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Stable Isotope Analyses of Food Web Structure and Fish Diet in Napoleon and Winam Gulfs, Lake Victoria, East Africa

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ABSTRACT. *The food web structures in Napoleon and Winam gulfs, Lake Victoria, were characterized using stable nitrogen and carbon isotope analyses. Similar biota in Napoleon Gulf had significantly lighter* $\delta^{15}N$ *values and heavier* $\delta^{13}C$ *values than similar biota in Winam Gulf, indicating different basal isotopic values. In both gulfs, Nile perch* (Lates niloticus) *was the top trophic predator while Nile tilapia* (Oreochromis niloticus) *was littoral and feeding at lower trophic levels.* Rastrineobola argentea *and* Yssichromis laparograma *had surprisingly high* $\delta^{15}N$ *values, close to those of Nile perch, which were not consistent with the high isotopic values of their assumed zooplankton prey.* Caridina nilotica, *a freshwater shrimp, had a wide range of* $\delta^{13}C$ *values but low* $\delta^{15}N$ *values, consistent with their appearance in nearly all habitants in the lake, and their presence in the stomaches of most fish species. Nile perch showed an increase in* $\delta^{15}N$ *and* $\delta^{13}C$ *values with size, signifying that piscivory increases and their dietary reliance on invertebrates decreases as they mature. Stable isotope values for Napoleon Gulf biota which were adjusted for different basal values were not statistically different from those of Winam Gulf biota, suggesting that stable carbon and nitrogen isotopes fractionate consistently through trophic transfers in Lake Victoria. The stable isotope data illustrate a short food web, with the top predator Nile perch feeding on a restricted set of fish and macroinvertebrate species, including its own young.*

INDEX WORDS: *Stable isotopes, Nile tilapia, Nile perch, Lake Victoria, aquatic food webs.*

INTRODUCTION

Lake Victoria has experienced dramatic changes in recent times, including eutrophication and deoxygenation, (Hecky 1993, Hecky *et al.* 1994), the extirpation of native cichlid species (Witte *et al.* 1992), an increase in Nile perch (*Lates niloticus*), Nile tilapia (*Oreochromis niloticus*), and *Rastrineobola argentea* fisheries (SEDAWOG 1999) and the upsurge and decline of water hyacinth, *Eichhornia crassipes* (Twongo 1996; R.E. Hecky *pers. comm.*). The food web structure in the lake is shifting, based on the volume and composition of the fish catch in the lake as well as on the stomach contents of fish (Balirwa 1998, Ogutu-Ohwayo 1995, Wanink 1998). There has to date been little actual quantification of the trophic interactions within the system beyond diet studies for selected species which are limited in spatial and temporal coverage. An understanding of the current food web structure in the lake, including site-to-site variability, is essential to support current and future management initiatives. This information will also complement on-going studies attempting to quantify the impacts of changing fish community composition on the economic and social well being of the people living in Lake Victoria's watershed. In this study, the food web structures in two gulfs of Lake Victoria, Winam (Kenya) and Napoleon (Uganda), are quantified using stable isotope relationships. The two gulfs have similar population and human usage patterns, although the morphometery

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TABLE 1. Selected water quality parameters for Lake Victoria, Napoleon Gulf, and Winam Gulf. Superscripts indicate the original data source of each parameter. Personal data (oxygen, Secchi depth, pH, conductivity, and temperature) were collected during the study period. Land use parameters and biological oxygen demand (BOD) are presented to give an idea of human impacts and possible pollution. Note that all references from Scheren* et al. *2000 include the* whole *shoreline in each country, not just specific gulfs.

Parameters	Napoleon Gulf	Winam Gulf
Chlorophyll-a (mg/m^3)—Dry season (June to Sept.)	22.1–51.4 [1]	9.3–21.0 [2*]
Chlorophyll-a (mg/m^3)—Wet season (March to May)	13.0–54.2 [3,4]	8.8–17.2 [2]
Surface dissolved oxygen (mg/L)	7.1 ± 0.8 (5.5–7.7)[4]	7.0 ± 1.3 (5.2–8.5)[4]
Secchi depth (m)	1.1 ± 0.3 (0.8–1.4)[4]	0.8 ± 0.2 (0.6–1.1)[4]
Surface pH	8.3 ± 0.2 (8.0–8.5)[4]	8.1 ± 0.2 (7.8–8.4)[4]
Surface conductivity (umho/cm at 20°C)	101 ± 2.7 (98–105)[4]	177 ± 3.9 (169–181)[4]
Surface temperature (°C)	26.8 ± 0.9 (25.6–28)[4]	26.9 ± 0.9 (25.8–28.4)[4]
Surface dissolved NH_4 (μM)	0.5[5]	0.4, 0.7, 6.8[6]
Surface dissolved NO_3 (μM)	0.5[5]	n.d., 0.3, 1.0[6]
Present population density (people/km^2)	246 (projected [7]	259[8]
% of dry land occupied by large-scale farms	2[7]	11[9]
Estimated % of catchment that is cultivated	40.0%[10]	30.2%[10]
Estimated production of industries in catchment (tonnes*/yr)	151,820[10]	875,770[10]
Most likely total BOD loading (tonnes*/yr)	4,540[10]	7,510[10]
Estimated % of BOD loading from domestic sources	75.9%[10]	88.1%[10]

[1] Muggide 1992; [2] Lung'ayia *et al.* 2000 (*extreme value of 71.5 excluded); [3] Ramlal *et al.* 2001; [4] Personal data; [5] Lehman and Branstrator 1994; [6] Gophen *et al.* 1995; [7] The Republic of Uganda 1999 Statistical Abstract. 2000; [8] Republic of Kenya 2000 Economic Survey. 2000; [9] Republic of Kenya 1997; [10] Scheren *et al.* 2000
*metric tons

and water chemistry differ (Table 1). Winam Gulf is an isolated gulf nearly closed to the main lake, and its waters have a higher conductivity (177 μmho/cm). Napoleon Gulf is open to the lake, is constantly flushed by the Nile River outflow, and has lower conductivity (101 μmho/cm) which is similar to Lake Victoria proper.

Characterization of trophic levels and food web structure has traditionally been based on dietary analyses of fish stomach contents. While dietary analysis provides valuable taxonomic information on fish diets, they can be complemented by the analysis of stable nitrogen ($\delta^{15}N$) and carbon ($\delta^{13}C$) isotope ratios of biota to characterize food web structure and trophic interactions (Peterson and Fry 1987). $\delta^{13}C$ and $\delta^{15}N$ values integrate long-term dietary patterns and can be used as numerical variables for statistical analyses. Stable isotope measurements have been successfully used to estimate feeding patterns and food web structure in several African lakes, including Lakes Kyoga in Uganda (Hecky and Hesslein 1995) and Malawi in southern Africa (Bootsma *et al.* 1996, Genner *et al.* 1999, Hecky and Hesslein 1995, Kidd *et al.* 2001).

Stable nitrogen isotopes are useful in determining the relative trophic position of biota. Nitrogen isotopes consistently fractionate in organisms: ^{14}N is selectively eliminated while ^{15}N is incorporated into body tissues. Consequently, with each successive trophic transfer, $\delta^{15}N$ values in the tissue of biota increase (become "heavier"). Many studies find that the average $\delta^{15}N$ difference between an animal and its food source is approximately 3 to 4‰ (DeNiro and Epstein 1981, Vander Zanden and Rasmussen 2001). This consistent change provides a powerful analytical tool to quantify relative trophic position, which can also be correlated with contaminant bioaccumulation or dietary changes in fish (Cabana and Rasmussen 1994).

In contrast, stable carbon isotopes fractionate very little in biota, with around 1‰ enrichment in $\delta^{13}C$ per trophic level (Peterson and Fry 1987, Vander Zanden and Rasmussen 2001). Because of these low fractionation rates, the stable carbon isotope values of organisms reflect the average $\delta^{13}C$ of their diets. $\delta^{13}C$ values can vary at the base of the food web due to differences in photosynthetic enzymatic fixation, growth rates, CO_2 and pH levels (Hecky and Hesslein 1995). Because free-floating pelagic algae close to the water surface have access to a large dis-

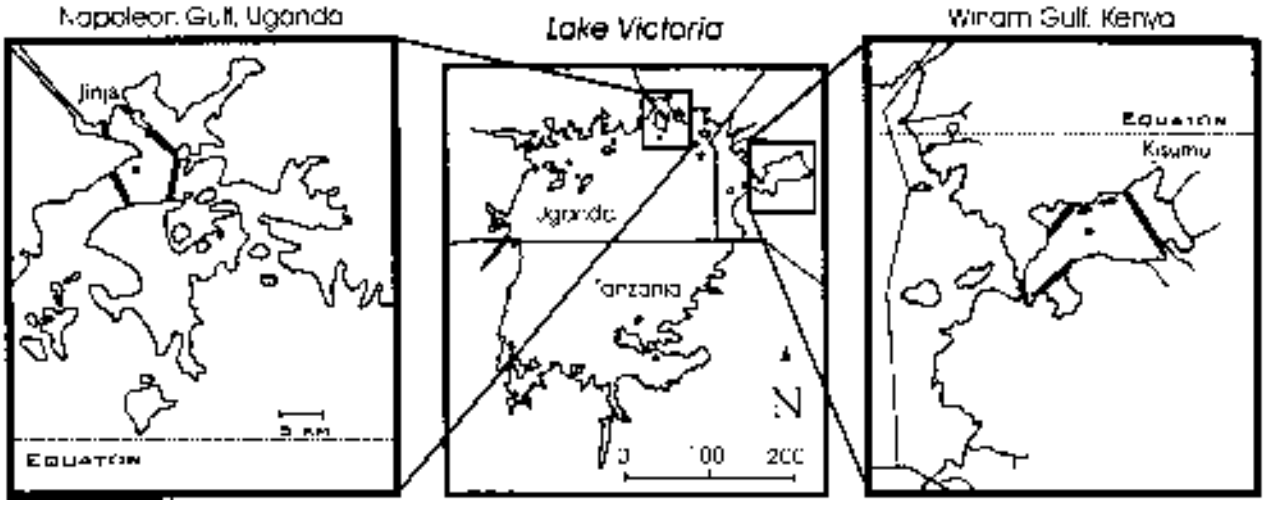

FIG. 1. Location of Napoleon Gulf (Uganda) and Winam Gulf (Kenya) in northern Lake Victoria, and the location of Lake Victoria in Africa. Regions bordered by thick lines indicate the sampling area.

solved CO_2 reservoir which fractionate only slightly, photosynthetic fixation can result in "lighter" (more negative) $\delta^{13}C$ values of –29‰ (Hecky and Hesslein 1995). At the sediment-water interface growth in a boundary layer restricts the CO_2 reservoir available, and the carbon-limited benthic algae are less isotopically discriminating, resulting in "heavier" (more positive) $\delta^{13}C$ signatures which may be between –25 to –10‰ (Hecky and Hesslein 1995, Bootsma *et al.* 1996). Emergent macrophytes obtain their carbon from the atmosphere, and their $\delta^{13}C$ values are influenced by their photosynthetic pathway (C-3 or C-4) and the need to conserve water (Hecky and Hesslein 1995). C-4 plants such as the tropical aquatic hippo grass *Vossia* spp. and papyrus *Cyperus papyrus* are less discriminatory against $^{13}CO_2$, which is reflected by their heavier $\delta^{13}C$ values (typically –12 to –14‰). C-3 plants, such as water hyacinth, are more discriminatory against $^{13}CO_2$ so their $\delta^{13}C$ values tend to be lighter (typically –26 to –28‰). As a result, there are differences in $\delta^{13}C$ values between organisms within a food-web based on different sources of primary production. These differences are passed up in the food chain, indicating the origin of organic carbon in organisms at higher trophic levels (Hecky and Hesslein 1995). This difference can be used to quantify the relative importance of pelagic versus benthic algal sources in an organism's diet (Bootsma *et al.* 1996), and to determine numerically the changes in carbon sources both over time and with growth.

