

Isotopic evidence of functional overlap amongst the resilient pelagic fishes of Lake Victoria, Kenya

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Abstract

The Lake Victoria ecosystem once hosted a diverse fish community dominated by a large species flock of haplochromine cichlids. Today this fish assemblage is highly altered by anthropogenic activities, with at least half of the indigenous species either extinct or very rare. The fauna and flora of the tropic's largest lake are still in flux, and little is known about even the most basic ecological questions, such as the source of carbon and nitrogen for its spectacular productivity. The actual food-web structure is difficult to determine with results based on traditional gut analysis. At the moment both scientists and conservationists are at odds as to whether there is any evidence of functional replacement or functional overlap amongst the resilient pelagic fishes of Lake Victoria. This study used a static stable isotope model to investigate the source of carbon and the extent of the trophic overlap amongst three pelagic fishes, *Rastrineobola argentea*, *Yssichromis laparogramma* and *Y. fusiformis* in the Kenyan waters of Lake Victoria. The $\delta^{13}\text{C}$ of plants ranged from -8.8 to -24.6‰ , while fishes ranged from -18.6 to -24.5‰ , suggesting assimilation of mostly C_3 sources for the fish species. On the basis of the isotope model, it is evident that *Yssichromis laparogramma*, *Yssichromis fusiformis*, and *Rastrineobola argentea* obtained from 90 to 97.5%, with an average of 94.2%, of their food from the same trophic level. The very high degree of overlap in the effective trophic level of these three zooplanktivores has important ecological and conservation implications.

Introduction

With a surface of 69 000 km², Lake Victoria is the world's largest tropical lake and is shared by the three East African countries (Kenya, Uganda and Tanzania). Together with Lake Malawi and Tanganyika, Lake Victoria contained one of the most diverse lacustrine fish faunas in the world (Goldschmidt et al., 1993). In the first half of the last century, Lake Victoria had a very diverse fish fauna comprising 28 genera (Greenwood, 1974). The haplochromine cichlids alone accounted for more than 500 species (Greenwood, 1974; Witte

et al., 1992b; Kaufman, 1993; Seehausen, 1996). Against the advice of ecological researchers, Nile perch, *Lates niloticus* (Linnaeus, 1958), was introduced to Lake Victoria in the late 1950s (Harrison, 1991) to feed on the abundant haplochromines and convert them into a larger fish of greater commercial and recreational value (Graham, 1929). In the early 1980s an explosive increase in Nile perch was observed, wiping out native fishes by feeding preferentially on the abundant species, then shifting to other (non-haplochromine) species as the density of the initial prey declined (Ligtvoet, 1989).

The fish community in the lake has changed radically to a current dominance by the introduced Nile perch, *Lates niloticus*, the endemic cyprinid *Rastrineobola argentea* and remnants of the zooplanktivorous (*Yssichromis* spp.) and rock-dwelling haplochromine species (Ogutu-Ohwayo, 1990; Kaufman & Ochumba, 1993; Seehausen et al., 1997; Wanink, 1991). Hitherto, the zooplanktivorous haplochromines constituted 25% of the total open water haplochromine biomass (Goldschmidt et al., 1993). Even though recent studies have reported reemergence and increase in biomass of some of the zooplanktivores (Witte et al., 2000; Getabu et al., 2003; Katunzi et al., 2003), it is nonetheless intriguing to speculate on a possible link between a fourfold increase in the biomass of a pelagic cyprinid, *R. argentea* and the even greater proportional decrease in catches of zooplanktivorous haplochromines (Wanink, 1991; Witte et al., 1992). One of the explanations for the success of *R. argentea* is that the disappearance of most of the zooplanktivorous haplochromines may have reduced competition for food (Witte et al., 1992a). Evidence that zooplanktivorous fishes in Lake Victoria are food-limited is wanting. The replacement of pelagic haplochromines by a native pelagic cyprinid could reflect simply that the cyprinid was better able than haplochromines to deal with the threat of predation from Nile perch. (e.g., Wanink, 1998).

