivity (umho cm^{-1})	582–623[c]	325[d]
Surface temperature (°C)	21–25[c]	22–24[d]

[a]Melack (1978), [b]L. Chapman, unpublished data, [c]Crisman *et al.* (2001), [d]Chapman *et al.* (1998).

Fig 1 Diagram of Lake Nukurba (lower left) and Lake Saka (lower right), and their location in Uganda. The grey areas around Lake Saka are wetlands

has a weak rim, 3–15 m high, so is exposed to direct light all day. The drainage basin, including several wetland areas, around the lake has been almost totally cleared for agricultural production, which has led to 'hyper-eutrophic' conditions with high chlorophyll ($>130 \ \mu g \ l^{-1}$) and low secchi depths ($\sim$0.5 m). Lake Saka has recently experienced increased phytoplankton productivity and severe algal blooms (Crisman *et al.*, 2001).

Fish were sampled in the months of May and July of 2000 using gill nets and funnel traps. With the exception of *A. alluaudi*, the haplochromine species in Lake Saka have not yet been formally identified; so descriptive names have been assigned to many species prior to the completion of taxonomic and genetic analyses (L. J. Chapman, unpubl. data). The diets of many Saka haplochromine species have also not yet been determined in taxonomic detail, but are known to be predominately primary consumers (O. Seehausen, Department Biological Sciences, University of Hull, personal communication). Plankton in Lake Saka were collected with a plankton net while benthic algae were scraped off rock surfaces. In Lake Nkuruba, terrestrial tree leaf litter deposited within the lake (*Prunus africana*, *Strychnos mitis* and *Erythrina abyssinica*), invertebrates, and tadpoles were collected in the littoral zone with kicknets. *Poecilia reticulata* are viviparous (live-bearing), and live young were removed from two adults as separate samples. Samples were held in acid-cleaned aluminium

(Al) foil trays, and dried for several days in a field 'drying oven' which was a metal closet containing mesh trays and a 60 W light bulb. Once dried, the biotic samples were double-wrapped in clean Al foil and stored in self-sealing bags with bagged desiccant crystals to prevent mould growth.

Samples were transported to Canada for analyses. Total Hg (THg) analyses on the fish samples were performed in the clean-room laboratory of the Dorset Research Centre, Ontario Ministry of the Environment, Dorset, ON, Canada. MeHg was not analysed due to unavailability of equipment. Dry weight samples were converted to wet-weight samples using the standard literature assumption of 80% water. (Water content of invertebrates can vary from 40% to 95%, averaging 80%, but there were no means of preweighing samples at the field station prior to drying.) Ultra-clean protocols were employed throughout the processing (Ontario Ministry of Environment, 1999) and are detailed in Campbell *et al.* (2003b). The Hg concentration in each biotic sample was determined via atomic fluorescence spectroscopy using the purge-and-trap procedure (Ontario Ministry of Environment, 1999). Samples were dried, weighed and hot-digested in a nitric-sulphuric acid mixture. Also included were the National Research Council (Canada) certified reference materials, DORM-2 (4.64 ± 0.26 mg Hg kg^{-1}, recovery, 110–125%) and DOLT-2 (2.14 ± 0.28 mg Hg kg^{-1}, recovery, 97–120%), as well as blanks (<0.5 pg total). The detection limit was

10 pg total Hg per sample. Replicate samples from archived Lake Victoria *L. niloticus* and *O. niloticus* were included in every run to determine between-run variation, which was 2–7%. The results reported here were not corrected for recovery.

To determine food web structure and biomagnification rates, stable nitrogen and carbon isotope ratios were analysed. The protocols for stable isotope analyses are described in detail in Campbell, Hecky & Wandera (2003c). Small subsamples were dried and ground. Stable nitrogen and carbon isotope ratios were measured concurrently using a Micromass VG-Isochrom Continuous Flow Isotope Ratio Mass Spectrometer at the Environmental Isotope Laboratory, University of Waterloo. The ratios of stable nitrogen isotopes were measured against nitrogen gas (N_2) in ambient air, as a reference, while stable carbon isotope ratios were measured relative to a PeeDee belemnite (CO_2) equivalent standard. The delta notation (δ) is used to indicate the part per thousand (‰) difference in the isotopic ratio of the sample from the reference standard. Analytical standards were inserted in every run, and included both International Atomic Energy Agency and in-house walleye and cellulose standards. Replicates of an archived Lake Victoria *L. niloticus* sample were included in every run to determine between-run variation (Campbell *et al.*, 2003c). Standard deviations for the standards were ±0.3‰ for $\delta^{15}N$ and ± 0.2‰ for $\delta^{13}C$, while standard deviations for replicate samples were ±0.16‰ for $\delta^{15}N$ and ±0.24‰ for $\delta^{13}C$.

