

Heterogeneity in food-web interactions of fish in the Mwanza Gulf, Lake Victoria: a quantitative stable isotope study

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Abstract Stable isotope analyses and derived population-level metrics were used to quantitatively analyse spatial and seasonal heterogeneity in the fish trophic dynamics in relation to environmental variables in Mwanza Gulf, Lake Victoria (Tanzania). The fish community in Lake Victoria, including the top predator Nile perch, is generally omnivorous with a heavy reliance on invertebrates. This is in contrast to findings based on stomach content analyses of Nile perch, which showed a stronger reliance on fish. We tested two hypotheses: (1) during the rainy seasons multiple carbon sources influence the food-web structure inside the Gulf, leading to increased carbon ranges and trophic diversity. (2) During dry periods,

the food-web structure mainly relies on pelagic primary production, reducing carbon ranges and trophic diversity. Carbon sources indeed varied seasonally and spatially, affecting the fish community at the highest trophic levels. With the onset of rains, carbon sources became spatially highly differentiated with enriched $\delta^{13}\text{C}$ values of fish in shallow water inside the Gulf and depleted $\delta^{13}\text{C}$ values in open waters. Metrics associated with niche size correlated significantly with seasonally varying environmental variables, while $\delta^{13}\text{C}$ ranges correlated with spatially varying environmental variables.

Keywords Tropical lake · Population-level metrics · Trophic level · Nile perch · Haplochromines

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Introduction

The food web of Lake Victoria underwent major ecological changes, including eutrophication (Hecky, 1993) and changes in the fish community. The endemic haplochromines declined (Witte et al., 1992a), followed by an upsurge of the introduced Nile perch (*Lates niloticus*, Linnaeus, 1758) in the 1980s. During the explosive population growth of Nile perch, there was also a population increase of the atyid shrimp *Caridina nilotica* (Roux, 1833), the small cyprinid fish Dagaa [*Rastrineobola argentea* (Pellegrin, 1904)] and the exotic Nile tilapia [*Oreochromis niloticus* (Linnaeus, 1758)] (Ogutu-Ohwayo, 1990; Witte et al., 1992b; Goldschmidt et al., 1993; Goudswaard et al., 2006). From the 1980s onwards, the Lake's fishery thrived, dominated by Nile perch as economically most important fish, and Dagaa and Nile tilapia as second and third most important target species (Wanink, 1999; Cowx et al., 2003; Njiru et al., 2005).

The former complex food web with more than 500 species of endemic haplochromines occupying every niche in the lake (van Alphen et al., 2003) was replaced by a simpler food web, dominated by omnivorous feeders (Ojwang et al., 2010), which opportunistically switched between available food sources. Traditional diet analyses showed that during the Nile perch boom, Nile perch preyed heavily on the endemic haplochromines and, when haplochromines declined, they switched their diet to the increasingly abundant *Caridina* shrimp, their own juveniles and Dagaa (Hughes, 1986; Mkumbo & Ligtvoet, 1992; Katunzi et al., 2006). Since the 1990s, a recovery of some pelagic haplochromine species was observed in the Mwanza Gulf in the south-east of Lake Victoria (Witte et al., 2000, 2007; Kische-Machumu et al., 2012) and Nile perch is observed to switch to haplochromines again (Kische-Machumu et al., 2012; Cornelissen et al., 2015). Other abundant species of Lake Victoria also changed their diets. Former specialist feeders such as the haplochromine species (specialized in detritus or zooplankton), Nile tilapia (algae), Dagaa (zooplankton) and *Brycinus sadleri* (Boulenger, 1906) (zooplankton) are now including larger invertebrate prey and even fish in their diet (Wanink, 1998; Wanink & Witte, 2000; Katunzi et al., 2003; Njiru et al., 2004; Wanink & Joordens, 2007; Kische-Machumu et al., 2008).

The increasing eutrophication facilitated the explosive population growth of Nile perch and increased fish production in Lake Victoria (Kolding et al., 2008). However, even though the food web simplified and Nile perch boomed, the lake still displayed great spatial heterogeneity in algal biomass and fish distributions (Getabu et al., 2003; Silsbe, 2004). Water quality and other abiotic factors varied spatially and seasonally within the Mwanza Gulf (Cornelissen et al., 2014). Nile perch distributions were primarily driven by water temperature, depth and oxygen and not by the availability of particular prey species (Goudswaard et al., 2011; Cornelissen et al., 2015). As a result the diet of Nile perch also varied spatially and temporally, since it feeds opportunistically on prey which is available in its abiotic-driven distribution range (Cornelissen et al., 2015).

Most studies in Lake Victoria focused on stock assessments and diet studies of a few commercial species, giving limited and 'snapshot' information on the organization of the food web and trophic interactions. Combined carbon ($\delta^{13}\text{C}$) and nitrogen ($\delta^{15}\text{N}$) stable isotopes provide information on food sources, trophic interactions and food-web structure of the entire communities, covering a longer integrated timespan (Peterson & Fry, 1987; Hesslein et al., 1993; Layman et al., 2012). However, only few isotopic studies on food-web dynamics of Lake Victoria have been conducted, and these were limited to two Gulfs in the northern part of Lake Victoria (Branstrator et al., 2003; Campbell et al., 2003; Ojwang et al., 2010).

In addition to identifying the resource use of individual organisms and species, community-wide metrics can be used to quantify trophic structure on a food-web level of the entire communities or populations in a number of diagnostic metrics (Layman et al., 2007). This approach has been used to compare food-web structures between ecosystems, seasons and habitats (Carlier et al., 2009; Jackson et al., 2012; Doi et al., 2013; Abrantes et al., 2014), and to study the effects of invasive species on trophic interactions of populations (Jackson et al., 2012).

The environment affects productivity rates and resources at the base of the food web which are supporting higher trophic levels. In ecosystems which are strongly affected by its hydrology such as wetlands, rivers, and estuaries, variation in environmental and physical conditions reflects variation in

food-web structure (Doi et al., 2013; Hyndes et al., 2013; Schriever, 2015; Thormar et al., 2016). At present little is known about how the environment structures the food web at higher trophic levels in large lake systems such as Lake Victoria.

Mwanza Gulf is spatially and seasonally heterogeneous in water quality and the distribution and diets of fish (Cornelissen et al., 2014, 2015). Therefore, we hypothesize that fish trophic interactions will also vary spatially and seasonally in relation to environmental variables (O'Neill & Thorp, 2014; Schriever, 2015). To test this, we used 8 metrics on population level to detect spatial and seasonal shifts of haplochromines and Nile perch and correlated them to several important environmental variables. We expected that during the rainy periods, when run-off is high, the fish community inside the Gulf will be more influenced by terrestrial and benthic/littoral carbon sources than during the dry season, when primary production will be mainly pelagic. These multiple carbon sources are expected to lead to increased carbon ranges and trophic diversity during the rainy periods, as compared to the dry season.