METHODS

Napoleon Gulf is situated in southeastern Uganda, and leads to the source of the Nile River located near the town of Jinja (Fig. 1). The town is lightly industrialized, with the Owen Falls Dam hydroelectric facility on the Nile River, a brewery, a sugarcane processing plant, a textile factory and several fish processing plants. The population density in districts around the gulf is estimated at 246 people per square kilometer (Table 1). Napoleon Gulf is eutrophic (Table 1), with a highly convoluted shoreline and numerous bays which provide a range of aquatic ecosystems from wetland to pelagic. Samples were collected in the vicinity of Jinja Bay and Buvuma Channel, which share similar environmental characteristics (Fig. 1).

Winam (Nyanza) Gulf in western Kenya is a shallow mesotrophic to eutrophic gulf (Table 1) nearly closed off to the main lake (Fig. 1). Kisumu, the main town in the region, is heavily industrialized (paint, solvent, and plastics manufacturing as well as sugar, food, and fish processing). Sewage effluent, usually untreated, enters the Kibos River near its mouth at Lake Victoria. The population density for the areas bordering the gulf is estimated at 259 people per square kilometer (Table 1). The Winam Gulf shoreline is less convoluted than that of Napoleon Gulf, and the waters are well mixed throughout the gulf. Samples for this study were taken from outside the Kisumu region toward the

TABLE 2. Fish, invertebrate and organic matter collected in this study with the assigned codes used in the figures. The number of samples from each location that were analysed are listed for each gulf, along with the mean values ± standard deviation for stable nitrogen ($\delta^{15}N$) and carbon ($\delta^{13}C$) isotope values and published diet information (Copley 1958, Greenwood 1966, Greenwood 1981, van Oijen 1995, and Balirwa 1998). Those separated by slashes indicate dietary changes occurring with growth and maturity.

		Napoleon Gulf			Winam Gulf			
Species	Code	n	$\delta^{15}N$	$\delta^{13}C$	n	$\delta^{15}N$	$\delta^{13}C$	Published diet composition
Organic matter								
Cyperus papyrus	U	2	0.2 – 0.6	–12.7 – –12.6	~	~	~	Photosynthesis (common name: papyrus)
Eichhornia crassipes	W	2	2.7 – 3.4	–27.8 – –26.4	~	~	~	Photosynthesis (common name: water hyacinth)
Suspended floc	F	2	2.7 – 3.2	–19.3 – –19.0	~	~	~	Photosynthesis
Phytoplankton (nearshore)	K	3	4.3 ± 0.8	–19.9 ± 0.7	~	~	~	Photosynthesis
Vossia spp.	V	2	0.5 – 0.8	–12.8 – –12.4	~	~	~	Photosynthesis (common name: hippo grass)
Invertebrates								
Caridina nilotica	C	17	4.4 ± 0.9	–19.0 ± 1.0	6	7.2 ± 0.7	–22.8 ± 0.4	Benthic algae, algal detritus, zooplankton
Small mussels	M	~	~	~	2	7.1 – 7.8	–24.05 – –23.4	Suspended particulates near benthic surfaces
Ephemeroptera nymph	E	5	2.6 ± 0.3	–18.9 ± 0.2	10	6.7 ± 0.7	–23.9 ± 0.4	Algae (common name: mayflies, lake-flies)
Odonata nymph	D	7	5.3 ± 0.8	–18.6 ± 0.8	5	6.0 ± 0.4	–27.0 ± 1.1	Algae, zooplankton, invertebrates (common name: dragonflies)
Prosobranch snail	N	1	5.6	–18.9	~	~	~	Water hyacinth epiphyton
Zooplankton (nearshore)	Z	3	7.1 ± 0.3	–17.6 ± 0.8	~	~	~	Suspended particulates
Zooplankton (offshore)	Z	2	7.7 – 7.8	–20.6 – –20.4	~	~	~	Suspended particulates
Fish								
Bagrus docmac F.	B	~	~	~	1	12.7	–21.3	Large invertebrates, Caridina / small fish
Clarias gariepinus B.	G	~	~	~	1	8.78	–25.02	Small fish, molluscs, insect larvae, and plant detritus
Haplochromis spp.	H	2	9.1 – 9.3	–18.5 – –18.1	5	9.2 ± 1.1	–24.1 ± 0.5	Presumed insectivores (species unknown)
Lates niloticus L.	L	12	8.0 ± 1.1	–18.9 ± 0.5	17	11.8 ± 1.4	–22.2 ± 1.2	Caridina / R. argentea, smaller Nile perch / larger fish
Oreochromis niloticus L.	O	11	5.9 ± 0.8	–18.1 ± 0.8	13	9.8 ± 1.1	–22.3 ± 1.9	Phytoplankton, detritus, Caridina, chironomids, molluscs
Immature *O. niloticus*	O’	5	7.0 ± 0.3	–17.1 ± 0.7	4	6.1 ± 0.5	–18.6 ± 1.0	Phytoplankton, benthic algae, detritus
Protopterus aethiopicus H.	P	2	7.3 – 7.7	–19.5 – –19.3	3	10.6 ± 0.4	–23.8 ± 0.5	Insects / Gastropoda, Caridina, small fish
Rastrineobola argentea P.	R	8	8.1 ± 0.6	–17.0 ± 0.7	3	11.3 ± 1.4	–23.8 ± 0.5	Copepods / chironomids and chaoborids / small Caridina
Schilbe intermedius L.	S	~	~	~	9	9.5 ± 0.7	–27.4 ± 1.5	Odonata / small fish (R. argentea and young Nile perch)
Synodontis afrofischeri H.	A	~	~	~	7	8.8 ± 1.5	–27.8 ± 3.0	Chironomids / molluscs
Tilapia zilli G.	T	1	8	–19.2	~	~	~	Phytoplankton, benthic algae, macrophytes
Yssichromis laparogramma G.	Y	5	7.9 ± 0.2	–19.9 ± 0.3	2	10.1 – 10.5	–26.7 – –24.7	Zooplankton or pelagic chironomids and chaoborids

mouth of the gulf, excluding Asembo and Homa bays (Fig. 1).

The species sampled included fish, invertebrates, macrophytes, and phytoplankton (Table 2). Commercially important Nile perch (*L. niloticus*) and Nile tilapia (*O. niloticus*) were collected from both gulfs, along with two pelagic fish species (the cyprind *R. argentea* and the haplochromid *Yssichromis laparogramma*), and the freshwater shrimp, *Caridina nilotica*. Other taxa were included whenever possible. Fish were obtained by trawling the region and supplemented by overnight gill net sets and fish purchased directly from the local fishermen. All fish were dissected, and for the large fish, a 10-cm^3 muscle sample was collected from the lateral muscle. Smaller fish were filleted. Near-shore and offshore zooplankton in Napoleon Gulf were collected with a Schindler trap and filtered through a mesh. Phytoplankton were collected with a 53 μm net. Suspended floc were collected off the surfaces of mesh bags suspended at 0.5 below the water surface near the Jinja Pier. Macrophytes collected in Napoleon Gulf were used as terrestrial endpoints potentially contributing to the lake's organic sources. Because samples were collected for both stable isotope and mercury analyses (Campbell *et al.* 2003), trace-metal clean protocols were followed during sampling. It was not possible to maintain the same sampling protocol and effort for each site due to logistical constraints, but every attempt was made to collect a broad and diverse sample set. Samples were wrapped in hydrochloric acid-cleaned aluminium foil, double-wrapped in Ziploc® bags, and frozen. The samples, transported to Canada on ice, were still frozen on arrival.

Small sub-samples of fish tissue and whole invertebrates were freeze-dried and ground into fine powder for $\delta^{15}N$ and $\delta^{13}C$ analyses using a Micromass VG-Isochrom Continuous Flow Isotope Ratio Mass Spectrometer (CF-IRMS) at the Environmental Isotope Laboratory, University of Waterloo. The ratios of the stable isotopes were then measured against the reference standards PeeDee belemnite for $\delta^{13}C$ and the nitrogen gas in ambient air for $\delta^{15}N$ (Eqn. 1). The delta notation (δ), the difference (‰, or parts per thousand) between the isotopic ratio of the sample and the standard, was calculated as:

$$\delta^{13}C \text{ or } \delta^{15}N = \{(R_{sample} - R_{standard})/(R_{standard})\} \times 1000 \quad (1)$$

where $R = {}^{13}CO_2 / {}^{12}CO_2$ for $\delta^{13}C$ or $R = {}^{15}N_2 / {}^{14}N_2$ for $\delta^{15}N$

Working standards used to determine inter- and intra-run variation and accuracy of the results included the International Atomic Energy Agency (IAEA) standards CH6 ($\delta^{13}C$ = –10.4‰), N1 ($\delta^{15}N$ = 0.36‰) and N_2 ($\delta^{15}N$ = 20.3‰), and the in-house standards: EIL-70 (powdered lipid-extracted Lake Ontario walleye; $\delta^{13}C$ = –19.34‰, $\delta^{15}N$ = 16.45‰) and EIL-72 (powdered Whatman cellulose fiber; $\delta^{13}C$ = –25.4‰). Replicate Nile perch samples were included in every run to determine between-run variation. Standard deviations for the standards were ± 0.3‰ for $\delta^{15}N$ and ± 0.2‰ for $\delta^{13}C$, and standard deviations of replicate samples were ± 0.16‰ for $\delta^{15}N$ and ± 0.24‰ for $\delta^{13}C$.

The food web structure was graphically represented by plotting $\delta^{15}N$ against $\delta^{13}C$ for all organisms collected from the two gulfs. Dietary information for all fish and invertebrate species was compiled from stomach content data and published sources to compare information derived from stable isotope analyses and stomach content data. Statistical analyses were performed using SYSTAT version 8.0 for Windows (SPSS Inc.). T-tests were done to determine if the stable isotope values were significantly different in adult Nile perch and Nile tilapia between the two gulfs and to compare the stable isotope values of R. *argentea and Y. laparogramma.*

Adult Nile tilapia and Nile perch $\delta^{13}C$ and $\delta^{15}N$ values were regressed against their total length (TL) to determine if there were isotopic changes with increasing fish size. TL ranged from 9 to 90 cm for adult Nile perch and from 15 to 60 cm for adult Nile tilapia. An extremely large Nile perch (TL = 158 cm) from Winam Gulf was excluded as an outlier. Grouped t-tests were used to demonstrate that "immature" Nile tilapia (≤ 5 cm) $\delta^{13}C$ and $\delta^{15}N$ values were different from those of adult Nile tilapia. Comparison of regression slopes and intercepts were completed in an ANCOVA model to determine if there were significant differences in stable isotope changes with adult fish growth in each gulf.

To determine the difference in basal $\delta^{13}C$ and $\delta^{15}N$ values between the two gulfs, the $\delta^{13}C$ and $\delta^{15}N$ values of selected taxa were compared, based on their assumed trophic position. Estimating the extent of the basal isotopic differences provides a means of adjusting the isotopic signatures of biota from one gulf to the basal values of another gulf. This could permit the direct comparison of food web structure and other aspects such as the trophic transfer of contaminants (Campbell *et al.* 2003). Taxa were selected by the following criteria: shar-

TABLE 3. Trophic numbers assigned to each taxon common to both Gulfs, based on diet. The taxon codes are in Table 2.

Taxon	Assigned trophic number	Reason for assigning trophic number
L	4	Top predator in Lake Victoria (fish and *C. nilotica*)
P	3	Feeds upon both fish and invertebrates (*C. nilotica*, snails and mollusks)
O	2	Strong preference for phytoplankton detritus, but will eat *C. nilotica*
C	1	Zooplankton and phytoplankton

ing overlapping $\delta^{13}C$ values, analogous taxa found in both gulfs, and relative food web position in both gulfs. The biota selected included *Caridina*, Nile tilapia, *P. aethiopicus* (lungfish), and Nile perch. Taxa were assigned a numerical value representing their "relative" trophic position, based on their known dietary patterns, which gradually ranged from planktivory to piscivory (Table 3). *Caridina*, an invertebrate commonly consumed by many fish species, was assigned the lowest trophic position (1) and Nile perch, a top predator, was assigned the highest trophic position (4). The $\delta^{13}C$ and $\delta^{15}N$ values for each taxon were then regressed against its assigned numeric trophic position. The differences between the slopes and intercepts were tested in ANCOVA and the difference between the intercepts for each regression ($\delta^{13}C$ and $\delta^{15}N$ vs. trophic position) was used to "adjust" Napoleon biota stable isotope values to those of Winam Gulf.

