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Food web structure and mercury trophodynamics in two contrasting embayments in northern Lake Victoria

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ABSTRACT

Nearshore regions of lakes are important sources of fish, and can be strongly influenced by anthropogenic inputs of nutrients as well as contaminants. This study characterizes food web structure, mercury concentrations, and biomagnification of mercury in two embayments in northern Lake Victoria that differ in their connectivity to the open lake, trophic status, and the influence of local anthropogenic pollution. Murchison Bay is a semi-confined hypereutrophic bay in a densely populated region, while Napoleon Gulf is mesotrophic and is well flushed with water from the open lake. Based on stable carbon and nitrogen isotope analysis, food web structure was similar at both sites, with short food chains and conspecific fish occupying similar trophic positions. However, there were strong differences in net phytoplankton $\delta^{15}N$ and $\delta^{13}C$ between sites; net phytoplankton $\delta^{13}C$ was largely related to trophic status, while $\delta^{15}N$ values appeared to be influenced by inputs of human waste and the prevalence of biological nitrogen fixation. Total mercury (THg) concentrations in fish were consistently below 200 ng/g wet weight, and despite elevated THg concentrations in water in Murchison Bay, THg concentrations in net phytoplankton and fish from both embayments did not differ, highlighting that THg in water is not always a good predictor of concentrations in fish. We also observed that biomagnification of mercury was occurring at a lower rate in Murchison Bay than in Napoleon Gulf, and we propose that the hypereutrophic state of Murchison Bay may be acting to reduce potential Hg exposure for higher trophic level fish.

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Introduction

Over the past decade, studies in several East African lakes have greatly increased our understanding of mercury concentrations and trophodynamics in tropical African lakes (Campbell et al., 2003b, 2006, 2008; Kidd et al., 2003; Ramlal et al., 2003). In particular, several studies have characterized food web structure and mercury concentrations in aquatic biota in Lake Victoria, which is home to the world's largest freshwater lake fishery (Kolding et al., 2008) and has been strongly affected by cultural eutrophication and the proliferation of exotic species including Nile perch (*Lates niloticus*), Nile tilapia (*Oreochromis niloticus*) and the water hyacinth (Hecky et al., 2010). Studies of Hg in Lake Victoria have largely centered on two embayments: Napoleon Gulf (Campbell et al., 2003b, 2004) and Winam Gulf (Campbell et al., 2003b), with some data from other regions of the lake, as reviewed by Campbell et al. (2003a).

Another embayment of interest in Lake Victoria is Murchison Bay, a semi-confined, highly polluted embayment (Haande et al., 2011) that is home to a substantial fishery that serves a large urban market (the nearby city of Kampala, Uganda) and provides fish for export. However, despite the presence of an important fishery, there have been no studies of food web structure in Murchison Bay; and despite the high potential for Hg contamination given the urban and industrial surroundings of this embayment and a high local reliance on fish protein, mercury concentrations have not been reported for fish from Murchison Bay.

Stable carbon and nitrogen isotope analysis can be used to characterize food webs and trophic interactions (Fry, 1991; Peterson and Fry, 1987). Stable nitrogen isotopic ratios ($\delta^{15}N$) are used as an indicator of trophic level because $\delta^{15}N$ values increase with increasing trophic level due to trophic fractionation (Minagawa and Wada, 1984; Peterson and Fry 1987). Stable carbon isotopic ratios ($\delta^{13}C$) from consumed food are largely retained or only slightly enriched from one trophic level to the next, and these values are often used as an indicator of dietary

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carbon source, particularly with respect to the primary producers that support the food web (Cabana and Rasmussen, 1994; Hecky and Hesslein, 1995; Peterson and Fry, 1987). Stable isotope analysis has also been applied extensively in food web contaminant studies in arctic, temperate and tropical aquatic ecosystems (Atwell et al., 1998; Campbell et al., 2003b; Kidd et al., 1995) to evaluate trophic transfer and biomagnification of contaminants in aquatic food webs.

Here we characterize food web structure and mercury concentrations in two large embayments in northern Lake Victoria: Murchison Bay and Napoleon Gulf. Murchison Bay is heavily impacted by industrial and municipal discharges and is Uganda's major port for lake transport. The inclusion of Napoleon Gulf in this study provides a minimally impacted embayment for comparison with Murchison Bay and allows for examination of long-term temporal stability of food web structure and mercury concentrations (compared to earlier results reported by Campbell et al. (2003b) for samples collected in 1998). Our objectives were as follows: 1) to establish putative food web structure and fish trophic position using stable isotope analysis, 2) to characterize mercury concentrations in water and aquatic biota, and 3) to identify differences in baseline $\delta^{13}C$ and $\delta^{15}N$, food web structure, mercury contamination and mercury trophodynamics between the two study sites.

Methods

Study sites

Murchison Bay and Napoleon Gulf (Fig. 1, Table 1) are both located on the northern coast of Lake Victoria in Uganda. Murchison Bay is located in a densely populated urban area. This embayment provides water to and receives waste from Kampala, Uganda's largest city (projected 2012 population of 1.7 million; Uganda Bureau of Statistics, 2002). Murchison Bay is shallow, hypereutrophic, and is the site of an important fishery. The inner bay is connected to the main lake via a small channel and is poorly flushed. Meanwhile, Napoleon Gulf is mesotrophic/eutrophic, deeper, and is situated in a mixed urban and agricultural region. Napoleon Gulf is well flushed with water from offshore Lake Victoria due to the outflow of the Victoria Nile from this embayment (Fig. 1). In Murchison Bay, municipal and industrial sources contribute to very high total phosphorus concentrations (Table 1). Meanwhile, Napoleon Gulf has similar TP concentrations to open Lake Victoria (Hecky et al., 2010).

The anthropogenic input of nutrients and consequent eutrophication of Lake Victoria has been well documented (Hecky, 1993; Hecky et al., 2010; Verschuren et al., 2002). Although Napoleon Gulf, which is flushed by the Nile river outflow, has suffered this nutrient enrichment, it is not affected by local anthropogenic wastes to the same extent as the semi-confined and poorly flushed urbanized catchment of Murchison Bay.

Table 1
Select physicochemical properties of Inner Murchison Bay and Napoleon gulf (total phosphorus and nitrogen, chlorophyll, phytoplankton biomass (based on microscopy)), Secchi depth and temperature data are from Poste *unpublished data*.