Materials and methods

Study area

Samples were collected at 6 stations in three areas in Mwanza Gulf (Fig. 1). Mwanza Gulf is located in south-east Lake Victoria in Tanzania and is about 60 km long, 2.5–11 km wide, 3–25 m in depth, and covers a surface area of approximately 500 km² (Witte & van Densen, 1995). Mwanza City is located in the north near the entrance of the Gulf (Fig. 1); here the shoreline is completely urbanized. Outside the city range, the littoral zone is characterized by a mixed vegetation of papyrus (*Cyperus papyrus* Linnaeus), reeds, e.g. [*Phragmites australis* (Cav.) Trin. ex Steud.] and water hyacinth [*Eichhornia crassipes*, (Martius) Solms-Laubach], and by rock formations. The bottom of Mwanza Gulf consists of soft, fine-grained sediment. The south of the Gulf at area 1 (station 1 and 2) is shallow with a depth of <5 m (Fig. 1). This area can be considered as a littoral habitat with benthic and terrestrial influences. Area 3 (station 5 and 6) is located in the open lake outside the Gulf with a depth of 15–25 m (Fig. 1). This area can

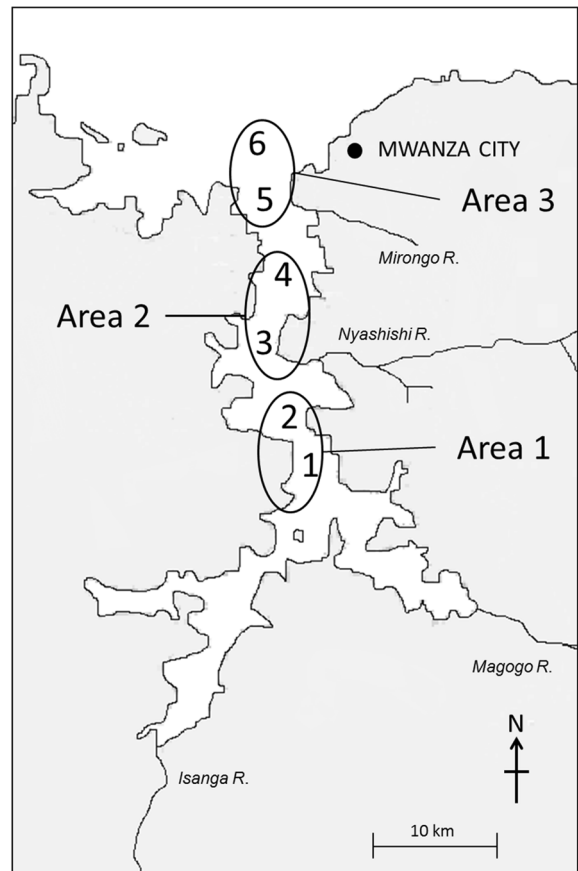


Fig. 1 Map of the Mwanza Gulf with six sampling stations. Stations were divided in three areas: (1) shallow = depth range of <5 m, (2) intermediate = depth range of 5–10 m and (3) deep = depth range of 15–25 m

be considered as a pelagic habitat. Area 2 (stations 3 and 4) has an intermediate depth range of 5–10 m with both littoral and pelagic habitat characteristics (Fig. 1).

Climate

The climate in Lake Victoria is characterized by three seasons, based on the yearly monsoon cycles. During the cooler dry season, from June to August, strong southerly winds and low precipitation keep the water well-mixed, isothermal and oxygenated (Talling, 1966; Akiyama et al., 1977). During the short rainy season, from September to December, winds decline and rainfall and temperature increase, warming up the surface layer of the water column, which becomes gradually stratified. During the long rainy season, from

Table 1 Number of individuals collected in the Mwanza Gulf during the study period from September 2009 to March 2011

Trophic group	Taxa	Common name	2009						2010						2011			Total
			September–Nov		April–May		July–August		April–May		July–August		Jan–March					
			A1 (2)	A2 (3)	A3 (3)	A1 (1)	A2 (1)	A3 (1)	A1 (2)	A2 (2)	A3 (2)	A1 (3)	A2 (3)	A3 (3)	A1 (3)	A2 (3)	A3 (3)	
Invertebrates	Zooplankton		3	2	3	1	1	1	1	1	1	1	1	2	1	1	1	17
	Gastropods	Snail	1	5	5	2	2	1	1	4	2	1	1	7	5	7	7	42
	<i>Caridina nilotica</i>	Shrimp			2	2	2	1	6	6	5	2	2	2	2	4	4	32
	Trichoptera nymph	Caddisfly nymph	1															1
	<i>Baetis</i> nymph	Mayfly nymph						1										1
	Zygoptera nymph	Damselfly nymph				1	1											2
	Anisoptera nymph	Dragonfly nymph				1					3							7
	Ephemeroptera nymph	Mayfly nymph		1														1
	Haplochromine cichlids		8	11	8	4	2	4	18	16	5	5	29	45	54	54	204	
	<i>Lates niloticus</i> Other fish	<i>Lates niloticus</i>	Nile perch	73	61	43	9	18	12	77	92	31	42	32	26	26	516	
<i>Labeo victorianus</i>		Ningu	1	1	1											3		
<i>Oreochromis niloticus</i>		Nile tilapia	1	8					1		2					12		
<i>Synodontis afrofscheri</i>		Marbled squeaker			2	1										3		
<i>Synodontis victoriana</i>		Victoria squeaker	3				2	1	1	4		5	15	13	13	44		
<i>Rastrineobola argentea</i>		Dagaa											5	10	5	20		
<i>Barbus</i> sp.		Barb											6			6		
<i>Brycinus sadleri</i>		Sadler's robber	17		7	4	4	3	9	7		6				57		
<i>Schilbe intermedius</i>		Butter catfish	8		1				2							11		
<i>Clarias gariepinus</i>		Deepwater catfish		1	1				3							5		
<i>Bagrus docmak</i>	Silver catfish														1			
<i>Mormyrus kannume</i>	Elephant-snout fish		1												1			
<i>Protopterus aethiopicus</i>	Marbled lungfish			3				1							4			

Table 1 continued

Trophic group	Taxa	Common name	2009			2010			2011			Total			
			September–Nov	April–May	July–August	Jan–March									
			A1 (2)	A2 (3)	A3 (3)	A1 (1)	A2 (1)	A3 (1)	A1 (2)	A2 (2)	A3 (2)	A1 (3)	A2 (3)	A3 (3)	
	<i>Caecomastacembelus frenatus</i>	Long tail spiny eel	1	112	83	66	19	26	20	112	119	38	93	102	98
Total number of fish			1												

Haplochromines and Nile perch were used for spatial and seasonal analysis of population-level metrics. The short rainy season was sampled from September to November 2009, the long rains from April to May 2010 and January to March 2011 and the dry season from July to August 2010. Areas are indicated as area 1 = A1, area 2 = A2 and area 3 = A3. Numbers of sampling days are indicated between parentheses

January to May, precipitation is high and stratification of the water column becomes strong (Talling, 1966). During the sampling period from 2009 to 2011, Mwanza Gulf had similar seasons, although during the long rains of 2010, there was twice as much rainfall as during the long rains of 2011 (Supplementary Fig. S1).

Data collection

Biological samples were collected from September 2009 to March 2011 during the short rains (September–November 2009), long rains (April–May 2010 and January–March 2011) and dry season (July–August 2010) (Table 1). The datasets gathered during the long rains of 2010 and 2011 were pooled together as isotope values did not differ between these years. Areas were sampled on 1–3 days each season (Table 1).

Fish were caught using gill nets and surface trawling at night. Fish were classified to species level, except for haplochromines, which, for this study, were classified as one group. This was justified by the fact that more than 94% of the haplochromines belonged to species classified as pelagic zooplanktivores or benthic detritivores, which, since their recovery in the 1990s, have similar broad diets in the Gulf including larger invertebrates (Kishe-Machumu et al., 2008, I. J. M. Cornelissen unpublished data) and also have similar habitat utilization. Invertebrates were collected during the day. *Caridina* shrimp and gastropods were collected by hauling a 1 m² square lift net from bottom to surface. Zooplankton was collected by hauling a 150-µm net from bottom to surface and stored in 50-ml jars.