Data were analysed in SYSTAT 10.0 for Windows (SPSS Inc.), with significance set at $P \leq 0.05$. The L_T of fish was selected as size parameter because it is easiest to measure accurately in the field by both scientists and fishermen and allows for recommendations on size limits for fish consumers in Uganda, if necessary. THg was log-transformed to normalize the data. Analysis of food web biomagnification of THg (using $\delta^{15}N$) in this study is limited to fish for two reasons. First, THg in invertebrates and primary producers can vary widely with season, species and environmental conditions, plus the proportion of bioavailable MeHg in invertebrates and primary producers can vary from 10% to 100% (Bloom, 1992; Lasorsa & Allen-Gil, 1995; Erickson *et al.*, 2003). However, THg in fish is usually consistently 85–100% MeHg (Bloom, 1992), allowing for relative ease of biomagnification analyses. Secondly, logistics made it difficult to collect a balanced set of samples from each lake representing entire food web (especially for invertebrates), and as such, fish formed the best subsample set for comparative purposes.

Results and discussion

This study represents the first attempt to quantify food web interactions and mercury transfer patterns in African tropical highland crater lakes. The configuration of the food web structure in both lakes indicates a very short food chain length, with all fish having only 1–2 trophic levels above primary producers (Fig. 2, Table 2). Assuming the
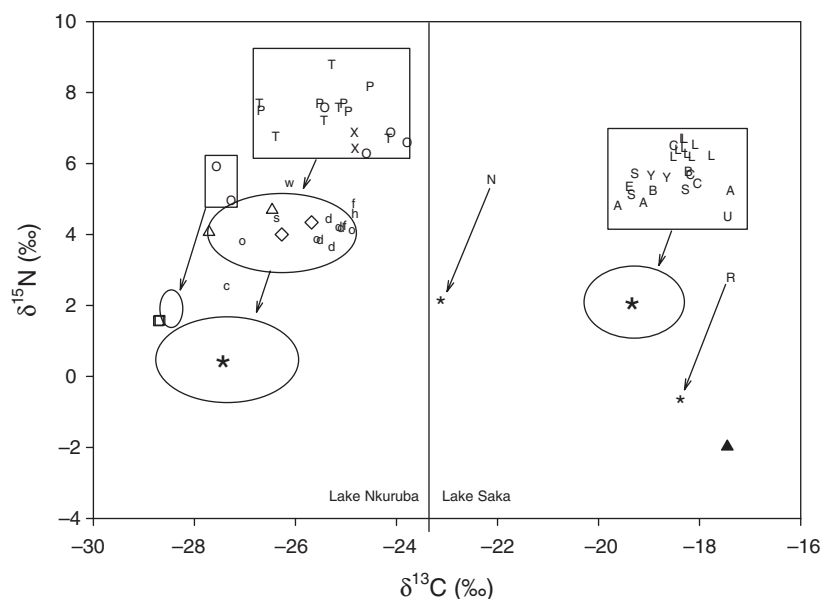
Fig 2 The relationship between $\delta^{15}N$, indicating trophic position and $\delta^{13}C$, indicating dietary carbon, for 27 taxonomic groups from lakes Nkuruba (left) and Saka (right). Each group is represented by a code defined in Table 2. Note the clear delineation in $\delta^{13}C$ signatures between lakes. Rectangles indicate isotopic clusters of fish, while circles and asterisks represent the estimated isotopic ranges of their diet

Table 2 Fish, invertebrates and plant species collected in this study, with assigned codes used in the figures. The haplochromine cichlids in Lake Saka have not yet been formally taxonomically categorized, so are temporarily identified by their color patterns and sex (F = female, M = male). Known feeding patterns are listed, along with the number of samples from each lake, mean values ± standard deviation for THg, δ^{13}C and δ^{15}N values. (Many of the species collected have not been studied in detail, so if dietary patterns are yet not known, a description of the sample is listed.)