Parameter	Inner Murchison Bay	Napoleon Gulf
Latitude	0°15′N	0°24′N
Longitude	32°39′E	33°14′E
Mean depth (m)	3.2	7.9
Site depth (m)	5.2	17.5
Total phosphorus (μg/L)	100.3 ± 22.5	60.0 ± 16.2
Total nitrogen (μg/L)	2108 ± 742	1644 ± 1022
Chlorophyll *a* (μg/L)	96.5 ± 38.1	24.7 ± 18.4
Phytoplankton biomass (mg/L)	155.3 ± 197.6	37.9 ± 29.2
Anabaena biomass (mg/L)	5.2 ± 4.3	10.0 ± 9.4
Microcystis biomass (mg/L)	99.4 ± 168.8	2.1 ± 2.5
Secchi depth (m)	0.72 ± 0.14	1.40 ± 0.23
Temperature (°C)	25.6 ± 0.5	25.7 ± 0.7
THg in water (ng/L)	1.30 ± 0.09 ($n = 3$)	0.53 ± 0.07 ($n = 3$)

Sample collection

Water and food web samples were collected from Murchison Bay and Napoleon Gulf between September 2008 and February 2009. Water samples for analysis of total mercury (THg) were collected at approximately 15 cm below surface. Certified trace-metal clean glass bottles were lowered to the sampling depth; then were opened, filled, and re-sealed at depth.

Plankton samples were collected (phytoplankton every two weeks; zooplankton on one occasion in Murchison Bay and three occasions in Napoleon Gulf) using vertical net hauls (20 μm mesh for phytoplankton, 80 and 153 μm mesh for zooplankton), and samples were subsequently filtered onto pre-combusted quartz-fibre filters (Whatman QM-A, nominal pore size 0.7 μm). Phytoplankton samples collected through net hauls will be referred to as "net phytoplankton", to distinguish between these samples and the phytoplankton community as a whole (which includes the <20 μm component). Debris was visually removed from plankton samples using clean forceps, and samples were examined microscopically to confirm sample composition. Benthic invertebrates were collected using a Ponar grab and shells were removed

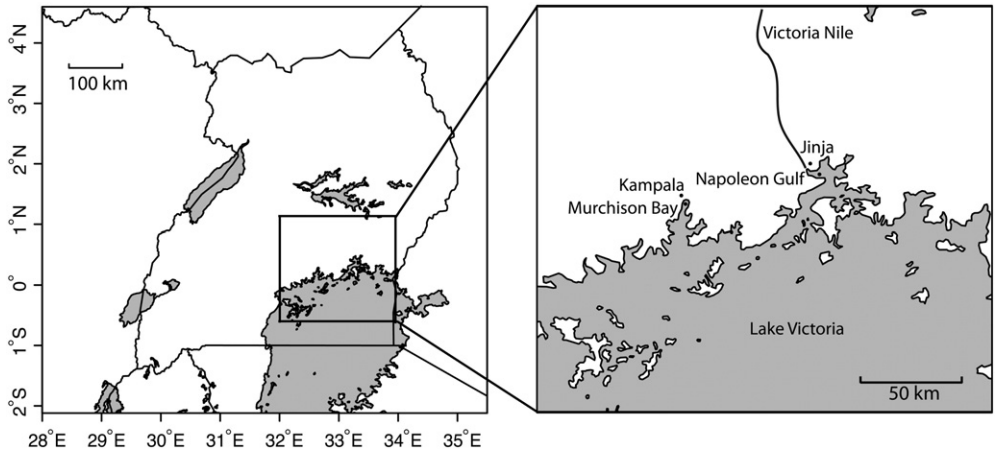

Fig. 1. Map of Uganda (left) and map of northern lake Victoria (right). The sampling sites in Inner Murchison Bay and Napoleon Gulf are shown. Note that the Victoria Nile (indicated on map) exits Lake Victoria via Napoleon Gulf.

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from gastropods before analysis. Plankton and benthic invertebrate samples were kept frozen until freeze-dried in Canada.

Fish were purchased directly from fishermen and general location of the catch was confirmed (although this was not always possible for Murchison Bay). Subsamples of epaxial muscle tissue were taken from fish and kept frozen until analysis in Canada. Where fish were too small to isolate epaxial muscle tissue, whole fillets of axial musculature were collected. For *Rastrineobola argentea* (where total length is typically less than 5 cm), fish were analyzed whole. Trace metal clean sampling protocols were used throughout.

Sample analysis

Stable carbon ($\delta^{13}C$) and nitrogen ($\delta^{15}N$) isotopic ratios were determined for all fish and food web samples as described in Campbell et al. (2003d). Stable isotope analysis was carried out at the Environmental Isotope Laboratory at the University of Waterloo. To determine variability between runs, standards for carbon (IAEA-CH6 (sugar), EIL-72 (cellulose) and EIL-32 (graphite)) and nitrogen (IAEA-N1 and IAEA-N2, both ammonium sulphate) were analyzed. Mean standard deviations from expected values for standard reference materials were ± 0.2‰ for $\delta^{13}C$ and ± 0.3‰ for $\delta^{15}N$. One in every ten samples was run in duplicate, and mean standard deviations of samples run in duplicate were ± 0.04‰ and ± 0.21‰ for $\delta^{15}N$ and $\delta^{13}C$ respectively.

Mercury analyses were carried out at the Canadian Centre for Inland Waters (Burlington, Canada). Total mercury concentrations in water were determined using EPA method 1631 (U.S. EPA, 1999). NIST 1641c was used as a standard and was on average within 3.1 % of the expected value. Quality control acceptance criteria (U.S. EPA, 1999) were met for all sample runs, and it was not necessary to discard any sample data. The precision for samples run in duplicate was on average ± 10.0 % and the mean standard deviation for replicates within study sites was ± 0.06 ng Hg/L.

Total mercury (THg) concentrations in biotic samples were determined according to EPA Method 7473 (U.S. EPA, 1998), using a DMA-80 direct mercury analyzer. Fish tissue was analyzed wet, and net phytoplankton filters were analyzed whole. Blank filters were also analyzed in order to account for the trace amounts of mercury present on filters, and a filter blank correction of 0.03 ng Hg was applied. Dry-weight THg concentrations for benthic invertebrates and plankton were converted to wet-weight concentrations by multiplying by 0.25 and 0.1 respectively (Chapra, 1997; Marshall and Hall, 2004).

For THg analysis of biotic samples, standard reference materials (SRMs) were analyzed in each run in order to determine between-run variability. SRMs used included DORM-1 (recovery of 100.6 ± 6.0 % of the certified value), NIST 1556b (95.7 ± 1.9 %), TORT-2 (102.7 ± 5.4 %), DOLT-2 (106.0 ± 2.5 %) and orchard leaves (10.0 ± 6.2 %); and reference materials were always within ± 10 % of the certified value. Also, approximately one in every ten samples was run in duplicate to estimate variability within runs, and the mean coefficient of variation for duplicated samples was 4.8 ± 4.1 %.