In fish >5 cm standard length, ca. 0.5 cm³ of skinned dorsal muscle tissue was collected. Fish <5 cm were entirely skinned and filleted. Fish tissue was rinsed in distilled water before preservation. Zooplankton was killed with ethanol and then transferred to 2-ml tubes. Gastropods were kept in regularly refreshed, distilled water for 24 h to allow for emptying their digestive tracts from food particles, after which their shells were removed and body tissue was preserved. *Caridina* and insect specimens were preserved entirely. All invertebrates and fish samples were preserved in 70% ethanol and stored at –20°C. The preserved samples were shipped to the laboratory of the Netherlands Institute of Ecology (NIOO) in the

Netherlands for further sample preparation and analyses. There, samples were drained off, freeze-dried and homogenized with stainless steel balls (4 mm in diameter) in 2-ml Eppendorf tubes. Of each sample, 300–500 µg of tissue powder was weighed before $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ isotope analysis. Stable isotopes of samples collected in 2009 were analysed with an Elemental analyser (Eurovector), interfaced with a Conflo 2 device for continuous flow and an Isotope Ratio Mass Spectrometer (IRMS) (Delta XP Advantage, Thermo, Germany). The samples collected in 2010–2011 were measured with an Elemental analyser Flash2000 (Thermo) interfaced with a Conflo 4 and an IRMS (Delta XP Advantage, Thermo, Germany). The isotope ratios were measured against reference standards of carbon and nitrogen using USGS40 L-glutamic Acid C5H9NO4, with $\delta^{15}\text{N}$ of -4.5‰ and $\delta^{13}\text{C}$ of -26.389‰ .

C:N ratios are related to lipid content (Post et al., 2007). Our mean C:N ratios varied from 3.13 to 4.44 between taxa (Supplementary Table S1). We therefore applied a posteriori mathematical normalization of $\delta^{13}\text{C}$ values using the lipid-correction equations given by Post et al. (2007). We corrected for consumer values (invertebrates and fish). The corrections ($\delta^{13}\text{C}$) rely on carbon to nitrogen ratios (C:N):

$$\delta^{13}\text{C}_{\text{corrected}} = \delta^{13}\text{C} - 3.31 + 0.99 \times \text{C:N}.$$

Environmental data of chlorophyll *a*, mean depth, K_{PAR} (attenuation coefficient) and water temperature were collected during this study in the Mwanza Gulf and calculated as described in Cornelissen et al. (2014). Mean wind speed and rainfall were based on data measured in Mwanza by the National Centers for Environmental Information (NOAA-NCEI data, retrieved on May 10, 2011). The environmental data are listed in Supplementary Table S2.

Nile perch diets were analysed by dissecting the stomachs. Stomach fullness was classified into five categories: 0–1% (empty), 1–25%, 25–50%, 50–75% and >75% (full) (Witte & van Densen, 1995). The relative volume per prey category of Nile perch was estimated into the same five categories. Prey were categorized as *Caridina* shrimp, haplochromines, Odonata, *R. argentea*, Nile perch and fish remains.

Data analyses

Baseline correction

$\delta^{15}\text{N}$ values of primary production sources vary in space and time. Therefore, to reliably compare trophic levels (TL) of consumers, their $\delta^{15}\text{N}$ values needed to be corrected with baselines. Since samples were collected in two distinct habitats, i.e. shallow, littoral waters inside the Gulf and open pelagic waters near the entrance, we used a two-end-member mixing model with a littoral and a pelagic source for calculating trophic levels (Post, 2002). The $\delta^{15}\text{N}$ baseline was identified by the two-end-member organisms in $\delta^{13}\text{C}$, which represent the littoral (baseline 1) and pelagic baseline (baseline 2). We used primary consumers as end members and identified these for each area and season separately (Supplementary Table S3). $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ of the littoral baseline did not show any seasonal or spatial variation (Supplementary Table S4) and therefore we used the mean littoral $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ to calculate trophic levels. The pelagic baseline of $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ varied across areas (Supplementary Table S4) and therefore we used a mean pelagic $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ of each area to calculate trophic levels. Trophic levels were calculated as (Post, 2002)

$$\text{TL} = \lambda + (\delta^{15}\text{N}_{\text{sc}} - [\delta^{15}\text{N}_{\text{b1}} \times \alpha + \delta^{15}\text{N}_{\text{b2}} \times (1 - \alpha)]) / \Delta_n,$$

where λ is the trophic position of the baseline organism, $\delta^{15}\text{N}_{\text{sc}}$ is the measured $\delta^{15}\text{N}$ of the consumer of interest, $\delta^{15}\text{N}_{\text{b1}}$ is the measured $\delta^{15}\text{N}$ of baseline 1, $\delta^{15}\text{N}_{\text{b2}}$ is the measured $\delta^{15}\text{N}$ of baseline 2, and Δ_n is the enrichment in $\delta^{15}\text{N}$ per trophic level. We used a λ value of 2 for the trophic position of the baseline organisms. We used 2.4‰ as enrichment per trophic level, which is used in Lake Tanganyika, a rift valley lake (Kilham et al., 2009), and also appropriate for Lake Victoria. The letter α represents the proportion of nitrogen derived from baseline 1 and can be estimated as (Post, 2002)

$$\alpha = (\delta^{13}\text{C}_{\text{sc}} - \delta^{13}\text{C}_{\text{b2}}) / (\delta^{13}\text{C}_{\text{b1}} - \delta^{13}\text{C}_{\text{b2}}),$$

where $\delta^{13}\text{C}_{\text{sc}}$ is the measured $\delta^{13}\text{C}$ of the consumer of interest, $\delta^{13}\text{C}_{\text{b1}}$ is the measured $\delta^{13}\text{C}$ of baseline 1, and $\delta^{13}\text{C}_{\text{b2}}$ is the measured $\delta^{13}\text{C}$ of baseline 2.

Population-level metrics

We used 8 diagnostic population-level metrics (Table 2) based on the $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ isotope data to reveal spatial and seasonal differences in niche use and trophic diversity of populations of haplochromines and Nile perch in Mwanza Gulf. The metrics nitrogen range (dNr), carbon range (dCr), corrected standard ellipse area (SEAc) and mean distance to centroid (CD) indicate the total isotopic space used in the $\delta^{13}\text{C}$ – $\delta^{15}\text{N}$ bi-space by a trophic group. The metrics nitrogen range (dNr) and carbon range (dCr) indicate the total carbon or nitrogen range used by a trophic group and are calculated as the difference between the lowest and highest values of $\delta^{15}\text{N}$ or $\delta^{13}\text{C}$ within a trophic group (Layman et al., 2007). We used SEAc as a measure of the core niche area. It is calculated from the variance and covariance between $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$, containing about 40% of the data points (Batschelet, 1981) and is corrected for small samples sizes according to Jackson et al. (2011). Mean $\delta^{13}\text{C}$ and mean $\delta^{15}\text{N}$ represent the centre of the core niche area. CD is calculated as the mean Euclidean distance of each individual to the $\delta^{13}\text{C}$ – $\delta^{15}\text{N}$ centroid, and is a metric of mean degree of trophic diversity (Layman et al., 2007).

The metrics packing density (MNND) and trophic evenness (SDNND) give information on the dispersion of isotopic values in the bi-space and are related to trophic redundancy. MNND is calculated as the mean of nearest neighbour distance between individual data points and measures the density of data point packing (Layman et al., 2007). A group of individuals with different trophic ecology will be more widely spread in isotopic bi-space and exhibit higher MNND values than a group of individuals with similar trophic ecology. Higher MNND values indicate decreased redundancy. SDNND indicates how evenly (low value) or clustered (high value) the isotope values are spread in isotopic bi-space (Layman et al., 2007). Clustering means that carbon sources and diets of organisms within a cluster are similar, whereas carbon sources and diets differ between separate clusters.

Jackson et al. (2011) developed a Bayesian statistical method to compare metrics across communities with the assumption of a normal distribution. However, in our study, normality of residuals of the isotope data could not be achieved directly or after transformations. In addition, sample sizes varied between areas and seasons. Therefore, bootstrapped means and

95% confidence intervals of the Layman metrics were calculated for each area and season. Spatial and seasonal differences in metrics were significant if 95% confidence intervals did not overlap. We used 10,000 replicates and a minimum of 8 observations to perform the bootstrap analysis (Table 2). As a comparison to the more standard analysis of Bayesian metrics, where normality is assumed, we also analysed Bayesian standard ellipses (SEAb) to compare to the bootstrapped version of SEAc. By comparing both methods, a robust result was acquired.