There have been a number of views regarding species composition and subsequent changes in faunal functional roles in Lake Victoria after the Nile perch boom. For example, the HEST (Haplochromine Ecological Survey Team) in Mwanza Gulf showed *R. argentea* to be an opportunistic feeder, taking zooplankton and several macro-invertebrate species as available (Wanink, 1998). This contradicts earlier studies (Graham, 1929; Corbet, 1961; Hoogenboezem, 1985), which indicated *R. argentea* to be an extreme specialist, feeding mainly on cyclopoid copepods. Wanink (1991) suggested that the original zooplanktivores (20 or more species of zooplanktivorous haplochromines, according to Witte & van Oijen, 1990) have been replaced by the native cyprinid *R. argentea*, plus juvenile ≤ 5 cm *Lates niloticus*. In all this it must be kept in mind that the original suite of zooplanktivorous haplochromines of Lake Victoria were themselves functionally diverse,

variously incorporating fractions of insect larvae, zooplankton, and cyanobacteria into their diets (Goldschmidt et al., 1990; Ebong, 1998).

Taken together, *R. argentea*, and pelagic haplochromines comprise a crucial but mysterious component of the modern Lake Victoria ecosystem. The functioning of the pelagic ecosystem and ultimate sources of materials for their subsistence has rarely been considered. A clear understanding of the ecosystem as a whole and interactions between species and various trophic levels is mandatory for proper resource management and sustainable utilization of a fast changing ecosystem such as Lake Victoria. In order to draw conclusions about the functional roles of individual species, a realized food web that reflects actual resource use is necessary. This is difficult to achieve. Different foods are absorbed at different rates in the gut, and it is not always clear from gut contents analysis how much a particular material will contribute to the production of the consumer concerned (Stoner & Zimmerman, 1988). For example some components, such as certain cyanobacteria, may be indigestible (Ribbink et al., 1983; Reinthal, 1990b). This problem is confounded in some fishes such as the cichlids and cyprinids, in which food is fragmented and rendered morphologically unidentifiable by grinding of the pharyngeal mill at the base of esophagus. There is therefore need to combine several lines of evidence to clarify trophic relationships and distinguish actual trophic links from those potentially possible.

One approach just gaining attention in Lake Victoria is to combine feeding observations with stable isotope measurements. Stable isotope analysis (SIA) methodology provides a slightly different perspective on trophic relationships and circumvents some of the problems encountered in the stomach content analysis (SCA). Stable isotope measurements of carbon and nitrogen have been helpful in determining the strength of food-web connections in a number of aquatic and terrestrial systems (Deniro & Epstein, 1978; Peterson & Fry, 1987). To date only a few studies on trophic dynamics in Lake Victoria have used both $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ stable isotopes to discern realized food web relationships in this fast changing ecosystem. It is not yet clear how much of the pelagic fish production is supported by pelagic (plankton)

versus benthic food sources. Our objective was to investigate the source of carbon and the extent of dietary overlap in the pelagic food web based on stable isotope analyses. The focus is on the three most abundant components of the pelagic fish assemblage in the Kenyan waters of the lake today: the endemic zooplanktivorous cichlids *Yssichromis laparogramma* and *Yssichromis fusiformis* and the indigenous minnow *R. argentea*. We used naturally occurring stable isotopes of carbon ($^{13}\text{C}/^{12}\text{C}$) and nitrogen ($^{15}\text{N}/^{14}\text{N}$).

Methods

Study site description

The study was carried out in the central open waters of Winam Gulf of Lake Victoria. It is a shallow bay (ca. 15 m maximum) in the north-eastern part of Lake Victoria, comprising most of the Kenyan portion of the lake. The Gulf covers an area of approximately 1920 km², reaches up to 30 km in width, and is joined to the main lake by a narrow (6 km) strait. The Nyando and Sondu/Miriu river systems are the major sources of water to the Gulf (Rinne & Wanjala, 1982). Winam Gulf is of particular interest as the purported area of initiation of the rapid increase in Nile perch population in Lake Victoria that took place in the mid-1980s, decades following its initial introduction (Ogotu-Ohwayo, 1988). Winam Gulf was also the first portion of Lake Victoria to exhibit shallow-water hypoxia and associated fish kills (Ochumba, 1990; Kaufman, 1992; Hecky et al., 1994), and it was the first area in Lake Victoria to experience overfishing of the Nile perch population. Winam Gulf is a bellweather for the lake as a whole.