Calculations and statistical analyses

Linear regressions were carried out in order to assess relationships between $\delta^{13}C$, $\delta^{15}N$, total length and log-transformed total mercury concentrations at the within-species level for fish. Pearson's correlation coefficients (r) were calculated to test for relationships between $\delta^{13}C$ and $\delta^{15}N$ in net phytoplankton from each embayment, and linear regression was used to determine relationships between net phytoplankton stable isotopic ratios and parameters including chlorophyll *a* concentrations, and biomass of nitrogen-fixing cyanobacteria (Table 1). Chlorophyll *a* concentrations (in whole water passed through Whatman GF/F filters) were determined fluorometrically following acetone extraction (as in Stainton et al., 1977), while total phosphorus and nitrogen were also determined as in Stainton et al. (1977). Phytoplanktons were identified and enumerated in whole water samples preserved with Lugol's iodine using an inverted microscope (Ütermohl, 1958). Cell volume was calculated as in Wetzel and Likens (1991), and biomass was estimated assuming a cell specific gravity of 1 g/cm^3 (Nauwerck, 1968).

Log-transformed mercury concentrations in fish were regressed against $\delta^{15}N$ values to generate an estimate of biomagnification rate in the fish food web at these study sites, and analysis of covariance was used to determine whether regression intercepts or slopes differed between embayments.

Welch's two sample *t*-tests were used to compare THg concentrations in water and net phytoplankton, as well as $\delta^{15}N$ and log transformed THg concentrations for fish species between Murchison Bay and Napoleon Gulf. Because $\delta^{15}N$ values at the base of the food web can differ greatly between study sites, $\delta^{15}N$ values for fish were standardized prior to comparison (using *t*-tests) by subtracting a site-specific $\delta^{15}N$ correction factor estimated as mean $\delta^{15}N$ of *Oreochromis niloticus*, a widely present tilapiine cichlid that is predominantly a primary consumer (Moriarty et al., 1973; Semyalo et al., 2011). All statistical analyses were carried out using R, version 2.11.1 (R Development Core Team, 2010).

Results

Food web structure

Net phytoplankton $\delta^{13}C$ values ranged from −18.5 to −11.9‰ (mean: −15.6‰) in Murchison Bay (Table 2), and were positively related ($r^2_{adj} = 0.23$, $P<0.05$) to chlorophyll *a* concentrations (mean: 96.5 µg/L; range: 55.9–186 µ/L). On average, net phytoplankton $\delta^{13}C$ values in Napoleon Gulf were lower than in Murchison Bay ($P<0.05$), with a mean of −16.9 ± 2.5‰ (range: -19.9 to −11.5‰). Net phytoplankton $\delta^{13}C$ in Napoleon Gulf was not related to chlorophyll *a* concentrations.

Net phytoplankton $\delta^{15}N$ was higher ($P<0.001$) in Murchison Bay (mean: 5.6 ± 1.0 ‰; range: 4.0–8.0‰) than in Napoleon Gulf (mean: 1.3 ± 1.0‰; range: 0.5–3.2‰) and was negatively related to log-transformed biomass of the nitrogen-fixing cyanobacterial taxa *Anabaena* in both embayments (Murchison Bay: $r^2_{adj} = 0.17$, $P<0.05$; Napoleon Gulf: $r^2_{adj} = 0.93$, $P<0.001$). Net phytoplankton $\delta^{13}C$ and $\delta^{15}N$ values were positively correlated in Murchison Bay (Pearson's $r = 0.72$, $P<0.001$); however, no such relationship was observed for Napoleon Gulf.

For both Murchison Bay and Napoleon Gulf, zooplankton had similar $\delta^{13}C$ and higher $\delta^{15}N$ values relative to net phytoplankton (Table 2). In Murchison Bay, $\delta^{13}C$ values for benthic invertebrates (−19.1 to −17.3‰) were consistently lower than mean net phytoplankton $\delta^{13}C$, and $\delta^{15}N$ for invertebrates ranged from 3.7‰ (chironomids) to 9.2‰ (leeches). The single pooled chironomid sample from Napoleon Gulf had a $\delta^{13}C$ value of −17.2‰ and $\delta^{15}N$ of 2.8‰ (Table 2).

Mean $\delta^{13}C$ values for fish species collected from Murchison Bay ranged from −17.1‰ to −15.9‰, with the exception of the one individual *Clarias gariepinus* collected, which had a $\delta^{13}C$ value of −18.7‰ (Table 2). Fish from Murchison Bay had mean $\delta^{15}N$ values ranging from 7.7 ± 1.5‰ (*Oreochromis niloticus*) to 10.5 ± 1.1‰ (*Protopterus aethiopicus*). In Napoleon Gulf, the lowest $\delta^{13}C$ values were observed for *Synodontis victoriae* (mean: −16.9 ± 0.3‰) and the highest values were observed for *Tilapia zilli* (mean: −13.6 ± 1.5‰), while *Oreochromis variabilis* had the lowest mean $\delta^{15}N$ value (4.0 ± 0.5‰) and *Bagrus docmac* had the highest mean $\delta^{15}N$ value (9.3‰). In Murchison Bay, fish $\delta^{13}C$ values were consistently lower than net phytoplankton $\delta^{13}C$ from this embayment; while in Napoleon Gulf, fish were slightly enriched in ^{13}C relative to net phytoplankton (Table 2, Fig. 2).

In Murchison Bay, $\delta^{15}N$ values were negatively related to total length for *O. niloticus* ($r^2_{adj} = 0.22$, $P<0.05$) and in Napoleon Gulf, $\delta^{15}N$ values were positively related to total length for *Lates niloticus*

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Table 2
$\delta^{13}C$, $\delta^{15}N$, total length and THg concentrations for aquatic food web samples from Inner Murchison Bay and Napoleon Gulf. Samples for *Rastrineobola argentea* (marked with an asterisk) each represent five pooled individual fish. Published diet is based on Greenwood (1958), and dietary items are labeled as follows: P: phytoplankton, Z: zooplankton, I: insects, BI: benthic invertebrates, M: macrophytes, Mo: mollusks, F: fish, PB: benthic primary producers, D: detritus, G: gastropods.