Moreover, we used Bayesian mixing models to estimate the relative contributions of resources to the diet of Nile perch as compared to results from stomach contents. We ran separate models with prior information on stomach content proportions of prey of each area and season. In this way, the spatial and seasonal variability in resources were included and corrected for the diet estimates. Based on main prey found in stomach contents, *Caridina* shrimp, Nile perch <10 cm TL, haplochromines, Odonata larvae and *R. argentea* were used as resources.

For some area–season combinations, resource isotope values were lacking (e.g. *Caridina* shrimp in areas 1 and 2 in the short rains). We then used the mean of $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ of the resource of samples collected during the study period in the remaining areas. Unfortunately, a similar analysis could not be performed for haplochromine diets, due to the lack of isotope values of detritus and phytoplankton, two major diet items of haplochromines (I. J. M. Cornelissen, unpublished data). We assumed a fractionation factor per trophic level of 2.4‰ for $\delta^{15}\text{N}$ (Lake Tanganyika) (Kilham et al., 2009) and 0.4‰ for $\delta^{13}\text{C}$ (Post, 2002).

Kendall tau correlations were used to relate significant differences in metric values of Table 2 with the environmental variables of Supplementary Table S2. R version 3.1.0 (R Core Team, 2014) was used for the Kendall tau correlations. Diet contributions were calculated using the SIAR package. Metrics were calculated using the SIBER analyses (Jackson et al., 2011) within the SIAR package (Parnell et al., 2008).

Results

The number of fish sampled varied between 20 and 119 for the different areas and seasons (Table 1). In

Table 2 Population-level metrics and 95% confidence intervals of haplochromine cichlids and Nile perch in the Mwanza Gulf

	Short rains			Long rains			Dry season		
	Area 1	Area 2	Area 3	Area 1	Area 2	Area 3	Area 1	Area 2	Area 3
Haplochromines									
dNr	3.00 ^a	3.46 ^a	4.61 ^a	4.24 ^a	3.82 ^a	3.78 ^a	3.47 ^a	2.91 ^a	
	0.51–4.34	1.00–4.19	0.96–6.36	1.83–6.27	1.18–9.68	1.82–7.72	2.17–4.51	1.43–3.47	
dCr	2.37 ^a	2.68 ^a	4.58 ^{ab}	6.25 ^{ab}	4.81 ^{ab}	5.32 ^{ab}	12.50 ^b	5.87 ^b	
	0.36–3.36	1.20–3.42	2.01–5.88	2.89–9.05	2.35–8.13	2.01–12.30	4.32–24.35	3.56–7.31	
SEAc	0.77 ^a	4.35 ^{ab}	6.99 ^{ab}	7.77 ^{ab}	6.83 ^{ab}	7.58 ^{ab}	17.93 ^b	7.34 ^b	
	0.01–1.58	0.51–7.83	0.72–13.67	0.92–15.12	0.42–16.13	1.01–15.37	3.15–39.57	1.73–12.08	
SEAb	2.86 ^a	5.11 ^{ac}	8.71 ^{acd}	8.34 ^{bc}	7.66 ^{bc}	8.06 ^{bc}	20.36 ^d	7.83 ^{ac}	
	1.22–4.96	2.48–8.29	3.72–15.14	5.67–11.26	5.58–9.91	6.07–10.19	11.59–30.01	4.36–11.77	
Mean $\delta^{13}\text{C}$	-14.22 ^c	-18.31 ^a	-19.47 ^a	-13.79 ^c	-15.83 ^{bc}	-18.09 ^{ab}	-17.46 ^{abc}	-17.64 ^{ab}	
	15.05–13.68	19.00–17.61	20.63–18.25	15.41–12.22	17.02–14.67	19.43–16.75	21.06–14.50	19.15–16.11	
Mean $\delta^{15}\text{N}$	7.94 ^{ab}	9.06 ^b	9.45 ^b	6.96 ^a	8.46 ^{ab}	9.18 ^b	8.68 ^{ab}	9.24 ^b	
	7.25–8.96	8.14–9.99	8.03–10.57	5.93–8.01	7.41–9.39	8.24–10.11	7.78–9.58	8.47–10.00	
CD	1.05 ^a	1.42 ^a	1.91 ^a	2.20 ^a	1.72 ^a	1.84 ^a	3.42 ^a	2.08 ^a	
	0.19–2.35	0.71–2.06	0.60–3.57	1.03–3.34	0.86–2.68	1.01–2.77	1.40–7.28	1.29–2.94	
MNND	0.32 ^a	0.49 ^a	0.59 ^a	1.07 ^a	0.97 ^a	1.11 ^a	1.62 ^a	0.75 ^a	
	0.00–0.75	0.07–0.94	-0.01–1.28	0.36–1.75	0.28–1.78	0.41–1.88	0.28–3.56	0.23–1.27	
SDNND	0.71 ^a	0.71 ^a	1.14 ^a	1.01 ^a	0.93 ^a	0.89 ^a	2.23 ^a	0.80 ^a	
	0.00–0.61	0.14–1.31	-0.01 to 2.57	0.26–1.81	0.20–2.18	0.22–1.89	0.33–5.53	0.26–1.36	
Nile perch (<i>Lates niloticus</i>)									
dNr	3.79 ^{ac}	5.81 ^c	4.29 ^{ac}	4.22 ^a	6.31 ^{ac}	6.73 ^{bc}	6.94 ^{ac}	5.78 ^{ac}	4.91 ^{ac}
	2.36–4.79	4.56–6.43	3.12–4.70	3.52–4.45	4.23–7.14	5.2–7.39	3.37–9.52	3.34–7.75	3.88–5.18
dCr	7.13 ^{ab}	6.61 ^a	6.81 ^{ab}	12.34 ^{ab}	9.64 ^{ab}	7.62 ^{ab}	8.49 ^{ab}	8.77 ^{ab}	8.82 ^b
	3.95–8.71	5.65–7.20	4.33–7.47	7.11–15.44	6.43–11.22	6.02–8.21	6.81–9.84	5.87–12.46	7.42–9.40
SEAc	4.18 ^a	9.47 ^b	7.12 ^{ab}	11.14 ^b	11.49 ^{ab}	12.85 ^b	11.08 ^{ab}	8.56 ^{ab}	8.97 ^{ab}
	1.66–6.59	6.96–12.00	4.52–9.61	7.43–14.68	5.90–15.01	9.09–16.31	4.85–17.21	3.97–13.14	5.55–12.23
SEAb	4.45 ^a	9.52 ^{bc}	6.98 ^{ab}	11.48 ^{bc}	11.15 ^{bc}	13.18 ^c	11.06 ^{bc}	8.74 ^{bc}	9.58 ^{bc}
	3.47–5.49	7.21–11.95	5.00–9.12	8.47–14.69	8.20–14.32	9.23–17.48	8.66–13.58	7.01–10.56	6.43–13.06
Mean $\delta^{13}\text{C}$	-14.89 ^e	-18.59 ^{ab}	-19.78 ^a	-14.54 ^c	-16.16 ^{de}	-17.72 ^{bc}	-16.64 ^{cd}	-17.45 ^{bcd}	-17.53 ^{bcd}
	15.50–14.30	19.25–17.92	20.40–19.15	15.55–13.54	16.94–15.39	18.49–16.94	17.46–15.83	18.20–16.70	18.37–16.71