Name	Code	Description	N	THg (ng g^{-1}, w/w)	δ^{13}C (‰)	δ^{15}N (‰)
Lake Saka						
Barbus neumaeyari	N	Benthivore	1	14.75	−22.12	5.56
Lates niloticus	L	Omnivore	9	14.00 ± 5.89	−18.24 ± 0.22	6.41 ± 0.20
Astatoreochromis alluaudi	A	Molluscivore	3	11.42 ± 7.70	−18.71 ± 1.17	4.99 ± 0.23
'Brassy Unknown' (F)	U	Haplochromine	1	8.38	−17.44	4.50
'Blue Unknown' (F)	E	Haplochromine	1	7.24	−19.39	5.34
'Blue Small Eye' (F)	S	Haplochromine	3	4.86 ± 1.66	−18.97 ± 0.60	5.37 ± 0.31
'Brassy Large Eye' (F)	B	Haplochromine	2	3.01	−18.92 to −18.22	5.25–5.76
'Blue Red Chest' (M)	C	Haplochromine	3	3.33 ± 0.73	−18.24 ± 0.24	5.88 ± 0.57
'Yellow Red Chest' (M)	Y	Haplochromine	2	2.5–2.7	−18.96 to −18.65	5.61–5.66
'True Blue' (M)	T	Haplochromine	1	–	−17.95	5.34
Oreochromis niloticus	R	Detritivore	1	2.79	−17.38	2.78
Benthic algae	▲	Algae	1	1.19	−11.50	−1.14
Pelagic algae	▲	Algae	1	1.08	−17.45	−1.98
Lake Nkuruba						
Poecilia reticulata	P	Zoobenthivore	5	22.65 ± 5.22	−25.34 ± 0.83	7.70 ± 0.28
Tilapia zillii	T	Detritivore	6	16.86 ± 9.40	−25.52 ± 0.92	7.46 ± 0.77
Oreochromis leucoticus	O	Detritivore	6	13.12 ± 6.70	−25.46 ± 1.62	6.36 ± 0.90
Anura (frog)	f	Tadpole	2	7.47–9.42	−25.02 to −24.94	4.24–4.86
P. reticulata young	X	Viviparous	2	0.33–2.02	−24.83 to −24.82	6.42–6.86
Hirudinea (leech)	h	Invertebrate	1	9.21	−24.82	4.58
Zygoptera (damselfly)	d	Invertebrate	5	3.18 ± 1.40	−25.27 ± 0.17	4.08 ± 0.32
Anisoptera (dragonfly)	o	Invertebrate	3	3.06 ± 1.76	−25.85 ± 1.11	3.95 ± 0.16
Chironomidae	c	Invertebrate	1	1.45	−27.36	2.55
Gerridae (waterstrider)	w	Invertebrate	1	n.d.	−26.12	5.47
Gastropoda (snail)	s	Invertebrate	1	n.d.	−26.37	4.49
Prunus africana	□	Tree leaf	2	2.75–2.92	−28.71 to −28.68	1.57–1.58
Strychnos mitis	△	Tree leaf	2	0.65–0.81	−27.71 to −26.46	4.07–4.69
Erythrina abyssinia	◇	Tree leaf	2	n.d.	−26.27 to −25.68	4.00–4.34

trophic isotopic fractionation rates in lakes Saka and Nkuruba are similar to those found for Lake Victoria: 3.6‰ and 1.0‰ for δ^{15}N and δ^{13}C, respectively (Campbell *et al.*, 2003c), it is possible to estimate the approximate isotopic values of the fish's diet, as indicated by circles and asterisks in Fig. 1.