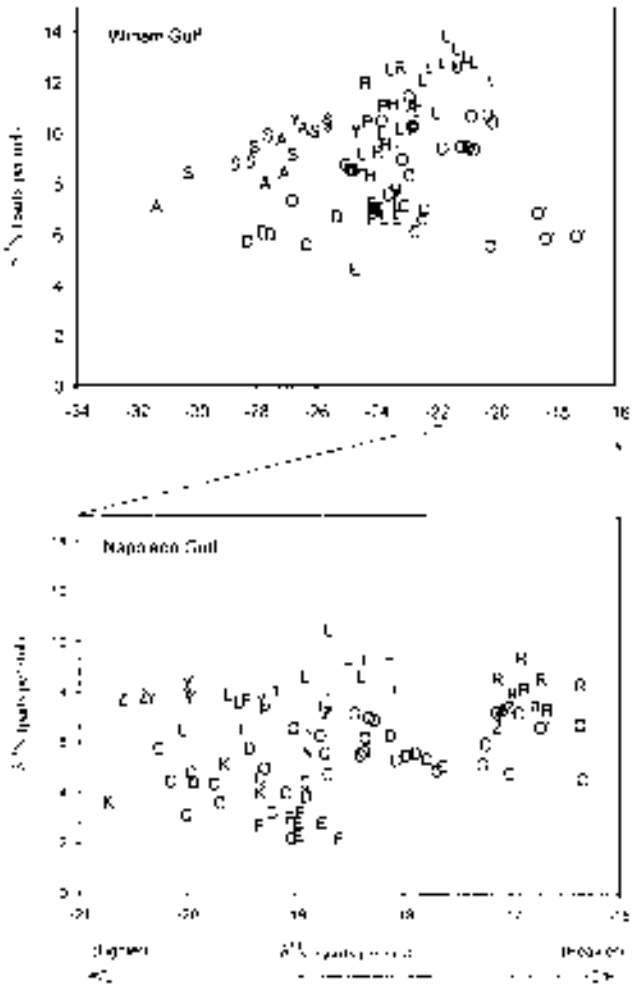

FIG. 2. The relationship between $\delta^{15}N$, indicating trophic position and $\delta^{13}C$, indicating dietary carbon source, for 21 taxa from Winam and Napoleon gulfs. Each taxa is represented by a code defined in Table 2. Note that the x-axis scales of the two figures are different, reflecting the wider range of $\delta^{13}C$ values in Winam Gulf.

RESULTS

Plotting $\delta^{15}N$ values against $\delta^{13}C$ values provides a visual characterization of the food web structure and can be used to assess predator-prey and cohort relationships (Fig. 2). The range of $\delta^{13}C$ and $\delta^{15}N$ values for Nile perch is wide, particularly in Winam Gulf, with these values extending over as much as 4‰ for $\delta^{13}C$ and 5‰ for $\delta^{15}N$. The range is supported by stomach content information, indicating a broad diversity of prey items ranging from *Caridina* to large fish (Table 2). In both gulfs, Nile perch stable isotope values overlap with many other fish species, including Nile tilapia and lungfish, although Nile perch tend to have higher $\delta^{15}N$ values and their $\delta^{13}C$ values are midway along the range of available prey organisms (Fig. 2, Table 2). The $\delta^{15}N$ values for Nile tilapia, lungfish and most pelagic haplochromids generally place these fish species between Nile perch and most invertebrates, including *Caridina*, Ephemeroptera, and Odonata (Table 2). The in $\delta^{13}C$ values for these fish species are varied, with Nile tilapia showing the most positive values, lungfish having median values and haplochromids having the most negative values. The low $\delta^{15}N$ values for most invertebrates and algae (including phytoplankton and floc) places them in a lower trophic position relative to fish (Fig. 2). In

TABLE 4. Results of grouped t-tests for $\delta^{15}N$ and $\delta^{13}C$ values for Napoleon and Winam Gulfs: between adult Nile perch (L),* R. argentea *(R) and* Y. laparograma *(Y) and between immature Nile tilapia (O′) and adult Nile tilapia (O). Mean values are given in Table 2. Significance is determined at* p*-value 0.05 and the alpha value is 0.027.

Gulf	Group	df	$\delta^{15}N$ t-test	$\delta^{15}N$ *p*-value	$\delta^{13}C$ t-test	$\delta^{13}C$ *p*-value
Napoleon	L–R	18	0.46	0.65	–9.63	0.00
	L–Y	12	–1.43	0.18	–1.44	0.18
	R–Y	8	–2.04	0.08	8.06	0.00
	O–O′	14	2.97	0.01	2.27	0.04
Winam	L–R	18	0.55	0.59	2.25	0.04
	L–Y	17	1.43	0.17	3.85	0.00
	R–Y	3	0.74	0.52	2.13	0.12
	O–O′	15	–6.38	0.00	3.73	0.00

Winam Gulf, *Schilbe intermedius* and *Syndodontis afrofischeri* both have $\delta^{13}C$ values that place them on the extreme negative end of the range of the food web (Fig. 2). T-test analyses indicate that the high $\delta^{15}N$ values of Y. *laparograma* and *R. argentea* (Fig. 2, Table 2) are not significantly different than $\delta^{15}N$ values of Nile perch in both gulfs (Table 4). The $\delta^{13}C$ values for Nile perch are significantly different from those for the pelagic fish species in Winam Gulf. In Napoleon Gulf, the $\delta^{13}C$ values for *Y. laparograma* and Nile perch are significantly different from each other (Table 4).

The difference between the two gulfs is visually discernible by the shift of Winam Gulf $\delta^{15}N$ values to the right (Fig. 3A), and the lighter biotic $\delta^{13}C$ values (and also wider range as indicated by wider standard deviation values) in similar species in Winam Gulf (Table 2, Fig. 3B). Furthermore, Nile perch and Nile tilapia in Napoleon Gulf have significantly lighter $\delta^{15}N$ and heavier $\delta^{13}C$ values than the same fish species in Winam Gulf (Table 5). Regressing the $\delta^{13}C$ and $\delta^{15}N$ values of common taxa against their assigned numerical trophic position (Fig. 4) illustrates the similarities and differences between the gulfs. The $\delta^{15}N$ regressions (Fig. 4A, Eqns. 2 and 3) are significant for both gulfs ($p, \leq 0.001$). The ANCOVA results indicate that the intercepts are significantly different ($p, \leq 0.000$), while the slopes are similar (p, 0.604).

$$\delta^{15}N \text{ (Napoleon Gulf)} = 3.3 + 1.2 \text{ (trophic position)} \quad (r^2_{adj} = 0.91) \qquad (2)$$

$$\delta^{15}N \text{ (Winam Gulf)} = 6.5 + 1.4 \text{ (trophic position)} \quad (r^2_{adj} = 0.93) \qquad (3)$$

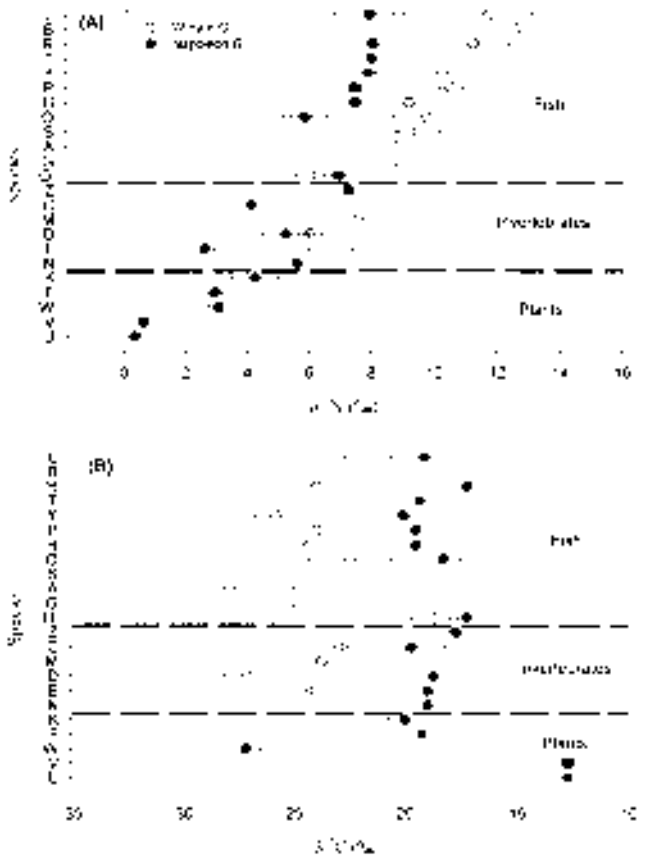

FIG. 3. Mean ± s.d. of $\delta^{15}N$ (A) and $\delta^{13}C$ (B) values in fish, invertebrates, and plants in Napoleon and Winam gulfs, Lake Victoria. Note that $\delta^{15}N$ values for biota in Winam Gulf tend to be higher than for similar biota in Napoleon Gulf. Note that $\delta^{13}C$ values for biota in Winam Gulf extend over a broader range and are lighter than those than for similar biota in Napoleon Gulf.

TABLE 5. Results of grouped t-tests for comparison of $\delta^{15}N$ and $\delta^{13}C$ values of Nile perch and Nile tilapia between Napoleon and Winam gulfs. The original $\delta^{15}N$ and $\delta^{13}C$ values of both fish species are compared between the two gulfs, and the adjusted $\delta^{15}N$ and $\delta^{13}C$ values for Napoleon Gulf (see text) are compared with original Winam Gulf values. Mean values are given in Table 2. Significance is determined at* p*-value = 0.05 and the alpha value is 0.027.

Gulf	Group	df	$\delta^{15}N$ t-test	$\delta^{15}N$ *p*-value	$\delta^{13}C$ t-test	$\delta^{13}C$ *p*-value
Nile perch	Unadjusted	27	–7.57	≤ 0.001	8.79	≤ 0.001
	Adjusted	" "	–0.25	0.8	0.38	0.71
Nile tilapia	Unadjusted	22	–9.75	≤ 0.001	6.45	≤ 0.001
	Adjusted	" "	–0.45	0.66	1.6	0.12

$\delta^{13}C$ values did not change significantly between assigned trophic values. The slopes of the $\delta^{13}C$:trophic position regressions are not significantly different (*p*, 0.394) while the intercepts are significantly different (p, ≤ 0.001).