Sample collection and analyses

The research vessel, R.V. Omena was used for bottom trawling with a net of 22.6-m head rope and a mosquito mesh cod end cover. The sampling was conducted from May to August 2002. The targeted fish species, haplochromines (*Y. laparogramma* and *Y. fusiformis*), *R. argentea* and the freshwater shrimp, *Caridina nilotica* were sampled from trawl catches from designated stations within

the Mid-Gulf (around Sukru Island and off Homa Bay). Fishes were examined soon after capture; white epaxial muscle tissue (5 g) of the fish species was removed from individuals after total lengths (TL) were measured. Individual samples were sealed in aluminum foil, and then frozen with dry ice. Other potential prey items, including zooplankton, phytoplankton, aquatic insects and various macrobenthic organisms were obtained synchronously with the fish samples. Zooplankton was obtained by filtering lake water into plankton net (mesh size 200 μm), and later picked under a dissecting microscope in the laboratory. Due to sampling difficulties, phytoplankton was collected as part of suspended particulate material, which was obtained on pre-ignited GF/F filters by filtering 0.5–1 l of lake water. Filters were then stored frozen. Mud samples and representative macrophytes (*Vossia cuspidata*, *Cyperus papyrus* and filamentous algae), were also collected from the stations and from nearby floating macrophyte islands. All samples were dried at 60 °C for 48 h in a drying oven, and ground to a fine powder using a mortar and pestle, then stored in clean glass vials. Samples were later shipped to the Boston University Stable Isotope Laboratory for analysis. $\delta^{13}\text{C}$, $\delta^{15}\text{N}$, %C and %N in the samples were determined using continuous-flow isotope mass spectrometry (Preston & Owens, 1983). Weighed samples of ground material (≈ 1 mg for animals and 2 mg for plants) were oxidized and the N₂ and CO₂ passed to a single inlet dual-collector mass spectrometer (Automated N C Analysis (ANCA) SL 20-20; PDZ Europa). Two samples of an internal reference material (glycine and peptone) were analyzed after every 10 tissue samples in order to calibrate the system and compensate for drift with time. The isotope ratios were expressed as parts-per-thousand (‰) deviation from the isotope standard using the equation:

$$\delta X = (R_{\text{sample}}/R_{\text{standard}} - 1) \times 10^3,$$

where X is ^{15}N or ^{13}C , R is the corresponding ratio $^{14}\text{N}:^{15}\text{N}$ or $^{12}\text{C}:^{13}\text{C}$ and δ is defined as the per mil (‰) deviation from isotope standard. A more positive δ value is said to be isotopically enriched, meaning the sample contains proportionately more of the heavy stable isotope (^{13}C or ^{15}N). The standard reference material for $^{13}\text{C}/^{12}\text{C}$ was Pee-dee Belemnite limestone (PDB), with atmospheric

N_2 being used for $^{15}N/^{14}N$. The analytical precision for ^{13}C and ^{15}N was within ‰, based on repeat measurement of a secondary standard. The following mixing model developed by Gu et al. (1996) was used to estimate the degree (f) of functional overlap or similarity between *Y. laparogramma*, *Y. fusiformis*, and *R. argentea* of specific size range (4.3–9.2 cm) (Table 2):

$$F(\%) = (1 - (x - y)/a) \times 100,$$

where x and y are the muscle $\delta^{15}N$ values for different comparisons between respective species and a is $\delta^{15}N$ enrichment factor. We used enrichment factors values of 3.0, 3.5 and 4.0. Enrichment factors for other fish species fall within this range (Minagawa & Wada, 1984; Hobson & Welch, 1992).

Results

$\delta^{13}C$ and $\delta^{15}N$ measurements

The mean values of the $\delta^{13}C$ determined for fishes and their potential prey are shown in Table 1. $\delta^{13}C$ values for the vascular and non-vascular plants ranged from -24 to -8 ‰. Filamentous algae were the most enriched with heavy carbon, at -8 ‰. Mean $\delta^{13}C$ values for *R. argentea*, *Y. laparo-*

gramma and *Y. fusiformis* did not vary significantly with an overall average of -21.5 ‰.