In Lake Nkuruba, there are no piscivorous fish. The detritivore *T. zillii* and *O. leucostictus*, and the zoobenthivorous *P. reticulata* shared overlapping δ^{13}C and δ^{15}N values (Table 2; Fig. 2). The hypothesized diets of Nkuruba invertebrates, as indicated by an asterisk, do not appear to support feeding upon terrestrial leaf detritus based on their isotopic composition (Fig. 2), but their diets likely include epiphytes and algae growing on litter where the invertebrates were collected. The inclusion of most invertebrates and the leaves from the N-fixing species *S. mitis* and *E. abyssinica* as dietary items for the fish *T. zillii*, *P. reticulata*, and most *O. leucostictus* is supported by the overlap of predicted and actual isotopic values of the dietary items (Fig. 2). Furthermore, there are two *O. leucostictus* with exceptionally low δ^{15}N and δ^{13}C values (~5‰; c. −28‰), which separates these individuals from the rest of the fish. *Prunus africana* δ^{15}N and δ^{13}C values are nearest to the hypothesized dietary range of those *O. niloticus* (Fig. 2). *Prunus africana* leaves are high in cyanogeneic glycosides, precursors of toxic cyanide compounds (Chapman & Chapman, 2002). Extrapolating from C : N ratios, *P. africana* (11.9–12.5) and *E. abyssinica*

(11.1–13.8) may have a higher protein content than *S. mitis* (15.6–18.9; L. M. Campbell unpubl. data). Because these two *O. leucostictus* are also the largest of their species, it is possible that larger individuals may have increased tolerance for glycosides, allowing them to consume more nutritious leaves, a hypothesis which deserves further examination.

In Lake Saka, *L. niloticus* occupied the highest trophic position, as indicated by their high δ^{15}N values around 6.4‰ (Fig. 2). However, the δ^{15}N values of the haplochromine cichlids species were only 0.5–1.5‰ lower than those for *L. niloticus*, negating the potential of haplochromines as *L. niloticus* prey (Table 2, Fig. 2). *Oreochromis niloticus* had the lowest δ^{15}N value of all fish species, while *B. neumayeri* had considerably lower δ^{13}C values than the other fish species (Fig. 2). Asterisks in Fig. 1 indicate possible dietary ranges for the fish species. Only pelagic algae come closest to possible dietary range, indicating that pelagic sources of carbon may be important to the Lake Saka food web.

The δ^{13}C values of all Lake Nkuruba specimens were markedly distinct (<−23‰) from those for Lake Saka (>−23‰; Fig. 2). This suggests that the basal isotopic values are different in each lake. This may be related to the trophic status of each lake, and the sources of carbon. Allochthonous carbon from tree litterfall is isotopically important in Lake Nkuruba, while pelagically produced carbon is probably more important in Lake Saka. Variation

in algal fixation and photosynthesis of available light can also significantly affect the basal isotopic values of phytoplankton (Fogel & Cifuentes, 1993; Hecky & Hesslein, 1995). The high algal biomass in Lake Saka (Crisman *et al.*, 2001) may be leading to increased demand for CO_2 and potentially N by photosynthetic algae, requiring additional N-fixation and bicarbonate uptake (Muggide, 2001). This would lead to lower δ^{15}N and enriched δ^{13}C values entering the food web relative to a less eutrophic lake. This is supported by similar results from Lake Victoria: the biota from the more productive Napoleon Gulf, with chlorophyll *a* ranging from 13 to 50 mg m^{-3}, had significantly lower δ^{15}N (mean difference of 3.14‰) and δ^{13}C values (mean difference of 4.02‰) relative to the same species in the less eutrophic Winam Gulf, which has chlorophyll *a* values range from 8 to 20 mg m^{-3} (Campbell *et al.*, 2003c).