Species	Code	Published diet	Murchison Bay					Napoleon Gulf				
			n	Total length range (cm)	$\delta^{15}N$ (‰) μ±s.d	$\delta^{13}C$ (‰) μ±s.d.	THg (ng/g ww) μ±s.d. (range)	*n*	Total length range (cm)	$\delta^{15}N$ (‰) μ±s.d	$\delta^{13}C$ (‰) μ±s.d.	THg (ng/g ww) μ±s.d. (range)
Astatoreochromis alluaudi	Aa	Mo	~	~	~	~	~	1	19.5	7.4	−16.0	7.3
Bagrus docmac	Bd	BI, F	~	~	~	~	~	1	26.5	9.3	−14.2	27.9
Brycinus sadleri	Bs	I	~	~	~	~	~	1	12.7	6.5	−16.7	85.3
Clarias gariepinus	Cg	F, Mo, I, D	1	57.5	8.8	−18.7	17.3	~	~	~	~	~
Haplochromis (?) spp.	H	P, I, BI, Z	9	6.0–14.8	9.8±1.1	−16.7±0.8	18.9±5.3 (12.9–25.9)	8	5.1–17.2	7.6±0.7	−15.4±1.5	30.4±18.5 (17.0–73.1)
Lates niloticus	Ln	F, I, BI, Z, P	18	19.0–96.0	9.4±1.6	−16.2±1.2	42.0±22.0 (17.6–101.1)	23	9.7–63.5	7.9±1.0	−15.3±1.2	34.8±13.0 (15.3–71.3)
Mormyrus kannume	Mk	BI	~	~	~	~	~	5	16.3–31.0	8.1±0.3	−14.6±0.5	31.7±29.1 (9.4–82.3)
Oreochromis leucostictus	Ol	P, D, BI	5	15.2–25.5	8.5±1.1	−17.1±0.8	11.0±5.7 (5.2–19.4)	2	21.1–25.3	4.3–4.6	−15.4 to −12.9	3.1±0.5 (2.8–3.5)
Oreochromis niloticus	On	P, D, BI	24	15.0–38.0	7.7±1.5	−16.3±1.5	14.1±18.8 (3.5–91.5)	24	13.5–34.5	4.6±0.7	−13.8±1.0	12.8±36.3 (2.7–182.5)
Oreochromis variabilis	Ov	P, D, BI	~	~	~	~	~	9	17.8–22.1	4.0±0.5	−14.5±0.6	3.2±0.7 (2.0–4.1)
Protopterus aethiopicus	Pa	I, G, F	9	46.0–77.0	10.5±1.1	−16.1±1.3	7.6±2.8 (4.4–13.9)	10	50.0–100.0	8.2±1.7	−16.4±0.9	7.1±5.6 (1.9–20.7)
Rastrineobola argentea	Ra	Z	1*	4.0	8.6	−15.9	49.1	5*	3.5–4.5	6.9±0.4	−14.0±0.8	17.0±9.5 (8.1–31.2)
Synodontis afrofischeri	Sa	Mo, BI	8	14.5–20.1	10.2±1.5	−17.0±0.6	40.8±19.9 (10.1–59.2)	3	13.0–15.4	8.3±0.1	−15.4±0.04	28.6±6.1 (22.7–34.9)
Synodontis victoriae	Sv	Mo, BI	7	17.1–24.5	9.0±0.8	−16.1±2.3	27.9±21.5 (6.2–69.6)	4	17.1–23.5	7.5±0.4	−16.9±0.3	111.5±152.9 (27.0–340.5)
Tilapia zilli	Tz	P, PD, B, M	7	15.3–26.5	8.7±1.3	−17.0±1.5	12.4±6.4 (7.0–25.4)	10	13.3–23.5	6.4±1.3	−13.6±1.5	9.3±3.8 (3.7–14.6)
Net Phytoplankton (all)	p	~	21	~	5.6±1.0	−15.6±1.5	~	6	~	1.0±0.8	−16.3±2.8	2.0±1.0 (0.6–3.1)
Net Phytoplankton (Hg analyzed)	p	~	6	~	5.8±0.9	−13.9±2.7	1.9±0.7 (1.3–2.7)	~	~	~	~	~
Zooplankton (>80 μm)	z	~	1	~	7.6	−15.3	~	3	~	5.3±0.4	−15.8±1.8	~
Zooplankton (>153 μm)	Z	~	1	~	7.7	−15.3	~	3	~	5.2±0.3	−15.3±2.0	~
Chironomidae	ch	~	1	~	3.7	−17.6	14.3	1	~	2.8	−17.2	17.1
Mayflies (*Povilla*)	m	~	1	~	6.1	−19.1	5.9	~	~	~	~	~
Leeches	h	~	1	~	9.2	−17.3	10.7	~	~	~	~	~
Snails (*Bellamya*)	b	~	1	~	7.7	−17.8	~	~	~	~	~	~

($r^2_{adj} = 0.40$, $P<0.001$). There were no other significant relationships observed between fish length and either $\delta^{13}C$ or $\delta^{15}N$ for either embayment.

Based on Welch's *t*-tests, there were no significant differences in standardized $\delta^{15}N$ values ("standardized" through subtraction of mean *O. niloticus* $\delta^{15}N$) for conspecific fish between Murchison Bay and

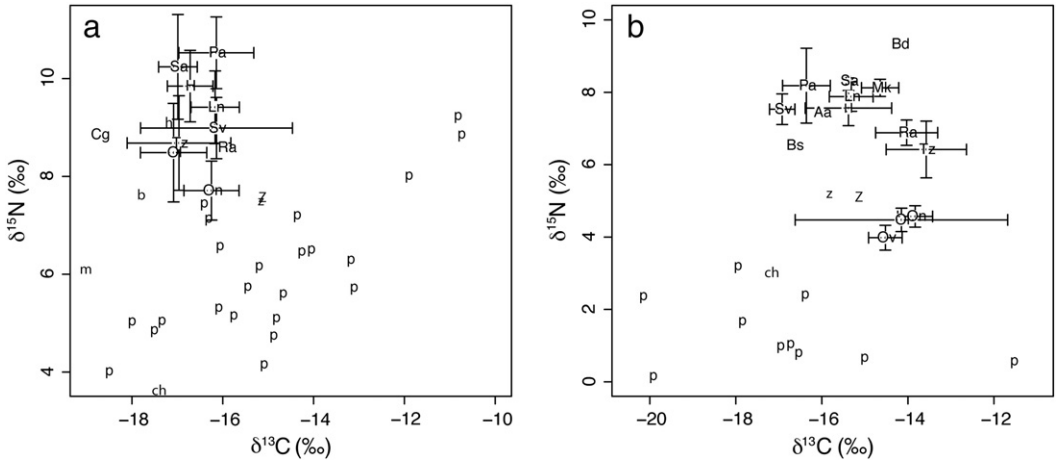

Fig. 2. Stable carbon and nitrogen isotope biplots for a) Murchison Bay and b) Napoleon Gulf. Means and 95 % confidence intervals are shown for fish, means are shown for benthic invertebrates, and individual data points are shown for net phytoplankton. Species codes used are defined in Table 2. Species for which only one individual was sampled do not have error bars.