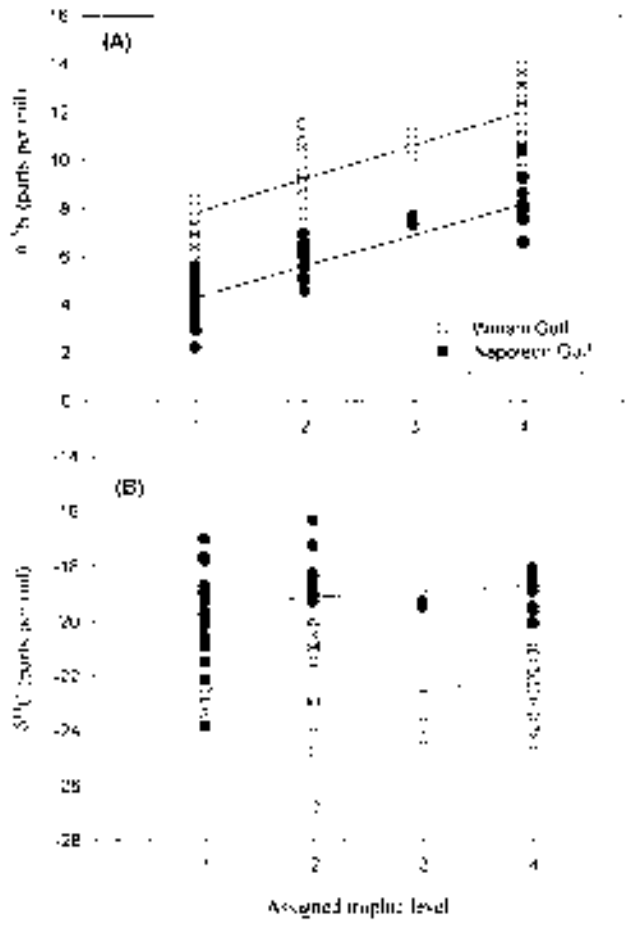

FIG. 4. $\delta^{15}N$ (A) and $\delta^{15}C$ (B) values of selected fish and* Caridina *versus their assigned numeric trophic position.

$$\delta^{13}C \text{ (Napoleon Gulf)} = -18.7 + 0.03 \text{ (trophic position)} \ (r^2_{adj} = 0.76) \quad (4)$$

$$\delta^{13}C \text{ (Winam Gulf)} = -22.7 + 0.09 \text{ (trophic position)} \ (r^2_{adj} = 0.85) \quad (5)$$

The difference between the two intercepts for Winam and Napoleon gulfs ($\delta^{15}N$ = 3.14; $\delta^{13}C$ = 4.02), provides a means of "adjusting" for the different values at the base of the food-web of one gulf to the other.

Using the intercept differences to "adjust" Napoleon Gulf stable isotope values to Winam Gulf values, a new set of stable isotope data was generated. Figure 5A compares the original stable isotope values of the two food-webs and 5B shows how the adjusted values for Napoleon Gulf become similar to Winam Gulf. $\delta^{15}N$ and $\delta^{13}C$ values after adjustment are not significantly different for both Nile perch and Nile tilapia (Table 5). The apparent differences in $\delta^{15}N$ and $\delta^{13}C$ values of the same species between the gulfs are largely eliminated by the correction for basal signatures.

Regressing stable isotope data against fish size enables the statistical interpretation of dietary shifts during fish growth. Nile perch length is positively correlated with $\delta^{15}N$ in both Napoleon (*p*, ≤ 0.001) and in Winam (*p*, 0.013; Table 6, Fig. 6A), indicating that Nile perch increase their trophic level as they mature. Dietary shifts are also indicated by significant correlations between Nile perch length and $\delta^{13}C$ in Napoleon (*p*, 0.027) and in Winam (*p*, 0.018; Table 6, Fig. 6B). ANCOVA analyses indicate that the slopes for $\delta^{15}N$ and $\delta^{13}C$ vs. Nile perch TL are not significantly different between the two gulfs (*p*, 0.903 and 0.702, respectively) but the intercepts are significantly different with *p*, ≤ 0.001 for both gulfs. Note the outlier points in Figures 6A

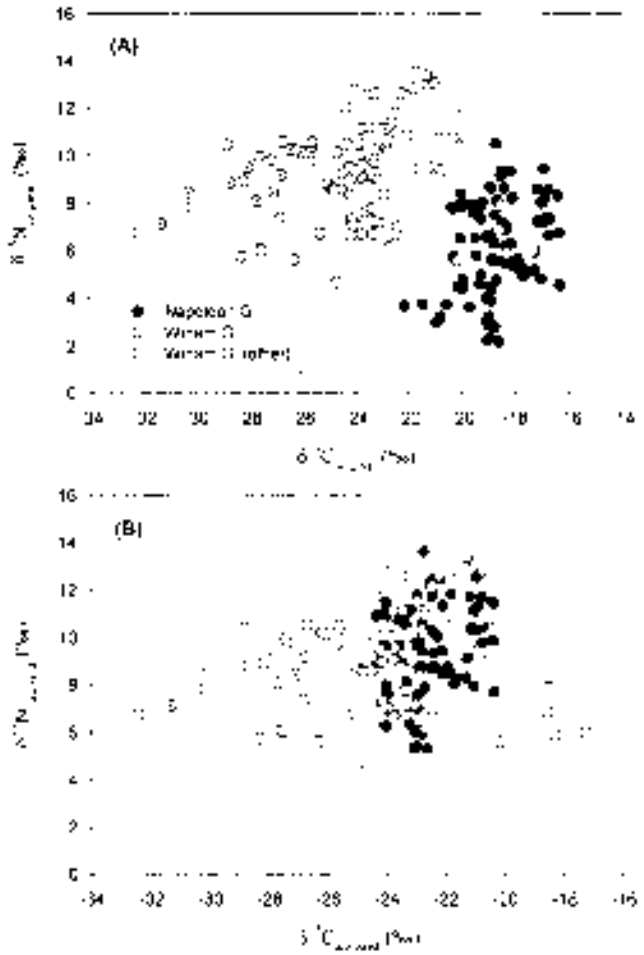

FIG. 5. The relationship between $\delta^{15}N$ and $\delta^{13}C$ values for biota from the Napoleon and Winam gulfs before (A) and after (B) calibration of the Napoleon values to Winam values using the intercepts in Figure 4. The dotted points represent* S. intermedius *and* S. afrofischeri *from Winam Gulf, which have very light $\delta^{13}C$ values and very likely do not make up a significant portion of Nile perch diets.

and B which represent the 158-cm long Nile perch from Winam Gulf—its $\delta^{13}C$ value and particularly its $\delta^{15}N$ value drops below the trend-line for the other Nile perch.

Adult Nile tilapia show a small but significant correlation between $\delta^{15}N$ and length (p, 0.022 and 0.028 in Napoleon and Winam Gulf respectively; Table 6). However, the correlation between Nile tilapia $\delta^{13}C$ and length is not significant in Napoleon Gulf (p, 0.903) but is significant in Winam Gulf (p, 0.032; Table 6). The slopes for $\delta^{15}N$ vs. TL are not significantly different between the gulfs (p, 0.086) but the intercepts are (p, 0.972). Due to the lack of significance for $\delta^{13}C$ vs. TL in Napoleon Gulf, an ANCOVA for $\delta^{13}C$ vs. TL between the gulfs was not carried out. Immature Nile tilapia stable isotope values are usually segregated from adult Nile tilapia in both gulfs; adult Nile tilapia usually have significantly heavier $\delta^{13}C$ values and their $\delta^{15}N$ values are significantly different (higher in Winam and lower in Napoleon) from those of immature Nile tilapia (Table 4).

DISCUSSION

The basal stable isotope values in Winam and Napoleon gulfs are different. Most of the external nutrient input of total nitrogen to the main body of Lake Victoria (including Napoleon Gulf) comes from biological N-fixation, especially in productive inshore waters (Muggide 2001), and carbon from the atmosphere through gas exchange. In a well-mixed lake, the basal stable isotope values would be relatively uniform, set by $\delta^{15}N$ and $\delta^{13}C$ values derived from terrestrial and atmospheric processes as well as from biological processes within the lake. However, in a lake as large as Lake Victoria, basal stable isotope values derived from algal photosynthesis can vary greatly from one region to another. The differences can arise from variation in recycling patterns of nutrients, which will affect the $\delta^{15}N$ of the inorganic nitrogen sources (Fogel and Cifuentes 1993), and from variability in the rates of algal growth rates and CO_2 availability affecting the $\delta^{13}C$ of phytoplankton (Hecky and Hesslein 1995). There are two ways that basal $\delta^{15}N$ and $\delta^{13}C$ values can be affected without external inputs. One is phytoplankton-driven and the other is nutrient-driven. If phytoplankton growth is low, then inorganic N compounds and CO_2 can be in excess relative to phytoplankton demand, leading to heavier $\delta^{15}N$ and lighter $\delta^{13}C$ basal values entering the food web (Keough *et al.* 1998, Schindler *et al.* 1997). This is the typical scenario for offshore stable isotope values produced in a deep light-limited mixed layer, and seems to be occurring in Winam Gulf with its higher turbidity (~20 NTU), leading to lower Secchi depths and lower chlorophyll concentrations (Table 1). Alternatively, when the algal biomass is high, CO_2 and N demand increases requiring N-fixation and bicarbonate uptake to meet algal demand. This would lead to lighter $\delta^{15}N$ (from increased N-fixation) and heavier $\delta^{13}C$ (from increased use of bicarbonate) basal values for the

TABLE 6. Regressions of $\delta^{15}N$ and $\delta^{13}C$ for Nile perch and Nile tilapia against total length (TL) for Winam and Napoleon gulfs. For each regression, the sample size (n), mean ± s.d. and range of TL, as well as the intercept, slope and adjusted r^2, are listed. A 158-cm Nile perch from Winam Gulf was excluded as an outlier. For each pair of regressions, ANCOVA analyses (α, 0.027) indicate that the intercepts ($p, > 0.05$) but not the slopes ($p, < 0.001$) are significantly different. The exception is $\delta^{13}C$ vs TL regression for Napoleon Gulf Nile tilapia, which is not significant.

Site	Object	Regression	n	TL (cm)	Intercept	Slope	r^2_{adj}
Napoleon	Nile perch	$\delta^{15}N$ vs TL	12	9.0–62.0	5.92	0.058	0.71
		$\delta^{13}C$ vs TL		(35.9 ± 16.4)	–19.73	0.022	0.40
Winam	Nile perch	$\delta^{15}N$ vs TL	16	10.4–87.8	9.11	0.053	0.72
		$\delta^{13}C$ vs TL		(47.9 ± 22.0)	–23.70	0.029	0.30
Napoleon	Nile tilapia	$\delta^{15}N$ vs TL	11	15.5–41.8	4.45	0.100	0.46
		$\delta^{13}C$ vs TL		(22.1 ± 7.9)	–18.24	0.010	0.00
Winam	Nile tilapia	$\delta^{15}N$ vs TL	13	25.5–52.1	7.08	0.100	0.17
		$\delta^{13}C$ vs TL		(41.3 ± 8.2)	–28.70	0.140	0.29

food web in near-shore environments with high algal biomass (Muggide 2001). Thus, increased abundance of rapidly growing phytoplankton in near-shore regions such as Napoleon Gulf can lead to lighter nitrogen and heavier basal carbon isotopic signatures. Possible external influences include increased animal waste and sewage which can also lead to heavier $\delta^{15}N$ and lighter $\delta^{13}C$ values due to the accumulation and increased availability of the ^{15}N and ^{13}C compounds in the aquatic environment (Cabana and Rasmussen 1996, Kwak and Zedler 1997). This also may be occurring in Winam Gulf with its large-scale farms and heavy industry and is reflected in its higher biological oxygen demand estimates (Table 1) relative to Napoleon Gulf. Differences in phytoplankton ecology and pollution levels may contribute to the offset in basal food web difference in $\delta^{13}C$ of 4.0 and $\delta^{15}N$ of 3.1 between Winam and Napoleon gulfs.

Once the Napoleon Gulf stable isotope data were "adjusted" to Winam Gulf data values, there were no significant differences between the $\delta^{15}N$ or $\delta^{13}C$ values for Nile perch or Nile tilapia between the two gulfs. This indicates that the fractionation of stable isotopes through trophic transfers in fish in each gulf remains consistent regardless of the basal isotopic differences between the two gulfs. This makes it possible to compare contaminant biomagnification patterns using stable isotopes between the two gulfs (Campbell *et al.* 2003). In this study a relatively arbitrary method of assigning trophic position was used, which was based upon known food relationships in Lake Victoria as supported by stable isotope data, to obtain the intercept values needed to "adjust" the food web stable isotope data. However, the calculated basal isotopic differences ($\delta^{15}N$: 3.1; $\delta^{13}C$: 4.0) are independently verified by the similarity of TL-$\delta^{15}N$ / $\delta^{13}C$ regression intercept differences (Table 6, Fig. 6) between the two gulfs. For example, the intercept differences for $\delta^{15}N$ and $\delta^{13}C$ are 3.2 and 4.0 respectively for Nile perch and for Nile tilapia, the TL-$\delta^{15}N$ intercept is 2.6. In addition, the food web structure of Winam and Napoleon gulfs are similar, so such a rough estimate is justified as long as its limitations are recognized.