Differences in $\delta^{15}N$ isotopic compositions among plant, invertebrates and fish material followed the typical trend for trophic enrichment. The mean $\delta^{15}N$ for zooplankton was 4.2 ‰ higher than for phytoplankton (Fig. 1). The sampled macro-invertebrates had $\delta^{15}N$ mean values ranging from 1.4 to 11.20 ‰, with Odonata being the most isotopically enriched among them, as expected for a predatory insect (Table 1). Muscle $\delta^{15}N$ mean values among *R. argentea*, *Y. laparogramma* and *Y. fusiformis* fell within an extremely narrow range from 11.9 ± 0.7 SD to 12.2 ± 0.6 SD, and did not vary significantly among species and was also not significantly correlated with the length of individuals within species. However, all three exhibited about 4 ‰ ^{15}N enrichment over zooplankton, which in turn was about 4 ‰ more enriched than phytoplankton (Fig. 1, Table 1).

Dietary overlap

The functional overlaps among *Y. laparogramma*, *Y. fusiformis* and *R. argentea* ranged from 90 to 96.7% on the basis of enrichment factor 3.0 (enrichment factors for other fish species fall within 3.0, 4.0 ranges). Using an enrichment factor

Table 1. Means (\pm SD), $\delta^{13}C$ and $\delta^{15}N$ signatures of *Yssichromis laparogramma*, *Y. fusiformis* and *Rastrineobola argentea* in the Kenyan waters of Lake Victoria

Biota	Sample-size n	$\delta^{13}C$ (‰)		$\delta^{15}N$ (‰)	
		Mean \pm SD	Range	Mean \pm SD	Range
<i>Y. laparogramma</i>	38	-21.4 ± 0.4	-22.4 to -20.9	11.9 ± 0.7	10.9–13.2
<i>Y. fusiformis</i>	32	-20.8 ± 0.7	-21.6 to -19.3	12.2 ± 0.6	11.3–13.1
<i>R. argentea</i>	27	-20.0 ± 1.2	-21.9 to -18.0	12.1 ± 0.6	11.0–13.5
Zooplankton	4	-20.7	-21.0 to -20.3	8.4 ± 1.5	8.0–8.8
<i>Caridina nilotica</i>	9	-18.7	-23.2 to -17.8	5.4 ± 0.4	5.3–7
Odonata	1	-26		11.20	
Phytoplankton	5	-24.1 ± 0.6	-24.6 to -23	4.1 ± 0.3	3.8–4.3
(suspended particulate material)					
Filamentous algae	1	-8.8		6.6	
<i>Eichhornia crassipes</i>	2	-28.1	-28.78 to 27.42	8.12	7.02–9.22
<i>Cyperus papyrus</i>	1	-13.46		9.12	
<i>Vossia cuspidata</i>	1	-14.08		2.83	
Mayflies	2	-21.70		5.90	
<i>Chaoborus</i> sp. (Midges)	2	-25.50		5.70	
Oligochaete	2	-23.80		3.90	

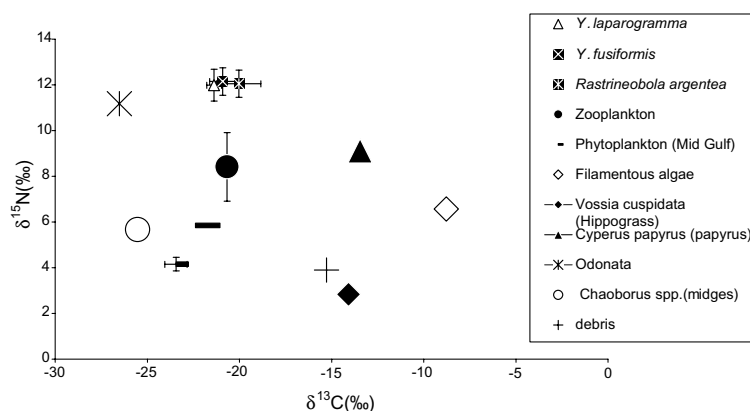


Figure 1. Scatterplot of $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ signatures (‰) of the pelagic fish assemblage and their potential prey in the Kenyan waters of Lake Victoria.

of 3.0 or 4.0 did not make a difference to functional overlap estimates for *Y. laparogramma*, *Y. fusiformis* or *R. argentea* (Table 2).