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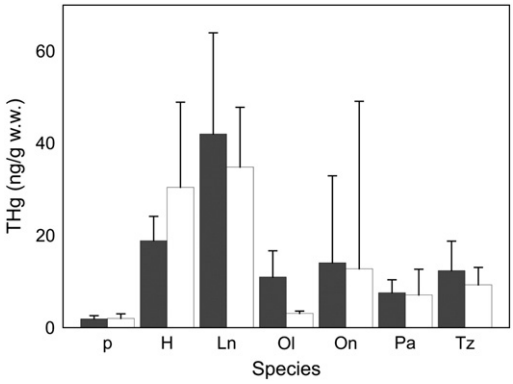

Fig. 3. Total mercury concentrations in net phytoplankton (p) and selected species of fish from Murchison Bay (dark bars) and Napoleon Gulf (white bars). Bar height represents mean THg concentration, error bars represent standard deviation. Species codes used are defined in Table 2.

Napoleon Gulf with the exception of *Synodontis victoriae* and *Lates niloticus*, which had lower standardized $\delta^{15}N$ values in Murchison Bay than in Napoleon Gulf ($P<0.05$).

Mercury concentrations

Total mercury (THg) concentrations in water were higher ($P<0.001$) in Murchison Bay (1.30 ± 0.09 ng/L, $n=3$) than in Napoleon Gulf (0.53 ± 0.07 ng/L, $n=3$, Table 1); however, THg concentrations in net phytoplankton did not differ ($P=0.77$) between the two embayments (1.3–2.7 ng/g wet weight (ww) for Murchison Bay and 0.6–3.1 ng/g ww for Napoleon Gulf; Table 2, Fig. 3). In Murchison Bay, mayflies, leeches and chironomids had THg concentrations of 5.9, 10.7 and 14.3 ng/g ww respectively; while chironomids from Napoleon Gulf had THg concentrations of 17.1 ng/g ww (Table 2).

THg concentrations in fish from Murchison Bay ranged from 3.5 to 101 ng/g ww and were highest in *L. niloticus* and *S. afrofischeri*; intermediate in *S. victoriae*, *Haplochromis* spp. and *C. gariepinus*; and lowest in tilapiine cichlids and *P. aethiopicus* (Table 2, Fig. 3). In Napoleon Gulf, THg concentrations in fish ranged from 1.9 to 341 ng/g ww and were highest in *S. victoriae* and *Brycinus sadleri*, intermediate in *L. niloticus*, *Haplochromis* spp. and *S. afrofischeri* and lowest in tilapiine cichlids and *P. aethiopicus* (Table 2, Fig. 3).

There were no significant differences in log-transformed total mercury concentrations in conspecific fish between Murchison Bay and Napoleon Gulf (based on Welch's *t*-tests), aside from *O. leucostictus* and *O. niloticus*, which both had lower THg concentrations in Napoleon Gulf than in Murchison Bay ($P<0.05$; Fig. 3).

Mercury trophodynamics

In Murchison Bay, mercury concentrations were positively related to fish length for *L. niloticus* ($r^2_{adj}=0.28$, $P<0.05$) and *S. victoriae* ($r^2_{adj}=0.80$, $P<0.01$), while in Napoleon Gulf a positive relationship was observed between total length and mercury concentrations only for *S. victoriae* ($r^2_{adj}=0.88$, $P<0.05$). It should be noted that given the absence of consistent length-THg relationships, we did not correct for length in our comparisons of fish THg between embayments.

Mercury concentrations for *L. niloticus* were significantly positively related to both $\delta^{15}N$ and $\delta^{13}C$ values for Murchison Bay, while in Napoleon Gulf mercury concentrations were negatively related to $\delta^{13}C$ for *Haplochromis* spp. ($r^2_{adj}=0.57$, $P<0.05$) and *Mormyrus kannume* ($r^2_{adj}=0.85$, $P<0.05$), and were positively related to $\delta^{15}N$ for *Tilapia zilli* ($r^2_{adj}=0.58$, $P<0.01$).

Slopes of regressions of log transformed total mercury concentrations against $\delta^{15}N$ values (as an indicator of relative trophic level) are often used as an estimate of biomagnification rate (Borgå et al., 2012). *P. aethiopicus* (lungfish) were excluded from regressions given their anomalously low THg concentrations despite high $\delta^{15}N$ values. We observed a significant positive relationship between $\delta^{15}N$ values and mercury concentrations for both Murchison Bay (slope: 0.13, $r^2_{adj}=0.32$, $P<0.001$) and Napoleon Gulf (slope: 0.20, $r^2_{adj}=0.55$, $P<0.001$; Fig. 4). Based on analysis of covariance there was no significant difference in regression intercepts between the two embayments ($P=0.21$), however, the slope of the log(THg)~$\delta^{15}N$ regression was significantly higher in Napoleon Gulf than in Murchison Bay ($P<0.01$). We also observed a significant negative relationship between mercury concentrations and $\delta^{13}C$ values for fish (excluding *P. aethiopicus*) from Napoleon Gulf ($r^2_{adj}=0.26$, $P<0.001$). A similar relationship was not observed for fish from Murchison Bay.

Given the significant relationship between net phytoplankton $\delta^{13}C$ and $\delta^{15}N$ for Murchison Bay, we tested whether applying a linear correction to fish $\delta^{15}N$ based on this relationship would alter the results of the comparison of fish $\delta^{15}N$ (standardized to *O. niloticus*) between study sites, the species specific relationships between $\delta^{15}N$ and fish length or THg, or the log(THg):$\delta^{15}N$ relationship for this embayment. We found that applying this correction did not affect the nature or magnitude of any of these observations, suggesting that such a correction would not affect the interpretation of the results in the current study, and as such, is not necessary and was not applied to the data analyzed.