It has been suggested that large Nile perch may be consuming young of the same species because of the decline in the availability of hapolochromine prey (Hughes 1992, Ogutu-Ohwayo 1994). The relatively low $\delta^{15}N$ values of Nile perch in this study would seem to support the cannibalization hypothesis. A Napoleon Gulf stomach content study found that Nile perch that are 60 to 100 cm tend to consume more Nile perch (usually < 20 cm; > 54 % frequency of occurrence) relative to other prey items (Ogutu-Ohwayo 1994). In Napoleon Gulf, the $\delta^{15}N$ difference ($\Delta\delta^{15}N$) between Nile perch ≥ 60 cm ($\delta^{15}N$, 10.5‰, n = 1) and smaller Nile perch (< 20 cm; $\delta^{15}N$, 6.6 ± 0.1‰; n,3) is 3.9‰. In Winam Gulf, the $\Delta\delta^{15}N$ value is 3.8‰ (60 to 100 cm, 13.1 ± 0.4‰, n = 6; < 20 cm, 9.3 ± 0.4‰, n = 6

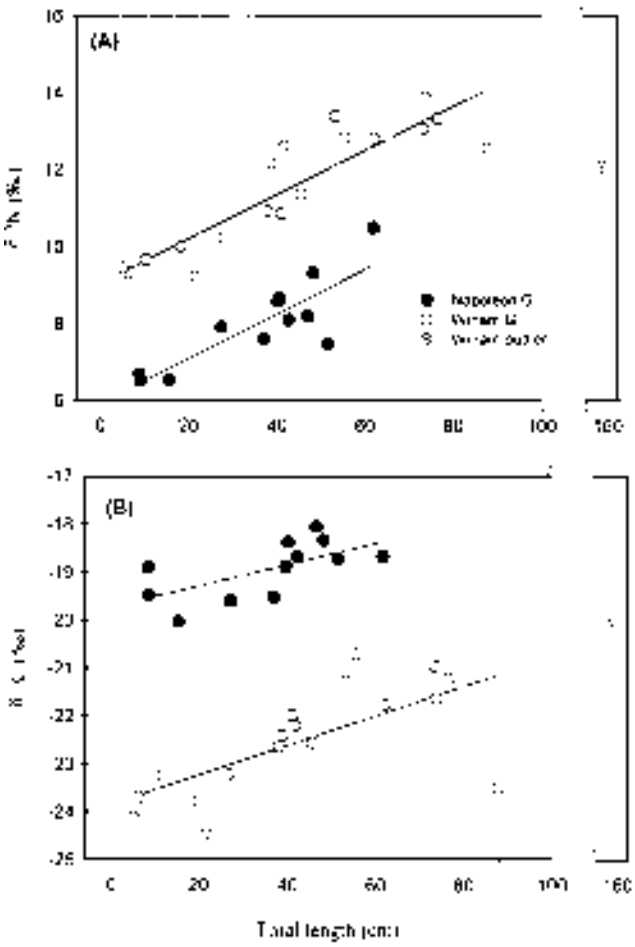

FIG. 6. $\delta^{15}N$ (A) and $\delta^{13}C$ (B) values in Nile perch versus their total length. The dotted outlier in each graph represents a very large Nile perch (TL = 158 cm) which was not included in the regression calculations.

respectively). These $\Delta\delta^{15}N$ values of 3.8 to 3.9‰ are remarkably similar to the $\Delta\delta^{15}N$ value of 3.7‰ found for cannibalizing Arctic char in a remote northern lake (Hobson and Welch 1995), and is in agreement with Nile perch stomach-content evidence (Hughes 1992, Ogutu-Ohwayo 1994). These $\Delta\delta^{15}N$ values represent only one trophic transfer if a mean enrichment of 3.5‰ per transfer is assumed. An alternative hypothesis is that Nile perch depends heavily upon *Caridina*. Nile perch from 20 to 60 cm have a high frequency of occurrence (29 to 55%) of *Caridina* in stomach contents (Ogutu-Ohwayo 1994), and the mean $\Delta\delta^{15}N$ is 3.8‰ between *Caridina* and Nile perch in that size class. These structures show that the dominant species in Lake Victoria, the Nile perch, has a wide dietary spectrum with a heavy dependence on invertebrates as juveniles and increasing piscivory as it ages and grows. The result of this broad spectrum and omnivory is a relatively short food chain length with a $\Delta\delta^{15}N$ of only about 4‰ between *Caridina* and Nile perch and no more than 8‰ between *Caridina* and the largest Nile perch. Assuming a mean enrichment of 3.5‰ per transfer, these $\Delta\delta^{15}N$ values represent only one to two trophic transfers between *Caridina* and the top predator.

Changes in stable isotope values with fish growth may occur due to shifts in diet with increased fish size. Nile perch in both gulfs have similar size-dependent dietary shifts and trophic position as evidenced by the similar slopes of the stable-isotope:TL regressions. Nile perch's diet selection is limited only by the size of the prey their gape size allows. Gape size consistently increases with the size of Nile perch (gape size $\cong$ 0.114 (TL)), which allows larger Nile perch to incorporate bigger prey items (Witte and van Densen 1995). This is supported by stomach content studies indicating that the size and type of prey changes consistently with the growth of Nile perch (Mkumbo and Ligtvoet 1992, Ogari and Dadzie 1988, Ogutu-Ohwayo 1994). Although the scatter in the stable isotope values indicates some degree of individual variability in feeding behavior within a size-class cohort, this does not negate the general trend of increasing $\delta^{15}N$ and $\delta^{13}C$ values with size in Nile perch. Differences in $\delta^{15}N$ and $\delta^{13}C$ values among Nile perch of similar sizes are more influenced by basal stable isotope values than by dietary differences. The higher $\delta^{15}N$ values of Winam Gulf Nile perch cannot be taken as an indicator of higher trophic position or different dietary patterns relative to Napoleon Gulf Nile perch.

Large Nile perch $\geq$ 100 cm incorporate more Nile tilapia (34%) relative to other prey items than the smaller size classes, and an equivalent amount of Nile perch (32%; Ogutu-Ohwayo 1994). This represents a potential decrease in trophic position for very large Nile perch because their intake of Nile perch decreases with size. This is supported by the observation that the $\delta^{15}N$ value (12.1‰) of the largest Nile perch (158 cm) sampled in Winam Gulf is lower than the mean $\delta^{15}N$ value (13.1‰) for the 60 to 100 cm class (Fig. 6A). The stomach contents of this giant individual were found to contain mostly Nile tilapia with a few *C. gariepinus*. According to Ogutu-Ohwayo (1994), Nile perch < 100 cm consume prey with a mean length of 16.7 ± 3.0

cm. Nile tilapia in this size class have a mean $\delta^{15}N$ value of 8.5 ± 0.5‰ (n, 3) leading to a $\Delta\delta^{15}N$ of 3.6‰ for this giant Nile perch, similar to the $\Delta\delta^{15}N$ values listed above. However, Nile perch ≥ 100 cm are increasingly rare in L. Victoria (Ogutu-Ohwayo 1999), and current populations likely have limited impacts on the aquatic ecosystem.

Detailed stomach-content analyses of Napoleon Gulf Nile tilapia from < 15 cm to > 35 cm primarily have shown that their diet consists of detritus and chironomids, and remains relatively constant, changing only with *in-situ* ecological, seasonal, or diel variation (Balirwa 1998). This has the effect of weakening any correlation between trophic level and fish size. In both gulfs, positive regressions between $\delta^{15}N$ values and TL indicate that adult Nile tilapia do increase their $\delta^{15}N$ values as they grow. In addition, immature Nile tilapia (less than 5 cm) have similar or significantly higher $\delta^{15}N$ values than adult Nile tilapia in both gulfs. This may be due to a shifting quality of detritus; larger Nile tilapia feed almost exclusively on detritus and chironomids away from the shoreline while smaller Nile tilapia feed upon a mix of detritus and invertebrates (including chironomids, mollusks, and *Caridina*) nearer to the shore (Balirwa 1998). Based on C/N ratios, it has been hypothesized that detritus further away from shore (C/N = 15:1 dry weight) have higher nutritional value compared to nearshore detritus (C/N = 40:1; Balirwa 1998). The lack of correlation between $\delta^{13}C$ values and TL for adult Nile tilapia in Napoleon Gulf suggests that their diets only shift in terms of improving quality, not composition. In Winam Gulf, there is a significant correlation of $\delta^{13}C$ and length in Nile tilapia, suggesting that their dietary carbon sources shift during growth. In Winam Gulf, as Nile tilapia become large enough to avoid predation by Nile perch, they may gradually move into the more open waters of the gulf and either move to a higher trophic position or consume food with higher $\delta^{13}C$ values.

The stable isotope values of *R. argentea* and *Y. laparograma* in both gulfs seem inconsistent with the simple food chain (algae → zooplankton → pelagic fish and *Caridina* → Nile perch) suggested by Kaufman (1992) among others. Prior to the haplochromine collapse, Nile perch preferred haplochromine fish to *R. argentea*, but after the collapse, *R. argentea* began to appear in Nile perch stomachs (Ogutu-Ohwayo 1994). *R. argentea* and *Y. laparograma*, however, have relatively high $\delta^{15}N$ values, comparable to top trophic Nile perch. There is no evidence of the 3 to 4‰ trophic fractionation between these predator and its putative prey, which precludes *R. argentea* and *Y. laparograma* as regular dietary items for Nile perch. If *R. argentea* were important to Nile perch diets, this should make Nile perch average $\delta^{15}N$ values around 11.7‰ in Napoleon Gulf and 14.9‰ in Winam Gulf, which is not the case. This may mean that these species form a smaller proportion of the Nile perch somatic growth than is indicated by dietary studies (Hughes 1992, Ogari and Dadzie 1998, Ogutu-Ohwayo 1994) or that the situation has changed significantly from the time of the earlier studies.

The high $\delta^{15}N$ values of *R. argentea* and *Y. laparograma* might be partially explained by the high $\delta^{15}N$ values of their commonly-invoked prey, zooplankton. The consistently high $\delta^{15}N$ values of zooplankton, regardless of their $\delta^{13}C$ values, seems to support this hypothesis. For example, the $\Delta\delta^{15}N$ (2.7 to 4.7‰) between zooplankton and phytoplankton / suspended floc indicates that the sampled zooplankton is about one trophic position above of phytoplankton. However, the $\Delta\delta^{15}N$ of the pelagic fish species and zooplankton is only 0.9‰, which indicate that other invertebrate species may be more important to *R. argentea* and *Y. laparograma* than zooplankton. In Mwanza Gulf, *R. argentea* is known to opportunistically feed upon lake-fly larvae (chironomids and chaoborids) and *Caridina* in surface waters (Wanink 1998). For example, the $\Delta\delta^{15}N$ value for pelagic fish and *Caridina* in Napoleon and Winam Gulfs are approximately 3.1 to 3.6‰, while for lake-flies, the $\Delta\delta^{15}N$ values are between 3.6 to 5.3‰. These are more plausible values, which provides strong lake-wide support for the hypothesis that these pelagic fish are currently not limited to feeding on zooplankton, but are opportunistic predators upon invertebrates.

In Napoleon Gulf, *Y. laparograma* has significantly lighter $\delta^{13}C$ values indicating an offshore pelagic diet relative to *R. argentea*, which has heavier $\delta^{13}C$ values. This is similar to the range of $\delta^{13}C$ values in zooplankton from offshore and nearshore sites in Napoleon Gulf. As seen in study, offshore zooplankton usually have lighter $\delta^{13}C$ values, which may be due to lighter $\delta^{13}C$ values in offshore phytoplankton (Hecky and Hesslein 1995, Ramlal 2002), and this is likely reflected in other planktivore invertebrates such as lake-flies. *Y. laparograma* and *R. argentea* in Napoleon Gulf may coexist by ecological segregation into near-shore and offshore habitats, which is consistent with their $\delta^{13}C$ values.