Table 2 continued

	Short rains			Long rains			Dry season		
	Area 1	Area 2	Area 3	Area 1	Area 2	Area 3	Area 1	Area 2	Area 3
	Mean $\delta^{15}\text{N}$	9.06 ^c	8.40 ^{abc}	9.07 ^{cd}	7.58 ^a	7.86 ^{ab}	8.07 ^{abd}	8.72 ^{bc}	9.06 ^c
CD	8.77–9.35	7.84–9.96	8.64–9.49	7.13–8.02	7.30–8.42	7.40–8.73	8.18–9.24	8.60–9.50	8.30–9.18
MNND	1.40 ^a	2.27 ^{ab}	1.81 ^{ab}	2.58 ^{ab}	2.21 ^{ab}	2.61 ^b	2.35 ^{ab}	2.12 ^{ab}	2.23 ^{ab}
SDNND	0.86–1.98	1.95–2.58	1.30–2.34	1.93–3.24	1.66–2.78	2.18–3.04	1.82–2.89	1.67–2.58	1.77–2.77
	0.35 ^a	0.40 ^a	0.31 ^a	0.45 ^a	0.42 ^a	0.41 ^a	0.54 ^a	0.51 ^a	0.34 ^a
	0.17–0.51	0.26–0.54	0.15–0.46	0.23–0.66	0.23–0.61	0.22–0.59	0.30–0.78	0.30–0.73	0.17–0.52
	0.58 ^a	0.43 ^a	0.51 ^a	0.72 ^a	0.65 ^a	0.60 ^a	0.73 ^a	0.65 ^a	0.58 ^a
	0.20–0.95	0.31–0.55	0.23–0.80	0.32–1.11	0.30–1.03	0.40–0.79	0.33–1.10	0.35–0.96	0.36–0.80

*dN*r nitrogen range, *dC*r carbon range, *SEAc* corrected standard ellipse area, *SEAb* Bayesian standard ellipse area, *mean* $\delta^{13}\text{C}$ mean $\delta^{13}\text{C}$, *mean TL* mean of trophic level, *CD* trophic diversity, *MNND* packing density, *SDNND* trophic evenness. Metrics were bootstrapped, except for *SEAb*, which was analysed with Bayesian methods. *SEAb* are presented with credibility intervals. Means with different letters indicate differences based on non-overlapping 95% confidence intervals, whereas similar letters indicate overlapping of confidence intervals

general, haplochromines and Nile perch were the most dominant fish taxa caught in Mwanza Gulf (7–55% and 27–82% of total numbers, respectively). 86% of Nile perch caught were juveniles (standard length of <40 cm) with a mean standard length of 21.8 cm and a size range of 2–67 cm, which did not vary significantly over space and time. Mean $\delta^{13}\text{C}$ isotope ratios of each taxon in Mwanza Gulf ranged from -21.4 [Caecomastacembelus frenatus (Boulenger, 1901)] to -14.2‰ [Bagrus docmak (Forsskäl, 1775)] (Fig. 2, Supplementary Table S5). The variation in the $\delta^{13}\text{C}$ isotope ratios caused taxa to overlap (see error bars in Fig. 2). Synodontis afrofisheri Hilgendorf, 1888 was most variable in $\delta^{13}\text{C}$ values, with standard errors ranging from -19.3 to -14.9‰.

Mean $\delta^{15}\text{N}$ values ranged from 4.9 (gastropods) to 10.1‰ (B. docmak) in Mwanza Gulf (Fig. 2, Supplementary Table S5). Zygoptera nymphs showed large variation in mean $\delta^{15}\text{N}$, with standard errors ranging from 3.3 to 7.3‰. Amongst the fish, Schilbe intermedius (Rüppell, 1832), Nile perch, haplochromines, Brycinus sadleri and Mormyrus kannume Forsskäl, 1775 had similar $\delta^{15}\text{N}$ values of ca. 8.5‰. Rastri-neobola argentea, Synodontis victoriae Boulenger, 1906, B. docmak and C. frenatus showed the highest $\delta^{15}\text{N}$ values (ca. 10‰) and Oreochromis niloticus the lowest (5.2‰).

The core niche area (*SEAc*-ellipses in Fig. 2) of all invertebrates combined was larger than that of haplochromines, Nile perch and other fish. These three fish groups showed large overlap amongst each other, but not with invertebrates.

Seasonal and spatial dynamics in fish interactions

We observed clear seasonal and spatial shifts along the $\delta^{13}\text{C}$ -axis in the position of core niche areas of Nile perch and haplochromines in Mwanza Gulf (*SEAc*-ellipses in Fig. 3, for seasonal and spatial mean $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values of all species see Supplementary Table S6). During the short rains, strong spatial differences between niches occurred along the $\delta^{13}\text{C}$ axis for both haplochromine cichlids and Nile perch (Fig. 3a, d). Seasonal mean $\delta^{13}\text{C}$ values were especially different in area 1 (highest values) compared to areas 2 and 3 (lowest values) (Table 2). This means that niches of both haplochromines and Nile perch were spatially differentiated (Fig. 3a, d). This differentiation was enhanced by the relatively small core

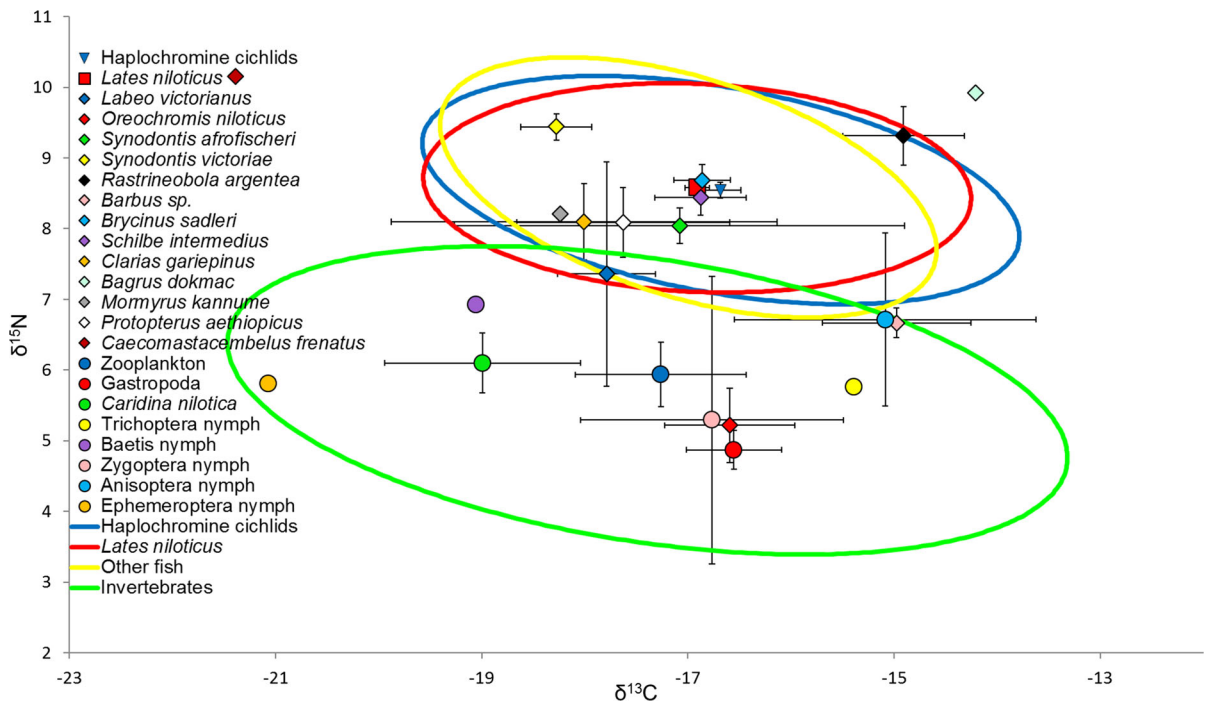


Fig. 2 Mean $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values with standard errors of taxa found in the Mwanza Gulf. Symbols represent trophic groups of taxa (haplochromine cichlids = reversed triangle, Nile perch = squares, other fish = diamonds and inver-

tebrates = circles). Core niche areas (SEAc-ellipses) of trophic groups are indicated for haplochromine cichlids (blue), Nile perch (red), other fish (yellow) and invertebrates (green). Details of trophic groups are listed in Table 1

niche area and carbon range in area 1 and/or areas 2 and 3 during the short rains (SEAc and dCr, Table 2). A similar, spatial effect was visible during the long rains, but less strong (Fig. 3b, e), because mean $\delta^{13}\text{C}$ values were more similar and in Nile perch also because of the relatively large core niche areas (SEAc, Table 2). During the dry season, mean $\delta^{13}\text{C}$ values and core niche areas of the three areas overlapped (Fig. 3c, f, mean $\delta^{13}\text{C}$, Table 2), with a large core niche area and dCr in area 1 of haplochromines (SEAc, dCr, Table 2).