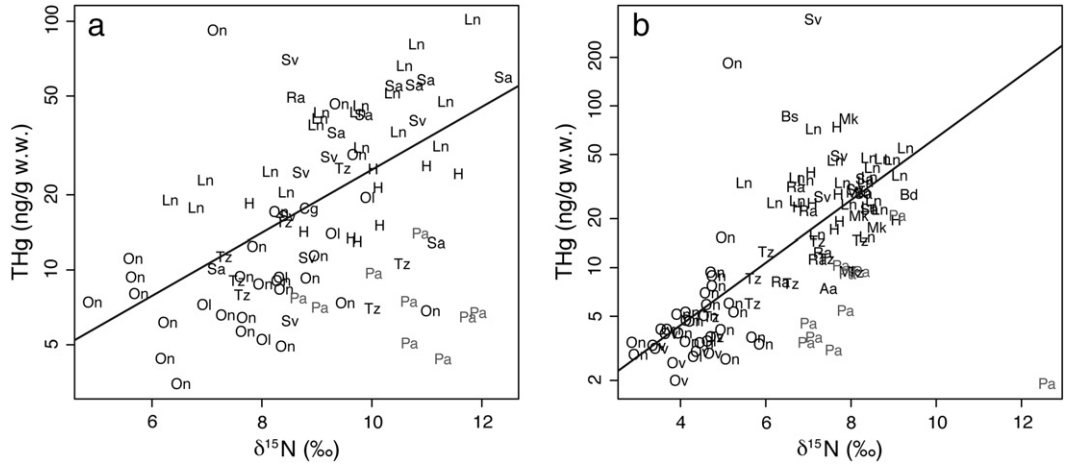

Fig. 4. Regressions of total mercury concentrations vs. $\delta^{15}N$ values for fish from a) Murchison Bay (slope: 0.13, $r^2_{adj}=0.32$, $P<0.001$) and b) Napoleon Gulf (slope: 0.20, $r^2_{adj}=0.55$, $P<0.001$). Species codes used are defined in Table 2. Data for *Protopterus aethiopicus* are shown in gray since these data were not included in the regression.

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Discussion

Net phytoplankton $\delta^{13}C$ and $\delta^{15}N$

Net phytoplankton $\delta^{13}C$ and $\delta^{15}N$ values for both Murchison Bay and Napoleon Gulf were within the range reported for suspended particulate matter from nearshore areas of the Tanzanian sector of Lake Victoria (Machiwa, 2010). The elevated $\delta^{13}C$ values in net phytoplankton from Murchison Bay relative to those observed in Napoleon Gulf (Table 2) are likely due to differences in phytoplankton biomass and growth rate between these embayments, with instantaneous CO_2 limitation which reduces isotopic discrimination of photosynthesis more common in hypereutrophic Murchison Bay (Hecky and Hesslein, 1995). Furthermore, the positive relationship observed between net phytoplankton $\delta^{13}C$ and chlorophyll *a* concentrations in Murchison Bay highlights the interaction between phytoplankton biomass (and carbon demand) and isotopic fractionation during photosynthesis in this embayment.

Net phytoplankton had much higher $\delta^{15}N$ values in Murchison Bay than in Napoleon Gulf (Table 2), likely because of the influence of the large amount of human waste that enters the inner bay from the city of Kampala. However, observed net phytoplankton $\delta^{15}N$ values are still below published $\delta^{15}N$ values for dissolved inorganic nitrogen from human waste (10–20‰; Harrington et al., 1998), suggesting that this influence may be counteracted by the occurrence of atmospheric nitrogen fixation (with $\delta^{15}N \sim 0‰$). In Napoleon Gulf, net phytoplankton $\delta^{15}N$ values were very low, highlighting the reduced importance of local anthropogenic nutrient inputs in this well-flushed embayment, and suggesting prevalent fixation of atmospheric nitrogen. Furthermore, based on microscopy, average biomass of *Anabaena* (the most common N-fixing cyanobacterial genus in these embayments) was two-fold higher in Napoleon Gulf than in Murchison Bay, where non N-fixing *Microcystis* dominated the phytoplankton biomass (Table 1). It is important to note that our net phytoplankton samples (>20 μm component) will not be wholly representative of the total phytoplankton community and are likely to predominantly select for larger colonial phytoplankton such as *Anabaena* and *Microcystis*, which would increase the relative influence of these larger taxa on net phytoplankton $\delta^{13}C$ and $\delta^{15}N$.

The role played by nitrogen fixation in influencing net phytoplankton $\delta^{15}N$ in both Murchison Bay and Napoleon Gulf is also supported by the significant negative relationships observed between net phytoplankton $\delta^{15}N$ and biomass of *Anabaena* spp. (based on microscopy), a cyanobacterial taxon capable of atmospheric nitrogen fixation. Over our study period, *Anabaena* spp. made up between 0.2–12 % and 2–65 % of the total phytoplankton biomass in Murchison Bay and Napoleon Gulf respectively (Poste *unpublished data*). Although *Anabaena* spp. does not generally dominate the phytoplankton biomass in either embayment, seasonal increases in *Anabaena* biomass appear to coincide with lower net phytoplankton $\delta^{15}N$, suggesting higher community N-fixation rates. These observations are consistent with the results of previous studies that have concluded that biological nitrogen fixation is an important source of fixed nitrogen in Lake Victoria (Mugidde et al., 2003) as well as other East African lakes (Horne and Viner, 1971).

The positive relationship between net phytoplankton $\delta^{13}C$ and $\delta^{15}N$ in Murchison Bay is of interest, as these ratios are often negatively correlated (e.g. Vander Zanden and Rasmussen, 1999; Poste et al. *unpublished data* from tropical Lake Edward; but see Post, 2002). This positive relationship may reflect that inputs of nutrients from sewage (with high $\delta^{15}N$ and soluble reactive phosphorus) may encourage increased phytoplankton growth rates, leading to decreased isotopic discrimination during photosynthesis (and possibly bicarbonate uptake) and associated increases in phytoplankton $\delta^{13}C$. In Murchison Bay, the relatively low biomass of *Anabaena* paired with the positive $\delta^{13}C$:$\delta^{15}N$ relationship for net phytoplankton suggest that net phytoplankton (primarily *Microcystis*) N-demand is largely being met by inputs from sewage, while atmospheric sources of N are meeting the N-demand of net phytoplankton in Napoleon Gulf (where *Anabaena* are prevalent).

Food web structure

Differences in phytoplankton $\delta^{15}N$ between Murchison Bay and Napoleon Gulf are reflected throughout the consumer food webs in these embayments, with fish from Murchison Bay tending to have higher $\delta^{15}N$ than conspecific fish from Napoleon Gulf (Table 2, Fig. 2). However, despite elevated $\delta^{13}C$ in net phytoplankton from Murchison Bay relative to Napoleon Gulf, fish from Napoleon Gulf were typically enriched in ^{13}C relative to conspecific fish from Murchison Bay (Table 2). Also, fish from Murchison Bay were generally depleted in ^{13}C relative to net phytoplankton; while in Napoleon Gulf, many species of fish were slightly enriched in ^{13}C relative to net phytoplankton (Fig. 2).

In many food web studies, stable carbon isotopic ratios are used to differentiate benthic and pelagic primary carbon sources, with organisms reliant on benthic sources of primary carbon tending to be enriched in ^{13}C (Hecky and Hesslein, 1995). However, in the current study, the benthic invertebrates sampled had $\delta^{13}C$ values that were generally lower than those observed for net phytoplankton, zooplankton and fish known to be reliant on pelagic food sources (such as *Rastrineobola argentea*).