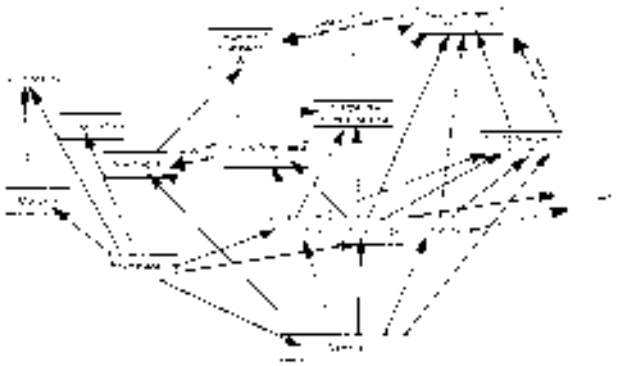

FIG. 7. A schematic food-web diagram of the food web structure based on stable isotope data from Napoleon and Winam Gulfs, Lake Victoria. The thin solid arrows demonstrate the energy flow from important dietary items to consumers. Dotted arrows indicate occasional dietary sources that are not isotopically important but are found in stomach contents of the predator fish. Dietary shifts from young to adult to very large adult Nile perch and for Nile tilapia are indicated.

In Winam Gulf, *S. intermedius* and *S. afrofischeri* exhibit $\delta^{13}C$ values which are lighter than most fish, and seem to form a group separate from other fish and invertebrates (Fig. 4). *S. intermedius* feed on Odonata larvae and small pelagic fish which partially explains their light $\delta^{13}C$ values. Stomach contents indicate that *S. afrofischeri* feed on mollusks and chironomids in the benthic environment (Table 1), and often feed on plankton by swimming upside down at the water surface. Mollusks and chironomids are often considered pelagic feeders because of their reliance on phytoplankton and pelagic organisms (Cabana and Rasmussen 1996), which explains the lighter $\delta^{13}C$ values of this fish species. Since these two fish species constitute a food chain that does not lead to Nile perch, and are not found in stomach contents (Ogutu-Ohwayo 1994), they can be eliminated from studies on Nile perch energetics.

In Lake Victoria today, Nile perch is dependent on a variety of macroinvertebrates and its own young for its growth through maturity and even into adulthood (Fig. 7). Young Nile perch and *Caridina* are isotopically consistent as prey items for larger adults and there is an increasing preference for piscivory with increasing size. Nile tilapia in Napoleon Gulf have isotopic signatures consistent with a strong preference for detritus throughout its life history, while in Winam Gulf, there are indications of shifting dietary patterns. *R. argentea* and *Y. laparogramma* cannot be contributing to somatic growth of Nile perch (Fig. 7) as the pelagic fish have $\delta^{15}N$ signatures indistinguishable from Nile perch (and in Napoleon Gulf, significantly different $\delta^{13}C$ values). Zooplanktivory appears to be relatively unimportant to many of the fish species in Lake Victoria, including *R. argentea* and *Y. laparogramma*. Several common fish species such as *S. intermedius* and *S. afrofischeri*, which coexist with Nile perch in the modern lake, are trophically isolated from Nile perch. This suggests that only a narrow group of fish species is available to sustain growth of larger Nile perch.

Overall, $\delta^{15}N$ and $\delta^{13}C$ values are different at the base of the food webs in Winam and Napoleon gulfs. However, the food web structures are very similar. The analysis of $\delta^{15}N$ and $\delta^{13}C$ values in biota is a powerful tool to study trophic position and dietary sources in Lake Victoria. One caveat to keep in mind—it should be understood that the $\delta^{15}N$ and $\delta^{13}C$ values of biota are relative to the basal stable isotope values. Comparisons of trophic position and food web structure between different locations should be undertaken with an understanding of the possible differences in basal stable isotope values. There remains much to be understood about the dynamics of fish and invertebrates in the Lake Victoria ecosystem, particularly during recent dramatic limnological and biotic shifts occurring in the lake. However, food web structures in two widely separated gulfs in Lake Victoria with differing water qualities and anthropogenic effects are similar, demonstrating that food web studies in one gulf may be extrapolated to another gulf.

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REFERENCES

Balirwa, J.S. 1998. *Lake Victoria Wetlands and the Ecology of the Nile tilapia, Oreochromis niloticus Linné.* Ph.D. thesis. Wageningen Agricultural Univ., Wageningen, NL.

Bootsma, H.A., Hecky, R.E., Hesslein, R.H., and Turner, G.F. 1996. Food partitioning among Lake Malawi nearshore fishes as revealed by stable isotope analyses. *Ecology* 77:1286–1290.

Cabana, G., and Rasmussen, J.B. 1994. Modelling food chain structure and contaminant bioaccumulation using stable nitrogen isotopes. *Nature* 372:255–373.

_____, and Rasmussen, J.B. 1996. Comparison of aquatic food chains using nitrogen isotopes. *Proc. Nat. Acad. of Sci.* 93:10844–10847.

Campbell, L.M., Hecky, R.E., Nyaundi, J., Muggide, R., and Dixon, D.G. 2003. Distribution and food-web transfer of mercury in Napoleon and Winam gulfs, Lake Victoria, East Africa. *J. Great Lakes Res.* 29 (Suppl. 2):267–282.

Copley, H. 1958. *Common Freshwater Fishes of East Africa.* London, UK: H. F. & C. Witherby Ltd.

DeNiro, M.J., and Epstein, S. 1981. Influence of diet on the distribution of nitrogen isotopes in animals. *Geochim. et Cosmochim. Acta* 45:341–351.

Fogel, M.L., and Cifuentes, L.A. 1993. Isotope fractionation during primary production. In *Organic Geochemistry*, eds. M.H. Engel and S.A. Macko, pp. 73–98. New York, New York: Plenum Press.

Genner, M.J., Turner, G.F., Barker, S., and Hawkins, S.J. 1999. Niche segregation among Malawi cichlid fishes? Evidence from stable isotope signatures. *Ecology Letters* 2:185–190.

Gophen, M., Ochumba, P.B.O., and Kaufman, L.S. 1995. Some aspects of perturbation in the structure and biodiversity of the ecosystem of Lake Victoria (East Africa). *Aquat. Living Res.* 8:27–41.

Greenwood, P.H. 1966. *The Fishes of Uganda.* Nairobi, Kenya: The Uganda Society (Kampala).

_____. 1981. *The Haplochromine Fishes of the East African Lakes.* Müchen, Germany: Kraus-Thomson Organization GmbH.

Hecky, R.E. 1993. The eutrophication of Lake Victoria. *Internat. Ver. Theor. Ang. Limnol. Ver.* 25:39–48.

_____, and Hesslein, R.H. 1995. Contributions of benthic algae to lake food webs as revealed by stable isotope analyses. *N. Amer. J. Benthol. Soc.* 14:631–653.

_____, Bugeny, F.W.B., Ochumba, P., Talling, J.F., Mugidde, R., Gophen, M., and Kaufman, L. 1994. Deoxygenation of the deep water of Lake Victoria, East Africa. *Limnol. Oceanogr.* 39:1476–1481.

Hobson, K.A., and Welch, H.E. 1995. Cannibalism and trophic structure in a high Arctic lake: insights from stable-isotope analysis. *Can. J. Fish. Aquat. Sci.* 52:1195–1201.

Hughes, N.F. 1992. Nile perch, *Lates niloticus,* predation on the freshwater prawn, *Caridina nilotica,* in the Nyanza Gulf, Lake Victoria, East Africa. *Environ. Biol. Fish.* 33:307–309.

Kaufman, L. 1992. Catastrophic change in species-rich freshwater ecosystem: The lessons of Lake Victoria. *BioScience* 42:846–858.

Keough, J.R., Hagley, C.A., Ruzycki, E., and Sierszen, M. 1998. ^{13}C composition of primary producers and role of detritus in a freshwater coastal ecosystem. *Limnol. Oceanogr.* 43:734–740.

Kidd, K.A., Bootsma, H.A., Hesslein, R.H., Muir, D.C.G., and Hecky, R.E. 2001. Biomagnification of DDT through the benthic and pelagic food webs of Lake Malawi, East Africa: Importance of trophic level and carbon source. *Environ. Sci. Technol.* 35:14–20.

Kwak, T.J., and Zedler, J.B. 1997. Food web analysis of southern California coastal wetlands using multiple stable isotopes. *Oecologica* 110:262–277.

Lehman, J.T., and Branstrator, D.K. 1994. Nutrient dynamics and turnover rates of phosphate and sulfate in Lake Victoria, East Africa. *Limnol. Oceanogr.* 39:227–233.

Lung'ayia, H.B.O., M'harzi, A., Tackx, M., Gichuki, J., and Symoens, J.J. 2000. Phytoplankton community structure and environment in the Kenyan waters of Lake Victoria. *Freshw. Biol.* 43:529–543.

Mkumbo, O.C., and Ligtvoet, W. 1992. Changes in the diet of Nile perch, Lates niloticus (L), in the Mwanza Gulf, Lake Victoria. *Hydrobiologia* 232:79–83.

Muggide, R. 1992. *Changes in phytoplankton primary productivity and biomass in Lake Victoria (Uganda).* M.Sc. thesis. Dept. Botany, University of Manitoba, MB.

_____. 2001. *Nutrient Status and Planktonic Nitrogen Fixation in Lake Victoria, Africa.* Ph.D. thesis. Dept. Biology, University of Waterloo, ON.

Ogari, J., and Dadzie, S. 1988. The food of Nile perch, *Lates niloticus* (L.) after the dissapperance of the haplochromine cichlids in the Nyanza Gulf of Lake Victoria (Kenya). *J. Fish Biol.* 32:571–577.

Ogutu-Ohwayo, R. 1994. *Adjustments in Fish Stocks and in Life History Characteristics of Nile Perch, Lates niloticus L. in Lakes Victoria, Kyoga and Nabugabo.* Ph.D. thesis. Dept. Zoology, University of Manitoba, MB.

_____. 1995. Diversity and stability of fish stocks in Lakes Victoria, Kyoga and Nabugabo after establishment of introduced species. In *The Impact of Species Changes in African Lakes*, eds. T.J. Pitcher and P.J.B.

Hart, pp. 59–82. London, Great Britain: Chapman & Hall.

_____. 1999. Deterioration in length-weight relationships of Nile perch, *Lates niloticus* L. in Lakes Victoria, Kyoga and Nabugabo. *Hydrobiologia* 403:81–86.

Peterson, B.J., and Fry, B. 1987. Stable isotopes in ecosystem studies. *Ann. Rev. Ecol. Syst.* 18:293–320.

Ramlal, P.S. 2002. *Sources, Transport and Sinks of Organic Matter in Two African Great Lakes.* Ph.D. thesis. Dept. Biology, University of Waterloo, ON.

_____, Kling, G.W., Ndawula, L.M., Hecky, R.E., and Kling, H.J. 2001. Diurnal fluctuations in PCO_2, DIC, oxygen and nutrients at inshore sites in Lake Victoria, Uganda. In *The Great Lakes of the World (GLOW): Food-web, health and integrity,* eds. M. Munawar and R.E. Hecky, pp. 65–80. Leiden, The Netherlands: Backhuys Publishers.

Republic of Kenya. 1997. *District Development Plans 1997–2001 for Kisumu, Homa Bay, Rachuonyo, Siaya, Suba, Busia and Migori* (7 separate reports). Office of the Vice-President and Ministry of Planning and National Development. Nairobi, Kenya.

_____. 2000. *Economic Survey.* Central Bureau of Statistics, Ministry of Finance and Planning. Nairobi, Kenya.

The Republic of Uganda. 2000. *The Republic of Uganda 1999 Statistical Abstract.* Uganda Bureau of Statistics. Entebbe, Uganda.

Scheren, P.A.G.M., Zanting, H.A., and Lemmens, A.M.C. 2000. Estimation of water pollution sources in Lake Victoria, East Africa: Application and eleaboration of the rapid assessment methodology. *J. Environ. Manage.* 58:235–248.