Trophic diversity (CD) varied less than core niche area (SEAc). Trophic diversity of haplochromines did not vary spatially and seasonally (Table 2). Trophic diversity of Nile perch was smallest in area 1 in short rains and largest in area 3 in long rains (Table 2).

There was no overall spatial and seasonal pattern in packing density (MNND), trophic evenness (SDNND) and mean $\delta^{15}\text{N}$ of haplochromines and Nile perch (Table 2). Mean $\delta^{15}\text{N}$ did show some variation with lowest values in area 1 during the long rains for both haplochromines and Nile perch. MNND and SDNND did not vary spatially and seasonally (Table 2).

Depth was negatively correlated with $\delta^{13}\text{C}$ values, whereas chlorophyll was positively correlated with $\delta^{13}\text{C}$ values for Nile perch and haplochromines (Table 3). Core niche areas (SEAc) and carbon range (dCr) correlated with seasonal environmental variables. Core niche area of haplochromines was negatively related to water temperature and carbon range was negatively related to rainfall and water temperature (Table 3). Core niche area, trophic diversity (CD) and carbon range of Nile perch were negatively related to wind speed (Table 3).

Haplochromines and *Caridina* both dominated the diet of Nile perch in stomach contents (Table 4). Haplochromines, *Caridina*, Nile perch and Odonata dominated the diet of Nile perch based on isotopes (Table 4). Relative contribution of *Caridina* to the diet of Nile perch based on both isotopes and stomach contents was highest in areas 2 and 3 in short and long rains (Table 4). Relative contribution of haplochromines decreased from area 1 to area 3 during the short and long rains and was similar for areas during the dry season based on isotopes and stomach content

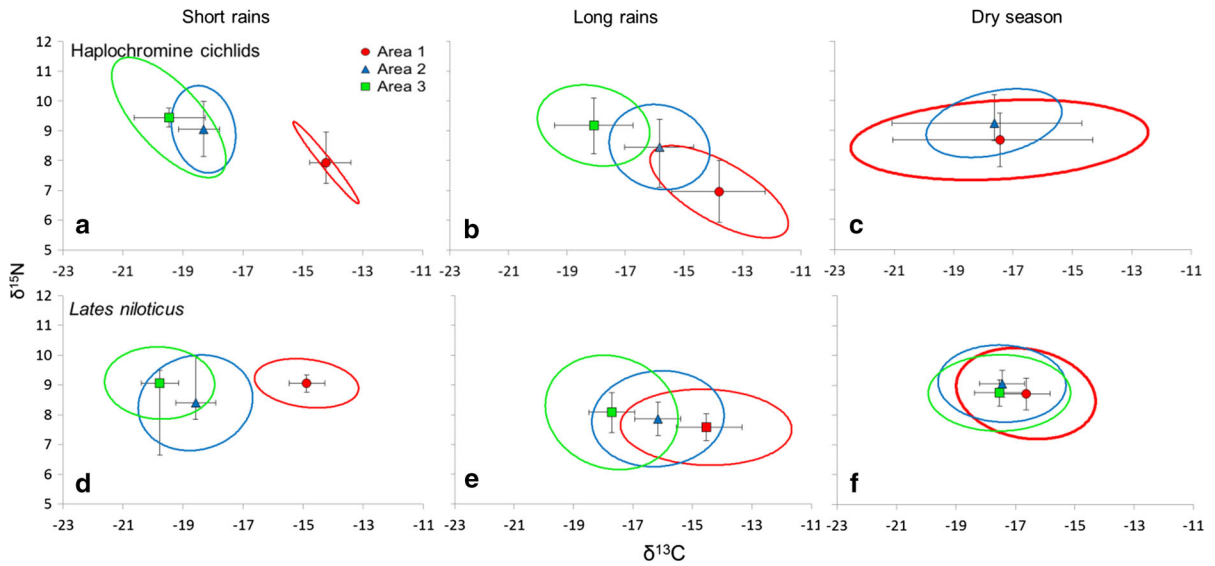


Fig. 3 Spatial and seasonal variation of mean $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values and core niche areas (SEAc-ellipses) of (a–c) haplochromines, d–f *Lates niloticus* (Nile perch). Error bars represent 95% confidence intervals. Means were bootstrapped. For location of sampling stations and the three areas see Fig. 1

Table 3 Kendall tau rank correlation between environmental variables (Mean depth, wind speed, rainfall, chlorophyll concentration, water temperature and K_{PAR}) and metrics of haplochromines and Nile perch from Table 2

Metric	Depth	Wind speed	Rainfall	Chlorophyll <i>a</i>	Temperature	K_{PAR}
Haplochromines						
dCr			-0.78		-0.93	
SEAc					-0.64	
SEAb					-0.57	
Mean $\delta^{13}\text{C}$	-0.70			0.71		
Mean $\delta^{15}\text{N}$	0.70			-0.5		-0.57
Nile perch (<i>Lates niloticus</i>)						
dCr		-0.67				
SEAc		-0.8				
SEAb		-0.8				
Mean $\delta^{13}\text{C}$	-0.67			0.72		
Mean $\delta^{15}\text{N}$		0.65				
CD		-0.55				

Only significant ($P < 0.05$) correlation coefficients are shown

(Table 4). The relative contributions of *R. argentea* were low for both isotopes and stomach contents (Table 4). The contributions of Odonata and Nile perch were higher based on isotopes than based on stomach contents, which resulted in lower contribution of haplochromines based on isotopes than on stomach contents (Table 4).

Discussion

We used $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ stable isotope ratios, quantitative population-level metrics and diets to investigate the trophic dynamics of fish species in Mwanza Gulf, Lake Victoria. However, there are some caveats, such as the fact that our samples were preserved in

Table 4 Relative resource contributions to the diet of Nile perch based on stable isotopes with 95% confidence intervals, and resource contributions based on stomach contents with standard deviations