In eutrophic lakes, benthic primary production is often greatly reduced due to light limitation in these low transparency systems, and food webs in these lakes are typically strongly reliant on planktonic primary carbon sources including phytoplankton and resultant detritus (Vadeboncoeur et al., 2003). In both of our study embayments light attenuation was high and the capacity for benthic primary production should be strongly limited by light availability (Murchison Bay has a mean depth of 3.2 m, while our observed mean Secchi depth was 0.7 m; Napoleon Gulf has a mean depth of 7.9 m, and our observed mean Secchi depth was 1.4 m). Increased reliance on planktonic carbon sources may explain the lack of strong differentiation in $\delta^{13}C$ between pelagic and benthic consumers at our eutrophic study sites.

It is also possible that the low $\delta^{13}C$ values observed for the benthic invertebrates sampled were due to the utilization of benthically generated methane-based carbon, which is highly depleted in ^{13}C (Bunn and Boon, 1993). The incorporation of ^{13}C-depleted methanotrophic bacteria has been reported for benthic invertebrates (mostly chironomids) from several freshwater lakes (Hershey et al., 2006; Kiyashko et al., 2001), and eutrophication-mediated oxygen depletion, particularly in hypereutrophic Murchison Bay, would be expected to favor the production of biogenic methane. As such, the depleted ^{13}C values observed for fish from Murchison Bay and the lack of substantial ^{13}C enrichment observed in typically benthivorous fish from Napoleon Gulf do not necessarily imply low levels of incorporation of benthic carbon, but may instead reflect dietary incorporation of low ^{13}C benthic invertebrates (that may be exploiting phytoplankton detritus and/or methane-based C sources).

This poor separation in $\delta^{13}C$ values between benthic and pelagic consumers makes it difficult to assess the relative importance of benthic and pelagic primary carbon sources to these food webs. However, in both study embayments low transparency (and light-limitation of benthic primary production) is likely to increase the relative importance of pelagic primary carbon sources to the food web as a whole (as has been observed for other eutrophic lakes; Vadeboncoeur et al., 2003).

In both Murchison Bay and Napoleon Gulf, fish $\delta^{15}N$ values generally agreed with expected trophic positions based on published dietary information (Greenwood, 1958; Table 2). Tilapiine cichlids (including the three *Oreochromis* species and *Tilapia zilli*), which are typically primary consumers, tended to have $\delta^{15}N$ values consistent with a diet based on phytoplankton and detritus; however, in Napoleon Gulf,

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T. zilli had elevated $\delta^{15}N$ values relative to the other tilapiine cichlids, suggesting some dietary inclusion of primary consumers. The remaining fish species all had $\delta^{15}N$ values consistent with being secondary consumers, although this was most apparent in Napoleon Gulf, where variability in fish $\delta^{15}N$ tended to be lower. It is also possible that omnivory, and in particular the dietary inclusion of phytoplankton and detritus, is more prevalent in hypereutrophic Murchison Bay than in Napoleon Gulf. Food web length in both embayments tended to be short, with no evidence of either strong piscivory or the presence of obligate tertiary consumers.

The negative relationship observed between total length and $\delta^{15}N$ for *O. niloticus* from Murchison Bay is consistent with previous observations that these fish can undergo ontogenetic dietary shifts, with smaller fish incorporating more benthic invertebrates in their diet, and adult fish tending to be strongly dependent on phytoplankton and detritus (Moriarty et al., 1973; Semyalo et al., 2011; but see Bwanika et al., 2006). *Lates niloticus* are also known to experience ontogenetic dietary shifts, whereby they are able to consume larger prey and become increasingly piscivorous as they grow (Campbell et al., 2003d). Although a positive relationship between total length and $\delta^{15}N$ was observed in Napoleon Gulf, this was not observed for Murchison Bay. Unlike tilapiine cichlids, which do not tend to have high mobility (Fryer, 1996), *L. niloticus* are highly mobile (Goudswaard et al., 2006). Migratory feeding by *L. niloticus* (and other highly mobile fish species) would be expected to complicate the relationship between total length and $\delta^{15}N$ in the Murchison Bay region given the strong differences in baseline $\delta^{15}N$ expected between the inner bay, the outer bay and the open lake (due to differences in influence of anthropogenic N and rates of atmospheric N-fixation; Hecky et al., 2010). However, in Napoleon Gulf, where conditions are much more similar to the open lake, these processes are less likely to strongly affect our ability to estimate fish trophic level from $\delta^{15}N$ values.

The food web structure of Napoleon Gulf was previously characterized using stable isotope analysis of samples collected in 1998 by Campbell et al. (2003d), providing a unique opportunity to explore the temporal stability of carbon and nitrogen isotopic ratios as well as trophic structure. In the current study, fish consistently had higher $\delta^{13}C$ (typically by ~3‰) and lower $\delta^{15}N$ values (typically by ~1‰) than was observed by Campbell et al. (2003d), which could reflect differences in baseline $\delta^{13}C$ and $\delta^{15}N$ values between studies. However, the relative trophic positions (as inferred from $\delta^{15}N$) and inferred trophic relationships for the current study are similar to those described by Campbell et al. (2003d), suggesting that the fundamental food web structure of Napoleon Gulf does not appear to have changed appreciably. Furthermore, there do not appear to be strong spatial differences in food web structure across nearshore Lake Victoria, given the similarities in trophic position and trophic relationships for fish from Murchison Bay and Napoleon Gulf in the current study (Fig. 2), and for fish from both Napoleon and Winam Gulfs in previous studies (Campbell et al., 2003d).

Mercury concentrations

We expected that mercury concentrations in water from Murchison Bay might be elevated given the region's dense urban and industrial development and the substantial inflow of wastewater to the bay. However, previously published THg concentrations for northern Lake Victoria were even higher than those that we observed for Murchison Bay (as reviewed by Campbell et al., 2003a,c); nevertheless, THg concentrations in Murchison Bay were nearly 3-fold higher than those that we observed in Napoleon Gulf (Table 1), suggesting that there is at least some localized anthropogenic Hg enrichment in Murchison Bay.

The highest THg concentrations were generally observed for fish that feed at higher trophic levels (based on $\delta^{15}N$ as well as published diet; Greenwood, 1958) such as *L. niloticus*, *S. afrofischeri*, *S. victoriae*, *R. argentea*, *Haplochromis* spp., as well as *M. kannume*. However, *P. aethiopicus* (lungfish) tended to have very low mercury concentrations, despite having some of the highest $\delta^{15}N$ values of any fish species sampled (Table 2). The anomalously low mercury concentrations may be due to differences in habitat and feeding strategies (*P. aethiopicus* is a benthic feeding omnivore that is primarily found in wetland areas; Goudswaard et al., 2002) or differences in mercury uptake or depuration.