Schindler, D.E., Carpenter, S.R., Cole, J.J., Kitchell, J.F., and Pace, M.L. 1997. Influence of food web structure on carbon exchange between lakes and the atmosphere. *Science* 277:248–250.

SEDAWOG. 1999. *The survey of Lake Victoria's fishers.* Socio-Economic Data Working Group (SEDAWOG), Lake Victoria Fisheries Research Project. Jinja, Uganda. Technical Document No. 5. LVFRP/TECH/99/05.

Twongo, T. 1996. Growing impact of water hyacinth on nearshore environments on Lakes Victoria and Kyoga (East Africa). In *The limnology, climatology, and paleoclimatology of the East African lakes*, eds. T.C. Johnson and E.O. Odada, pp. 633–642. Amsterdam, The Netherlands: Gordon and Breach Publishers.

van Oijen, M.J.P. 1995. Key to Lake Victoria fishes other than haplochromine cichlids. In *Fish Stocks and Fisheries of Lake Victoria: A Handbook For Field Observation*, eds. F. Witte and W.L.T. van Densen, pp. 209–300. Cardigan, UK: Samara Publishing Ltd.

Vander Zanden, M.J., and Rasmussen, J.B. 2001. Variation in ^{15}N and ^{13}C trophic fractionation: Implications for aquatic food web studies. *Limnol. Oceanogr.* 46:2061–2066.

Wanink, J.H. 1998. *The pelagic cyprinid Ratrineobola argentea as a crucial link in the disrupted ecosystem of Lake Victoria.* Ph.D. thesis. Sociale Wetenschappen. Univ. of Leiden, NL.

Witte, F., and van Densen, W.L.T. 1995. *Fish Stocks and Fisheries of Lake Victoria: A Handbook for Field Observations.* Cardigan, UK: Samara Publishing Limited.

_____, Goldschmidt, T., Goudswaard, P.C., Ligtvoet, W., van Oijen, M.J.P., and Wanink, J.H. 1992. Species extinction and concomitant ecological changes in Lake Victoria. *Netherlands J. Zool.* 42:214–232.

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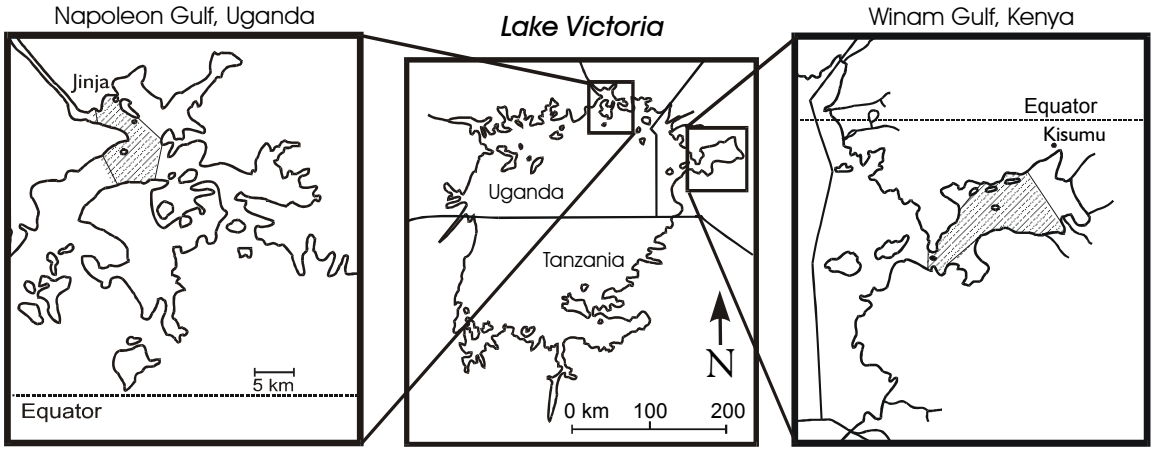
Napoleon Gulf, Uganda
Lake Victoria
Winam Gulf, Kenya
Jinja
5 km
Equator
Uganda
Tanzania
N
0 km 100 200
Equator
Kisumu

Figure 1.

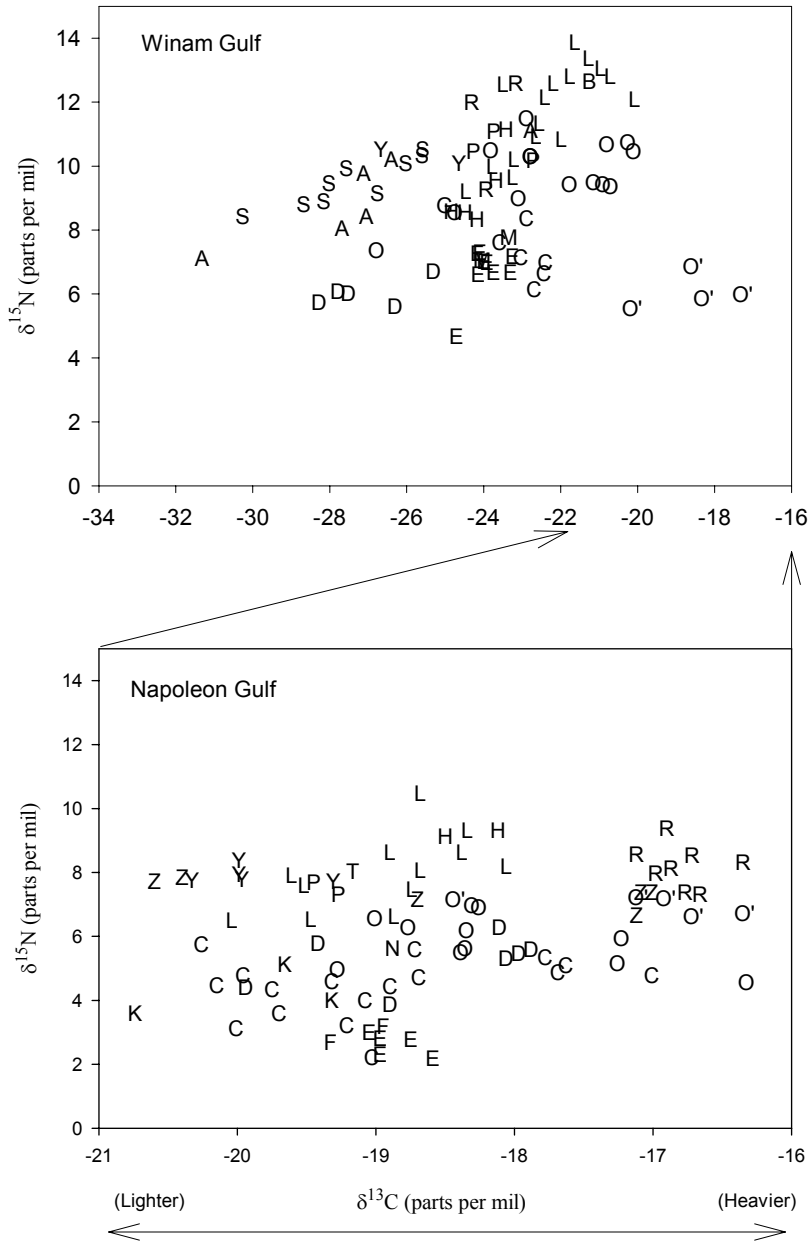
Winam Gulf
Napoleon Gulf
δ15N (parts per mil)
δ13C (parts per mil)
(Lighter)
(Heavier)

Figure 2.

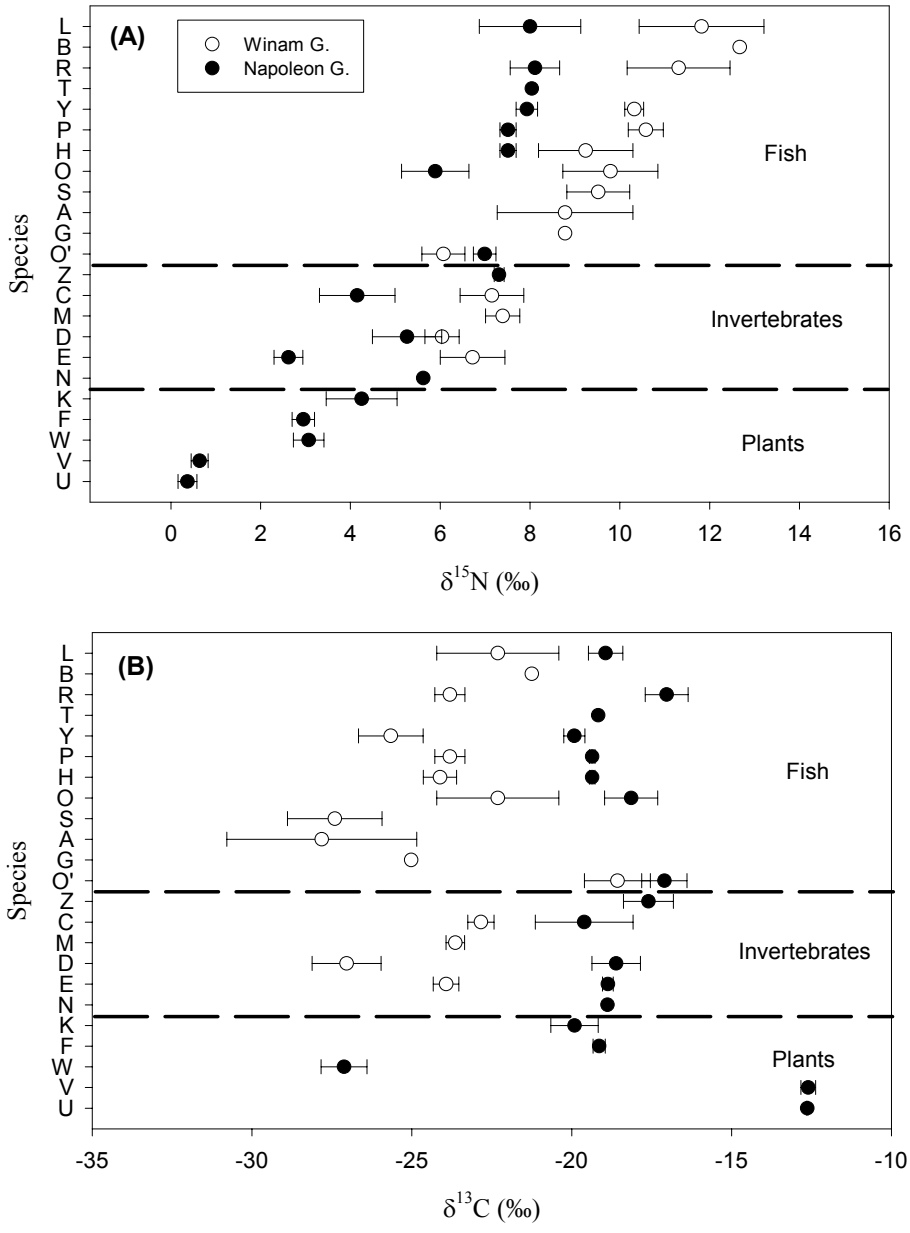
(A)
Winam G.
Napoleon G.
Species
L
B
R
T
Y
P
H
O
S
A
G
O'
Z
C
M
D
E
N
K
F
W
V
U
Fish
Invertebrates
Plants
0
2
4
6
8
10
12
14
16
δ15N (‰)
(B)
-35
-30
-25
-20
-15
-10
δ13C (‰)

Figure 3.