Season	Area	Resource	Isotope diet contribution			Stomach diet contribution	
			Mean	Lower CI	Upper CI	Mean	Std
Short rains	1	<i>Caridina nilotica</i>	0.27	0.20	0.33	0.31	0.45
		Haplochromines	0.23	0.02	0.41	0.46	0.36
		Nile perch	0.10	0.00	0.29	0.09	0.17
		Odonata	0.21	0.10	0.32	0.03	0.14
		<i>Rastrineobola argentea</i>	0.19	0.01	0.33	0.10	0.18
	2	<i>Caridina nilotica</i>	0.51	0.42	0.58	0.55	0.47
		Haplochromines	0.06	0.00	0.26	0.31	0.27
		Nile perch	0.24	0.00	0.55	0.09	0.15
		Odonata	0.20	0.00	0.34	0.01	0.10
		<i>Rastrineobola argentea</i>	0.00	0.00	0.03	0.04	0.11
	3	<i>Caridina nilotica</i>	0.57	0.47	0.70	0.80	0.38
		Haplochromines	0.06	0.00	0.24	0.16	0.21
		Nile perch	0.19	0.00	0.40	0.01	0.06
		Odonata	0.16	0.02	0.30	0.01	0.07
		<i>Rastrineobola argentea</i>	0.02	0.00	0.17	0.01	0.06
Long rains	1	<i>Caridina nilotica</i>	0.07	0.00	0.27	0.15	0.34
		Haplochromines	0.12	0.00	0.51	0.59	0.42
		Nile perch	0.40	0.00	0.67	0.02	0.08
		Odonata	0.36	0.27	0.49	0.05	0.19
		<i>Rastrineobola argentea</i>	0.05	0.00	0.39	0.19	0.27
	2	<i>Caridina nilotica</i>	0.56	0.38	0.70	0.43	0.48
		Haplochromines	0.04	0.00	0.28	0.42	0.40
		Nile perch	0.17	0.00	0.46	0.01	0.08
		Odonata	0.21	0.00	0.49	0.02	0.12
		<i>Rastrineobola argentea</i>	0.02	0.00	0.11	0.12	0.22
	3	<i>Caridina nilotica</i>	0.53	0.41	0.66	0.56	0.49
		Haplochromines	0.00	0.00	0.01	0.31	0.34
		Nile perch	0.44	0.18	0.47	0.02	0.09
		Odonata	0.03	0.00	0.30	0.00	0.00
		<i>Rastrineobola argentea</i>	0.00	0.00	0.01	0.10	0.21
Dry season	1	<i>Caridina nilotica</i>	0.27	0.18	0.35	0.16	0.32
		Haplochromines	0.17	0.00	0.33	0.53	0.42
		Nile perch	0.04	0.00	0.07	0.04	0.13
		Odonata	0.38	0.24	0.49	0.24	0.39
		<i>Rastrineobola argentea</i>	0.13	0.00	0.36	0.02	0.10
	2	<i>Caridina nilotica</i>	0.55	0.47	0.62	0.31	0.43
		Haplochromines	0.11	0.00	0.38	0.45	0.39
		Nile perch	0.34	0.05	0.47	0.01	0.04
		Odonata	0.01	0.00	0.03	0.20	0.37
		<i>Rastrineobola argentea</i>	0.00	0.00	0.02	0.04	0.12
	3	<i>Caridina nilotica</i>	0.17	0.00	0.31	0.25	0.41
		Haplochromines	0.19	0.00	0.40	0.59	0.44
		Nile perch	0.16	0.00	0.47	0.11	0.22

Table 4 continued

Season	Area	Resource	Isotope diet contribution			Stomach diet contribution	
			Mean	Lower CI	Upper CI	Mean	Std
		Odonata	0.46	0.34	0.60	0.05	0.17
		<i>Rastrineobola argentea</i>	0.01	0.00	0.06	0.00	0.00

Table 5 Observations of trophic positions of main taxa in the Tanzanian part of Lake Victoria (LV) and Mwanza Gulf (MW) according to different authors

Taxa	MW 1977 Downing (2012)	LV 2000 Matsuishi et al. (2006)	MW 2005 Downing (2012)	MW 2009–2011 This study
Zooplankton	2.1	2	2.1	2.2
<i>Caridina nilotica</i>	2	2.3	2.4	2.1
<i>Oreochromis niloticus</i>	2.2	2.6	2.2	2.2
Haplochromines	2–3	3	3.2	3.3
<i>Rastrineobola argentea</i>	3.1	3.1	2.9	3.4
Nile perch (<i>Lates niloticus</i>) (juvenile, ≤ 40 cm)		3.5	3.6	3.2
Nile perch (<i>Lates niloticus</i>) (adult, >40 cm)	3.4	3.9	4.2	3.3

Observations for Lake Victoria (Matsuishi et al., 2006) and Mwanza Gulf from 1977 and 2005 (Downing, 2012) were based on stomach contents and estimated by ECOPATH. Observations for Mwanza Gulf from 2009 to 2011 were based upon $\delta^{15}\text{N}$ stable isotope values (this study)

ethanol before isotope analyses. Although samples were preserved consistently, ethanol could have affected isotope values. Ethanol reduces lipid content of tissue and, therefore, ethanol mostly affect $\delta^{13}\text{C}$ (Kaehler & Pakhomov, 2001; Cummings et al., 2010; Syvärante et al., 2011; Ford et al., 2016) and effects are species-specific (Kelly et al., 2006; Syvärante et al., 2008). The C:N ratios of our taxa ranged between 3.1 and 4.4, indicating relatively low lipid contents between taxa (Supplementary Table S1) and thus a minimal lipid effect on $\delta^{13}\text{C}$ values. Furthermore, we used a lipid normalization (Post et al., 2007), which corrects for variable lipid contents affecting $\delta^{13}\text{C}$ values. We are convinced that in this way ethanol effects were minimal.

We used bootstrapped metrics instead of the commonly used Bayesian metrics. We compared the bootstrapped standard ellipse area (SEAc) with the Bayesian standard ellipse area (SEAb) for validation. In general, SEAc corresponded well with SEAb, especially when sample sizes were large as in the case of Nile perch. This validates our use of bootstrapped metrics.

Most fish in the Mwanza Gulf were positioned mid-range compared to the carbon ranges of invertebrates

in the food web. This indicates omnivory at higher trophic levels and fish relying heavily on invertebrates. This is in contrast with the large diversity of species occupying many different feeding niches, based on stomach and gut analyses, observed in Lake Victoria before the Nile perch upsurge (van Alphen et al., 2003). Many abundant fish species, for instance *O. niloticus*, *B. sadleri*, *R. argentea* and haplochromines, that were originally known as phytoplankton, zooplankton or detritus feeders extended their diets with larger invertebrates, such as insects, *Caridina* shrimps and even small fishes (Wanink, 1998; Wanink & Witte, 2000; Katunzi et al., 2003; Njiru et al., 2004; Wanink & Joordens, 2007; Kische-Machumu et al., 2008).

Lake Victoria's top predator, Nile perch, showed relatively low $\delta^{15}\text{N}$ values in the food web of Mwanza Gulf compared to other consumers. Similar $\delta^{15}\text{N}$ values between Nile perch and haplochromines and an enrichment of 2–3‰ between Nile perch and invertebrates indicate that Nile perch relies more on invertebrates than fish. This agrees with a diet of *Caridina* shrimps found in stomachs of juvenile Nile perch after the decline of haplochromines (Katunzi

et al., 2006). However, more recent diet analyses of stomach contents in the Mwanza Gulf revealed that haplochromines and *Caridina* both dominated the diet of juvenile Nile perch of <40 cm (Kishe-Machumu et al., 2012). This is confirmed by stomach analyses in this study. We therefore observed large differences in the diet estimations between stomach content and isotope analyses. The contribution of haplochromines to the diet of Nile perch was smaller based on isotopes than based on stomach contents. Odonata and small Nile perch showed a considerable contribution in isotope diets, whereas in stomach contents they were only contributing little to the diet of Nile perch.

There are several reasons that might explain the discrepancy between isotopes and stomach contents. Firstly, the Bayesian models used for estimating isotope diets might have resulted in some bias in estimates. Most datasets were not normally distributed. The model also showed difficulties distinguishing between sources, especially between diets of small Nile perch and haplochromines, Odonata and *Caridina*. This was mainly caused by a high variability within sources in each area and season, which results in a under- or over-estimation in sources, i.e. higher contributions of Odonata and Nile perch and lower contributions of haplochromines to the isotope diets. This highlights the importance of incorporating resource variation in mixing models (Hyndes et al., 2013). Furthermore, we used a constant enrichment in $\delta^{15}\text{N}$ between Nile perch and the different prey types in the model. However, enrichment varies between different trophic transfers because of differences in $\delta^{15}\text{N}$ assimilation between types of prey (McCutchan et al., 2003). Still, this cannot fully explain the similar $\delta^{15}\text{N}$ levels we observed between Nile perch and its haplochromine prey, because the enrichment is larger for fish predators feeding on high-protein preys such as fish, than for fish feeding on invertebrate prey (McCutchan et al., 2003).