Despite significantly higher THg concentrations in water in Murchison Bay than in Napoleon Gulf, mercury concentrations in both embayments did not differ for either net phytoplankton or most fish species (Fig. 3). This suggests that total mercury concentrations in water are not a particularly good predictor of mercury concentrations in fish in northern Lake Victoria (as was observed by Campbell et al., 2003a), and that there may be differences in the bioavailability of Hg (i.e. MeHg concentrations) or Hg trophodynamics between these embayments. It is also possible that in hypereutrophic Murchison Bay, where phytoplankton biomass is much higher than in Napoleon Gulf (Table 1), greater biomass dilution of THg is taking place (Pickhardt et al., 2002), leading to reduced THg concentrations in phytoplankton (and consequently at higher trophic levels).

The THg concentrations observed in fish from the current study fall within the range reported in the literature for Lake Victoria (Campbell et al., 2003a). It is of particular interest to compare THg concentrations in fish from Napoleon Gulf in the current study with those reported for fish collected from this embayment in 1998 by Campbell et al. (2003b). Mean mercury concentrations reported by Campbell et al. (2003b) were typically higher than for the same species in the current study; including THg concentrations that were 2- to 3-fold higher for *L. niloticus* and *O. niloticus*.

A previous study of mercury concentrations in two sediment cores from Lake Victoria (one from Napoleon Gulf and one from the central offshore region of the lake) revealed a decline in THg concentrations that appeared to begin in the 1980s (Campbell et al., 2003a). Despite the evidence for declining THg in sediments, this study was not able to determine whether this decline was attributable to decreasing mercury inputs to the lake, or an increase in sedimentation rate due to eutrophication of the lake. Given that mercury concentrations in water and fish from Napoleon Gulf were lower in the current study than for samples collected in the late 1990s by Campbell et al. (2003b) and Ramlal et al. (2003), our observations provide additional evidence that mercury concentrations in Napoleon Gulf are declining. However, it is important to note that possible differences in sampling season, specific sampling location, or methodology could also complicate comparison between these two studies.

Mercury trophodynamics

Both ontogenetic dietary shifts (Campbell et al., 2003b,d) and long-term accumulation of Hg in fish (MacCrimmon et al., 1983) can contribute to a positive relationship between total length and mercury concentrations in fish. The positive relationship observed between total mercury concentrations and both fish length and $\delta^{15}N$ for *L. niloticus* (Nile perch) from Murchison Bay is consistent with our understanding of the ontogenetic dietary shift experienced by this species, with larger fish feeding on higher trophic level prey, which increases dietary mercury exposure (Campbell et al., 2003d). At both study sites, THg concentrations in *Synodontis victoriae* also increased with fish length; however, given that there was no corresponding relationship between total length and $\delta^{15}N$, this increase is likely to be primarily attributable to long-term accumulation of mercury in fish over time, rather than ontogenetic dietary shifts.

The regression slope of log transformed THg concentrations against $\delta^{15}N$ (as a measure of trophic level) has been widely used to quantify and compare the biomagnification rate of mercury in aquatic food webs (see Kidd, 1998). Although there are many limitations to direct comparison of such regression slopes (e.g. when the species composition of the data set or the trophic fractionation of nitrogen stable isotopes differs between lakes), given the similarity in the species sampled and the

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food web structure between sites, we feel that such a comparison can be informative for the current study.

The significant positive relationships observed between log(THg) and $\delta^{15}N$ for fish in both Murchison Bay and Napoleon Gulf confirm that biomagnification of mercury is taking place in both of these embayments (Fig. 4). Despite strong similarities in food web structure between embayments, the biomagnification rate (as represented by the slope of the log(THg):$\delta^{15}N$ regression) for Murchison Bay (slope: 0.13) was lower than the rate observed for Napoleon Gulf in the current study (slope: 0.20), which may account, at least in part, for the similar mercury concentrations in conspecific fish for the two embayments despite differences in THg in water.

We hypothesize that the difference in biomagnification rate between Murchison Bay and Napoleon Gulf could be due to growth dilution at consumer trophic levels (Herendeen and Hill, 2004; Simoneau et al., 2005), whereby fish growth is faster and more efficient in hypereutrophic Murchison Bay than in the less productive Napoleon Gulf, leading to relatively lower dietary exposure to mercury in consumer trophic levels in Murchison Bay. Also, if there are substantial differences in fishing pressure between the two embayments, this could also drive differences in fish growth rate and therefore mercury accumulation (Simoneau et al., 2005; Surette et al., 2003; Verta, 1990).

Conclusions

The results of this study have highlighted that in northern Lake Victoria, lake trophic status appears to play a central role in determining $\delta^{13}C$, $\delta^{15}N$ and THg in phytoplankton and consumer organisms. In particular, net phytoplankton stable carbon and nitrogen isotopic ratios were strongly influenced by lake trophic status and the prevalence of N-fixing cyanobacteria, and differences in net phytoplankton $\delta^{13}C$ and $\delta^{15}N$ between embayments were transferred throughout the food web. Also, in these highly productive lakes, low transparency reduces the relative contribution of benthic primary production and increases the importance of pelagic primary carbon to the benthic food web, resulting in poor separation in $\delta^{13}C$ between organisms known to rely on benthic or pelagic food sources. Our results also suggest that trophic status, and high phytoplankton biomass and productivity, may be acting to mediate mercury concentrations at the base of the food web (Pickhardt et al., 2002) and in consumer trophic levels (Herendeen and Hill, 2004; Simoneau et al., 2005).

Murchison Bay and Napoleon Gulf are critical sources of fish both for export and for local consumption. In the current study, no fish from Murchison Bay exceeded the WHO recommended guideline for at-risk population of 200 ng/g, and with the exception of the largest specimen of *S. victoriae*, no fish from Napoleon Gulf exceeded this threshold either. These results are in agreement with the conclusion of Campbell et al. (2003a), that in general, risk of Hg intoxication from consuming fish from Lake Victoria is low, even for fish from Murchison Bay, where industrial and urban pollution has led to elevated THg concentrations in water.

Our results are also consistent with previous reports that mercury concentrations in fish from African lakes tend to be low (as reviewed by Black et al., 2011). This may be attributable to several factors including shorter life spans and higher growth rates of tropical fish relative to temperate fish (Harris and Bodaly, 1998; Kidd et al., 2003), and relatively short food chain lengths (as observed in the current study); however, there remain many unknowns with respect to Hg biogeochemistry, bioavailability and trophodynamics in tropical lakes. In particular the role of lake trophic status in determining mercury concentrations in fish from tropical African lakes deserves further consideration.

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