It is usual for larger fish to exhibit ontogenetic changes in δ^{15}N, δ^{13}C and THg burdens, as evidenced by significant regressions listed in Table 3. This can be attributed to shifts in trophic level of prey types (larger prey tend to be derived from higher trophic levels) and to older fish accumulating THg over a longer period of time (Cabana *et al.*, 1994). In Lake Saka, log-THg concentrations in *L. niloticus* are correlated with δ^{15}N values but not with δ^{13}C values. This suggests an increasing THg burden with increasing trophic level, but still consuming prey from the same basic carbon

Table 3 Regressions of log-THg against δ^{15}N and δ^{13}C values for all fish from Saka and Nkuruba are listed. One outlier for Nile perch was removed. Additionally, regressions for log-THg, δ^{15}N and δ^{13}C values against L_T are also shown for individual fish species in each lake. For each regression, the sample size (n), the intercept, slope and adjusted r^2 are listed. The values listed in bold are significant at $P < 0.05$

Lake	Regression	Object	n	Intercept	Slope	r^2_{adj}	P-value
Saka	log THg versus δ^{15}N	All fish	27	0.075	0.138	0.107	0.061
Nkuruba			**17**	**0.190**	**0.140**	**0.273**	**0.032**
Saka	log THg versus δ^{15}N	*L. niloticus*	**8**	**6.008**	**0.025**	**0.694**	**0.010**
	log THg versus δ^{13}C	*L. niloticus*	8	−18.11	−0.009	−0.073	0.520
Nkuruba	log THg versus L_T	*O. leucostictus*	**6**	**0.843**	**0.020**	**0.611**	**0.041**
		T. zillii	**6**	**0.753**	**0.034**	**0.338**	**0.112**
		P. reticulata	**5**	**1.078**	**0.071**	**0.549**	**0.034**
		Zygoptera	5	0.680	−0.163	0.000	0.559
Nkuruba	δ^{13}C versus L_T	*O. leucostictus*	**6**	**−23.07**	**−0.187**	**0.745**	**0.017**
		T. zillii	6	−23.81	−0.148	0.532	0.062
		P. reticulata	5	−25.65	0.080	0.000	0.869
		Zygoptera	5	−25.21	−0.050	0.000	0.836
Nkuruba	δ^{15}N versus L_T	*O. leucostictus*	6	6.890	−0.041	0.000	0.488
		T. zillii	6	0.046	6.931	0.000	0.574
		P. reticulata	5	7.465	0.063	0.000	0.702
		Zygoptera	**5**	**3.222**	**0.658**	**0.717**	**0.045**

sources. Furthermore, the slope of the log-THg : δ^{15}N regression for all fish of the same species can indicate the rate of THg uptake and the influence of changes in prey selection on THg uptake. The log-THg : δ^{15}N slope for Lake Saka *L. niloticus* (0.387) is higher than those seen for the same fish species (0.066–0.092) from Lake Victoria (Campbell *et al.*, 2003b). This suggests that the rate of THg uptake with trophic position is quite different in Lake Saka than in Lake Victoria, implying that there is either a more rapid shift in prey selection with size in Lake Saka due to a more diverse prey base, or a high degree of stunting in the Lake Saka *L. niloticus* population resulting in less tissue growth and more concentrated THg per unit tissue mass.

There may be two factors in Lake Saka affecting the growth of Nile perch: poor dietary quality and chronic exposure to cyanobacterial toxins, which are known to affect fish physiology (Oberemm *et al.*, 1999). Preliminary assessment of water samples using the Microtox© semi-quantitative screening kit (AZUR Environmental, Newark, DE, U.S.A.) has indicated that concentrations of the cyanobacterial toxin, microcystin, exceed 3.0 p.p.b. (L. M. Campbell and L. J. Chapman, unpubl. data). Those levels are known to delay fish development and hatching rates as well as interfere with invertebrate physiology (Oberemm *et al.*, 1999; Pietsch *et al.*, 2001). In contrast, Lake Nkuruba only had microcystin concentrations <0.5 p.p.b. The growth of *L. niloticus* in Lake Saka may be stunted due to high concentrations of algal toxin and resultant poor dietary quality throughout the food chain.