Secondly, the discrepancy between isotope diet estimations and stomach contents may be caused by Nile perch's feeding behaviour. The relative high proportions of fish found in stomachs were of Nile perch caught at night and only represent its night-time feeding behaviour. As Nile perch exhibits a diel feeding pattern of consuming more shrimps during the day and more fish at night (Mkumbo & Ligetvoet, 1992; Goudswaard et al., 2004), the contribution of fish in its diet as based on stomach content analyses is probably overestimated.

Thirdly, isotopes cover an integrated timespan of weeks compared to the timespan of hours in diets of stomach analyses. A Nile perch sampled in the Gulf may have been feeding on haplochromines there, resulting in a higher proportion of fish in stomach analyses, but may have been feeding previously on *Caridina* shrimps outside the Gulf where *Caridina* densities are higher and where it is still a major prey in Nile perch diets (Ngupula & Mlaponi, 2010; Cornelissen et al., 2015). Nevertheless, Nile perch isotope values correspond more to an invertebrate-based diet and haplochromines are a less important food source for Nile perch than is suggested by stomach content analyses alone. This highlights the importance of both isotope and stomach content methods to study resource use in consumers.

After the Nile perch upsurge in the late 1980s, the Lake Victoria food web simplified with *Caridina* shrimp, *R. argentea*, *O. niloticus*, zooplanktivorous and detritivorous haplochromine cichlids and Nile perch dominating the food web. When comparing our estimates of isotopic trophic positions, most taxa in our study correspond with the estimates reported for 1977, 2000 and 2005 in Lake Victoria (Table 5) (Matsuishi et al., 2006; Downing, 2012). Therefore, despite the loss of biodiversity in Lake Victoria since the Nile perch upsurge in the 1980s (Witte et al., 1992a), the overall trophic structure of the food web seems unchanged since 1977 when haplochromines still dominated the food web. Yet, Nile perch in our study, especially of >40 cm, showed lower trophic levels than in 1977, 2000 and in 2005 (Table 5). However, the higher trophic levels observed in those years for Nile perch were all solely based on stomach content analyses and are therefore probably overestimates.

We found large seasonal differences in carbon sources of fish in Mwanza Gulf. In contrast to our hypothesis, differentiation in the niche position characterized fish during the short rainy season, because of a large spatial differentiation in carbon sources and smaller carbon ranges and core niche area especially in area 1 during the short rains (dCr, SEAc, Table 2; Fig. 3). This spatial differentiation of carbon sources was probably caused by the increased run-off from the land into the Gulf, the effect of which was greatest in area 1, deep inside the Gulf and decreased towards area 3 in the open water outside the Gulf. The negative $\delta^{13}\text{C}$ values found in the open water outside the Gulf

indicate that isotopic composition of fish here was mainly influenced by pelagic phytoplankton (France, 1995; Hecky & Hesslein, 1995; Keough et al., 1996; Schindler et al., 1997).

The extreme positive $\delta^{13}\text{C}$ values inside the gulf in shallow water indicate an increased effect of littoral/benthic influence and/or increased primary production on fish (France, 1995; Casey & Post, 2011). Littoral primary producers such as macrophytes, benthic algae and increased phytoplankton growth often seen in shallow inshore areas all result in enriched $\delta^{13}\text{C}$ values. However, macrophytes probably contribute little to the food chain of haplochromines and Nile perch in Mwanza Gulf because they do not feed on macrophytes (Katunzi et al., 2003; Kische-Machumu et al., 2008; Cornelissen et al., 2015), nor do their prey that feed on detritus, phytoplankton, zooplankton and invertebrates. This is consistent with studies in a satellite lake of Lake Victoria, where macrophytes contribute little to consumers in the food web (Hecky & Hesslein, 1995; Mbabazi et al., 2010).

In eutrophic water, like Mwanza Gulf, phytoplankton production often causes light limitation for the benthic primary production pathway in the food web (Vadeboncoeur et al., 2003). Therefore, benthic algae are probably of minimal influence on fish. High primary productivity and high rates of N-fixation with associated phytoplankton blooms may also result in an enrichment of $\delta^{13}\text{C}$ (Mugidde, 2001; Casey & Post, 2011). The higher phytoplankton biomass in shallow waters compared to deep waters (Supplementary Table S2) indicates higher primary production rates in shallow waters, which might have contributed to an enriched $\delta^{13}\text{C}$ of fish in shallow water. N-fixation rates were low in Mwanza Gulf (Cornelissen et al., 2014) and, therefore, N-fixing bacteria are unlikely to be a major carbon source for fish. Terrestrial carbon also has typically enriched $\delta^{13}\text{C}$ values. The rainfall in September to November 2009 probably increased the run-off of terrestrial carbon and therefore might also explain the spatial differentiation in carbon sources and the enriched $\delta^{13}\text{C}$ values of fish in shallow waters during the short rains. The long rains showed a similar, but less extreme spatial shift in carbon sources as the short rains, indicating a more mixed use of carbon sources by fish. The long rains seemed to represent a transition period where carbon sources start to diffuse over the Gulf, before becoming mixed during the dry season.

The dry season showed similar $\delta^{13}\text{C}$ ranges of fish between areas which resulted in overlapping niches between areas (Fig. 3). This indicates that during this time fish were omnivorous, using a mixture of carbon sources regardless of their location in the Gulf. This can be explained by the combination of increasing winds and little rainfall during the dry season (Fig. S1), which resulted in a well-mixed column and no run-off. This caused a mixed carbon environment throughout the gulf at the base of the food web.

Diet analyses of isotopes and stomach contents showed decreasing proportions of *Caridina* shrimp and increasing proportions of haplochromines in the diet of Nile perch from shallow to deep water during the rainy periods. This was probably caused by spatial variation in Nile perch size at which ontogenetic diet shifts occur (Cornelissen et al., 2015). The seasonal high abundance of *Caridina* in deep water and the corresponding high occurrence of *Caridina* in their diets indicate here a late dietary shift of Nile perch from invertebrates to fish (Cornelissen et al., 2015). In shallow water, Nile perch shifted from *Caridina* to fish at a much smaller size (Cornelissen et al., 2015), leading to a higher contribution of haplochromines in shallow water.

Spatial and seasonal changes in carbon sources at the base of the food web affected carbon use and in some extent niche size and trophic diversity of fish at higher trophic levels. In our study, depth and chlorophyll *a* correlated with the spatial distribution of available carbon sources. This is also observed in estuaries where abiotic factors such as nutrients and light reflect the spatial variability of carbon sources (Hyndes et al., 2013). In our study, seasonal environmental factors such as wind, rainfall and temperature correlated with trophic diversity and niche size. In estuaries, seasons also influence trophic diversity of food-web structures where higher variabilities of carbon sources due to primary production and terrestrial inputs result in increased trophic diversities after rainy periods (Abrantes et al., 2014).

Conclusion

We conclude that fish in the food web of Lake Victoria's Mwanza Gulf are omnivorous with a heavy reliance on invertebrates and that environmental factors influence the higher trophic levels of the food

web on spatial and seasonal scales. The significant effect of environmental factors on food-web dynamics has previously been shown in highly fluctuating systems such as ponds along a hydroperiod gradient, rivers, wetlands and coastal areas (Zeug & Wine-miller, 2008; Hyndes et al., 2013; O'Neill & Thorp, 2014; Schriever, 2015; Thormar et al., 2016). The patterns of heterogeneity in food webs of lakes should be investigated further in order to explain responses to environmental changes such as eutrophication. Eutrophication often results in a loss of diversity and a simplified food web (Coll et al., 2011; Thormar et al., 2016; Xu et al., 2016). In Lake Victoria, the increasing eutrophication and introduction of Nile perch led to a high degree of omnivory and functional redundancy in the food web and the dominance of resilient species (Ojwang et al., 2010). However, a simplified food web with few trophic links is more vulnerable for collapse and as eutrophication continues in Lake Victoria, it is unknown how this will affect food-web dynamics in the future.

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