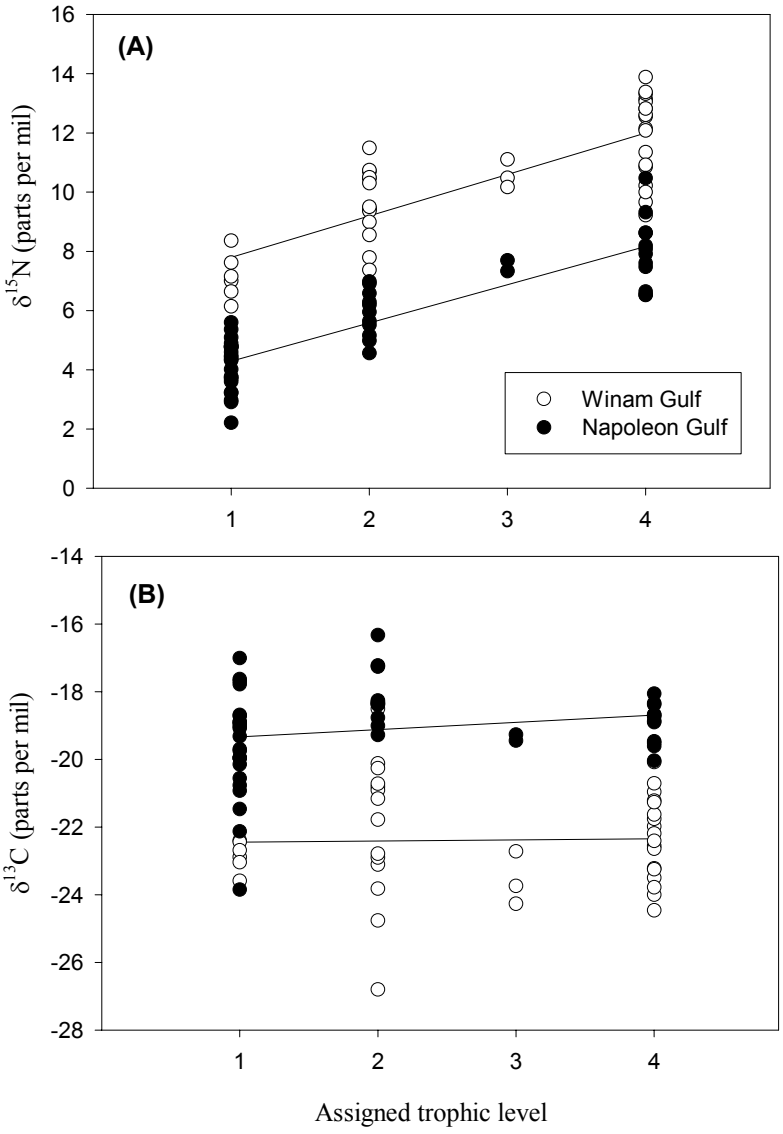
(A)
δ15N (parts per mil)
16
14
12
10
8
6
4
2
0
1
2
3
4
Winam Gulf
Napoleon Gulf
(B)
δ13C (parts per mil)
-14
-16
-18
-20
-22
-24
-26
-28
1
2
3
4
Assigned trophic level

Figure 4.

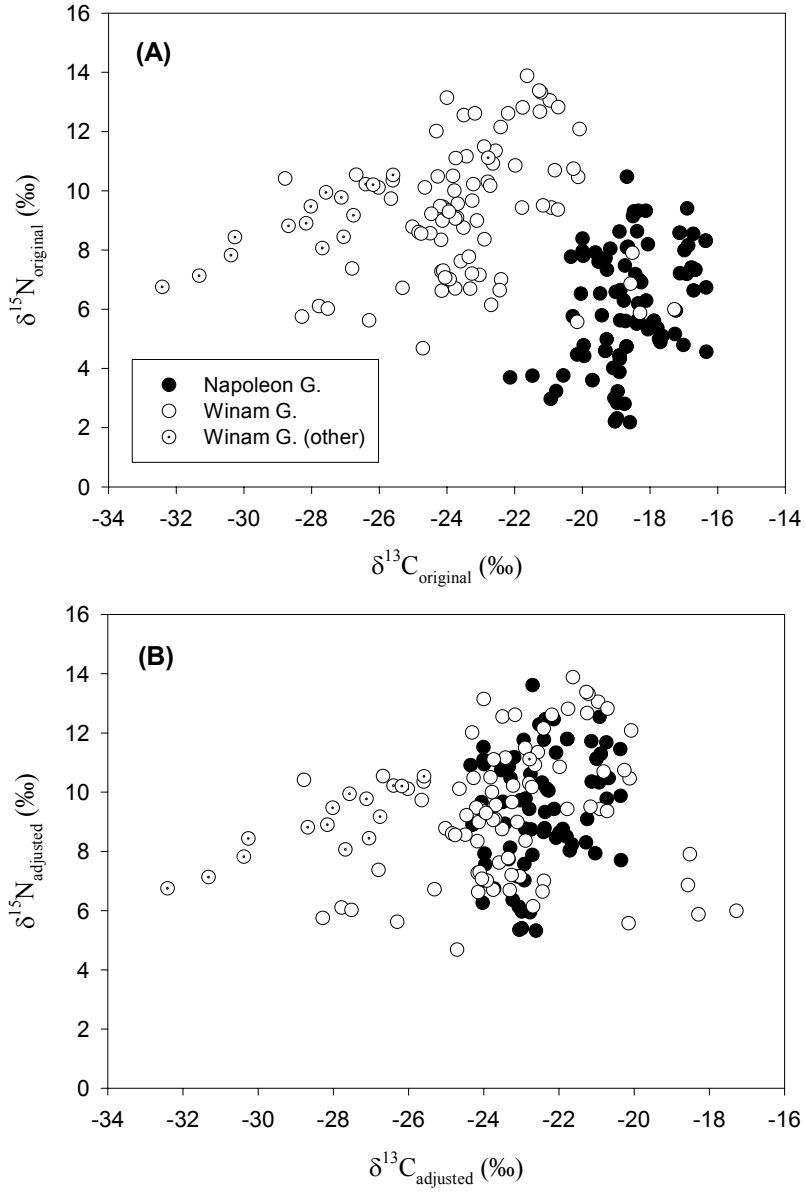
(A)
Napoleon G.
Winam G.
Winam G. (other)
$\delta^{15}N_{original}$ (‰)
$\delta^{13}C_{original}$ (‰)
(B)
$\delta^{15}N_{adjusted}$ (‰)
$\delta^{13}C_{adjusted}$ (‰)

Figure 5.

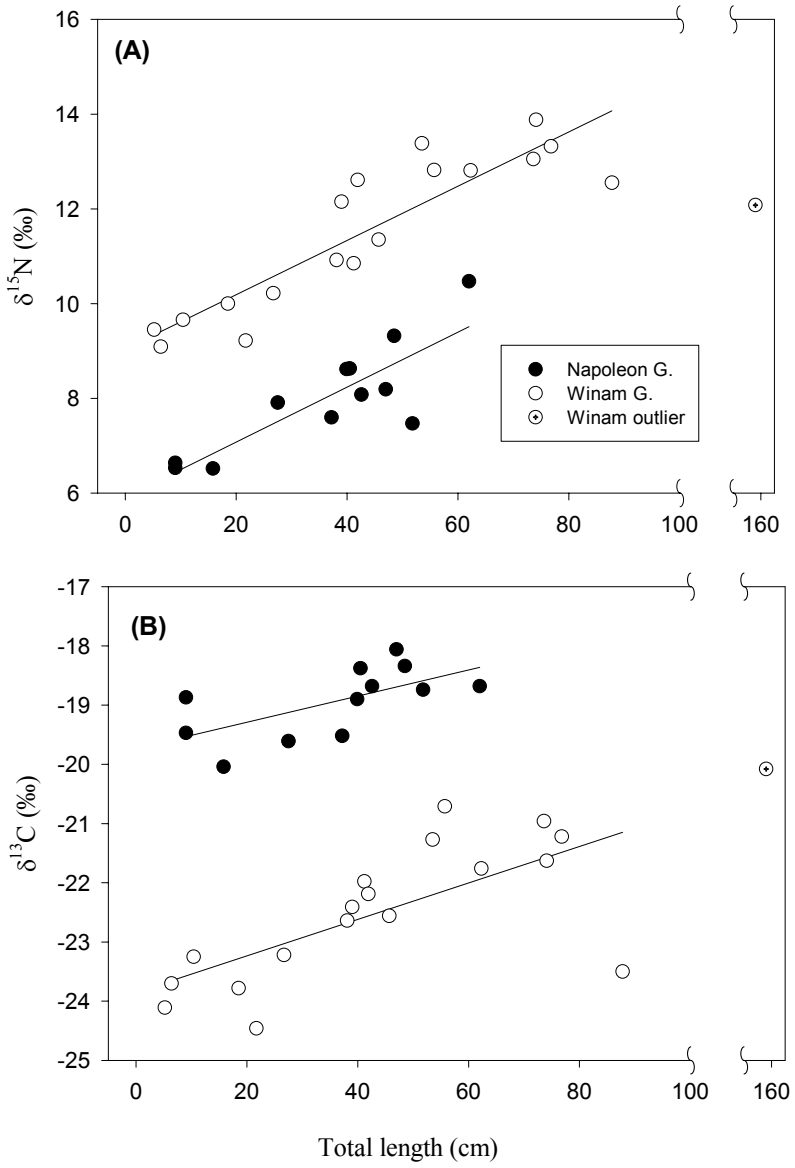
(A)
(B)
Napoleon G.
Winam G.
Winam outlier
δ15N (‰)
δ13C (‰)
Total length (cm)

Figure 6.

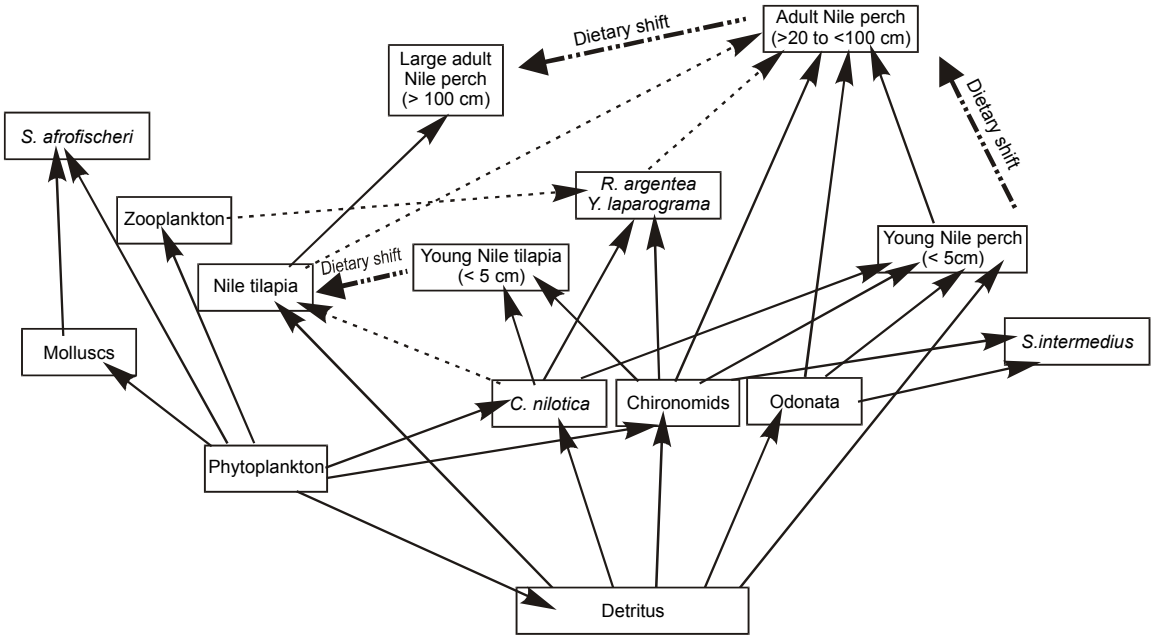
Dietary shift
Adult Nile perch
(>20 to <100 cm)
Large adult
Nile perch
(> 100 cm)
Dietary shift
S. afrofischeri
R. argentea
Y. laparogramma
Zooplankton
Young Nile perch
(< 5cm)
Dietary shift
Young Nile tilapia
(< 5 cm)
Nile tilapia
Molluscs
S.intermedius
C. nilotica
Chironomids
Odonata
Phytoplankton
Detritus

Figure 7.