In Lake Nkuruba, the log-transformed THg concentrations and δ^{13}C values in *O. leucostictus* were positively correlated with L_T (Table 3); although there were no significant correlations between δ^{15}N values and L_T for any fish species. This suggests that increasing THg in *O. leucostictus* is not due to significant ontogenetic shifts in trophic position, but simply to age (as indicated by size) and dietary shift linked with increasing size of the consumer. Previously, we discussed the possibility of large *O. leucostictus* consuming a greater dietary proportion of *P. africana* leaves due to the higher nutritional quality and despite the elevated cyanogenic glycoside concentrations. As the leaves of *P. africana* have a higher THg concentration than those of other leave species, the increasing THg concentrations with size in *O. leucostictus* is consistent with the presence of more *P. africana* leaves in the diet of larger *O. leucostictus.*

In Lake Nkuruba, the young removed from two adult *P. reticulata* had similar δ^{13}C values but slightly lower δ^{15}N values (Table 2) than the adults. Furthermore, the *P. reticulata* young had much lower THg concentrations (0.3–2.0 ng g^{-1}) than their parents (22.7 ng g^{-1}; Table 2). This indicates that despite the isotopic link in nutrient transfer between adult and young *P. reticulata*, maternal transfer of THg to viviparous young from the parent may be limited.

Zygoptera (damselflies) showed a positive relationship between size and δ^{15}N, but there were no relationships between size, THg burdens and δ^{13}C values (Table 3). This seems to indicate that damselflies will increase their trophic level with size (i.e. shift to larger prey), but the underlying basal carbon source and the mean THg burden in prey do not change.

In Nkuruba, significant correlations were observed for log-THg versus δ^{15}N regressions among all combined fish species, while Saka fish exhibited weakly significant regressions (Table 3, Fig. 3). This indicates that THg is biomagnifying through the food web in Nkuruba and probably in Saka, despite the very short food web length. The slope of the log-THg versus δ^{15}N regressions have been interpreted as a quantitative measure of biomagnification rate through the food web (Kidd, 1998). The slope values for Lake Saka and Lake Nkuruba (0.134 and 0.140 respectively) are lower or similar to published log-Hg : δ^{15}N slopes for other African lakes elsewhere, which range from 0.12 to 0.26, seen in other African lakes (Campbell *et al.*, 2003b, 2004; Kidd *et al.*, 2003). Worldwide, slopes range from 0.11 to 0.35 in marine and aquatic systems (Bowles *et al.*, 2001; Power *et al.*, 2002; Campbell *et al.*, 2005).

While the biomagnification rate of THg are similar in both lakes, Nkuruba fishes tended to have higher THg concentrations (13–23 ng g^{-1}) than Saka fishes (2–15 ng g^{-1}), even including the Saka *L. niloticus* (Table 2). This was surprising; the original hypothesis was that *L. niloticus* in Lake Saka would have the highest THg concentrations of all fish from both lakes. This was based on observations of some of the highest THg concentrations and trophic position consistently found for *L. niloticus* from other African lakes in Kenya and Uganda (Campbell, Hecky & Dixon, 2003a; Campbell *et al.*, 2003b,d, 2004). Instead, the detritus-feeding tilapiines and *P. reticulata* from Nkuruba tended to have higher THg concentrations than Saka fishes, which seem to point to more bioavailable THg at the base of the food web in Lake Nkuruba. The length of the food chain appears to be similar in both lakes (1–2 trophic levels). Food chain length has been invoked to explain higher THg in top trophic fish species: the longer

(a)

(b)
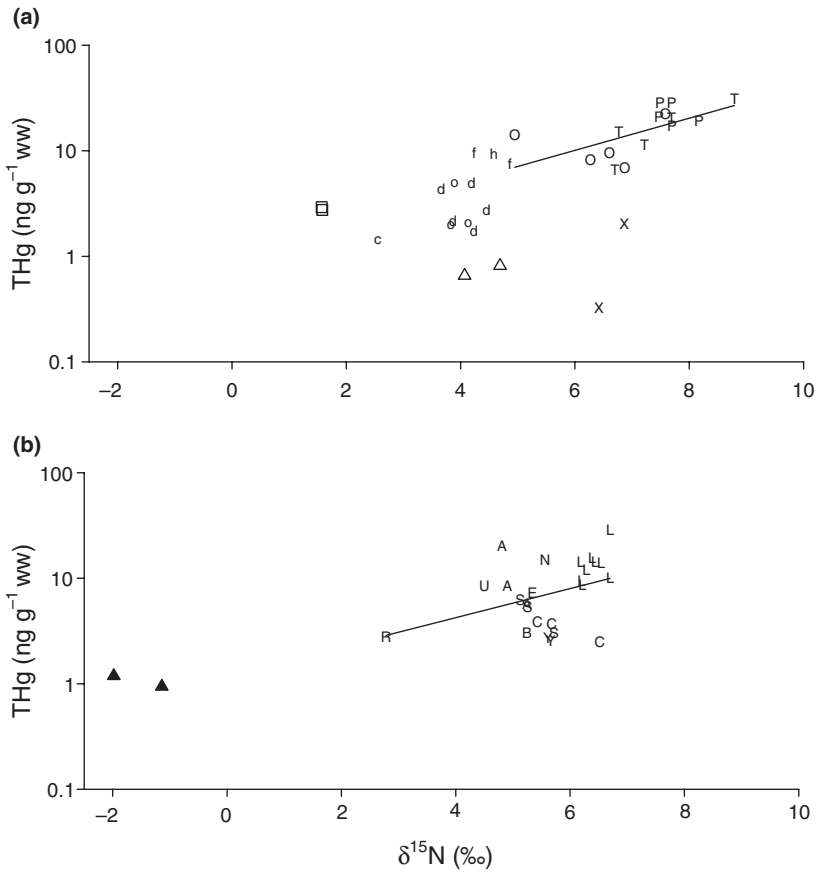
Fig 3 THg concentrations versus $\delta^{15}N$ values in the food web of Lakes Nkuruba (a) and Saka (b). Note the logarithmic scale for THg concentrations. Regression lines indicate significant relationships between log-THg and $\delta^{15}N$ values among all fish species in each lake. Each taxonomic group is represented by a code defined in Table 2

the food chain, the higher THg concentrations in top trophic predators (Cabana & Rasmussen, 1994), but does not seem to be a factor in this situation.

There are two possible environmental factors that could explain the apparent differential in THg concentrations in fish from each lake, if we assume that the bioavailability is an important factor and that the total input of THg to both lakes are atmospherically derived and constant across the region. The first factor could be the higher area of riverine wetlands surrounding Lake Saka relative to Lake Nkuruba (Crisman *et al.*, 2001). In East Africa, wetlands can have a high storage capacity for heavy metals (Kiremire, 1998; Makundi, 2001). Temperate wetlands and reservoirs are well known for being excellent sites of mercury methylation, thereby acting as mechanisms for increasing bioavailable MeHg for uptake by aquatic biota (Hecky *et al.*, 1991; St. Louis *et al.*, 1994). However, fish from wetland-rich regions in East Africa such as Lake Kyoga and Thruston Bay in Lake Victoria and from Tanzanian reservoirs have exceptionally low THg concentrations (Ikingura & Akagi, 2003;

Campbell *et al.*, 2004). As a result, it has been proposed that in East African wetlands, THg could be retained in sediments with high ferric content, removing Hg from *in-situ* methylation processes and in turn, made less bio-available to biota (Campbell *et al.*, 2003a; Ikingura & Akagi, 2003). The second factor could be 'biomass dilution', the dilution of Hg in by higher densities of phytoplankton and organic matter. Meili, Iverfeldt & Håkanson (1991) found that the uptake of THg in fish was inversely proportional to the biomass at the base of the food web. This hypothesis was recently supported by laboratory studies examining THg uptake in zooplankton relative to phytoplankton biomass in aquaria (Pickhartdt *et al.*, 2002). Lake Saka is much more eutrophic, with higher chlorophyll concentrations than Lake Nkuruba (Table 1). Subsequently, the higher algal biomass in Lake Saka exposed to constant ambient Hg concentrations, could be leading the 'biomass dilution' of Hg within the higher algal biomass, resulting in the introduction of lower Hg concentrations to primary producers at the base of the food web.

THg concentrations in all fish species from lakes Nkuruba and Saka are significantly below the World Health Organization's recommended limit (200 ng THg per gram wet weight) for groups at risk, including frequent fish consumers, pregnant women and young children (World Health Organization, 1990). Low fish THg concentrations are common for most African aquatic ecosystems, especially those with short food chain lengths (Campbell *et al.*, 2003a). Fish from lakes Saka and Nkuruba do not represent any significant human or wildlife health risk in the Fort Portal region.

Acknowledgements

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