Discussion

Stable carbon isotope measurements indicate the types of plants that are important sources of carbon to consumers in food webs (Peterson & Fry, 1987). As shown in Table 1, the $\delta^{13}\text{C}$ values for *Y. laparogramma*, *Y. fusiformis* and *R. argentea* compared to those of plants analyzed had $\delta^{13}\text{C}$ ranges suggesting mainly C_3 sources for these fishes. Carbon values for C_3 plants generally range from -31 to -22 ‰ (Michener & Scherr, 1994) with a much smaller isotopic fractionation across trophic levels than is seen in ^{15}N (0 – 1 ‰) per trophic

level (Fry & Sherr, 1984). The most likely source of fixed carbon for these fishes is lacustrine phytoplankton (which are C_3 photosynthetic protists), via herbivorous zooplankton prey (Fig. 1). It is unlikely that these fishes derived much of their carbon from benthic algae, which generally show high levels of $\delta^{13}\text{C}$ enrichment. France (1995), attributed greater ^{13}C enrichment in benthic compared to planktonic algae to differences in exposure to water turbulence. Estimation of energy sources for consumers are at times masked significantly by different lipids contents of the $\delta^{13}\text{C}$ signal among organisms as noted by Wada et al. (1987). However, for small freshwater tropical fish species lipids in epaxial musculature (i.e., belly flap muscle excluded) have not presented a major problem in our experience. Therefore based on our data, we surmise that carbon sourcing for these

Table 2. Mean dietary overlap between *Yssichromis laparogramma* (L), *Y. fusiformis* (F) and *R. argentea* in the Kenyan waters of Lake Victoria as estimated using differences mean muscle $\delta^{15}\text{N}$ and three enrichment factors (a)

Run	Difference	Dietary overlap (%)		
		$a = 3.0$	$a = 3.5$	$a = 4.0$
L and F	0.3	90.0	91.4	92.5
L and R	0.2	93.3	94.3	95.0
F and R	0.1	96.7	97.1	97.5
Key	Length range (cm)	Muscle $\delta^{15}\text{N}$		
L – <i>Yssichromis laparogramma</i>	5.1–7.8	11.9 ± 0.7		
F – <i>Yssichromis fusiformis</i>	5.4–9.2	12.2 ± 0.6		
R – <i>Rastrineobola argentea</i>	4.3–8.6	12.1 ± 0.6		

Note: Values of $\delta^{15}\text{N}$ are given as the mean ± SD.

three zooplanktivorous fishes is (a) very similar, and (b) derived mostly from the open-water food web.

The mean $\delta^{15}\text{N}$ for zooplankton averaged 4.2‰ higher than for phytoplankton. This is in good agreement with several studies on $\delta^{15}\text{N}$ enrichment factors specific to zooplankton (Montoya et al., 1990; Kling et al., 1992; Gu et al., 1994). Other studies have also indicated $\delta^{15}\text{N}$ enrichments between fish and their diets do typically range from 3.0 to 4 ‰ (Minagawa & Wada, 1984; Hobson & Welch, 1992). Therefore on the same basis, the isotopic differences in *R. argentea*, *Y. laparogramma* and *Y. fusiformis*, compared to those of zooplankton and phytoplankton (Fig. 1), suggest that the three fishes largely assimilated zooplankton and not the phytoplankton sometimes seen, especially in the gut contents of the zooplanktivorous haplochromine guild. Ebong (1998) using stomach content analysis reported both *Y. laparogramma* and *Y. fusiformis* to be incorporating fractions of algae into their diet. Other studies in Mwanza Gulf showed phytoplankton to form a considerable amount of the diet of other pelagic haplochromine species (Goldschmidt et al., 1990). Wanink et al. (1998) concluded that *R. argentea* is an opportunistic feeder, which feeds basically on zooplankton but takes several macro-invertebrates whenever available. However, the differences in $\delta^{15}\text{N}$ enrichment between *R. argentea* and macro-invertebrates analyzed in our study pointed out the importance of zooplankton and relative unimportance of predatory macro-invertebrates such as *Chaoborus* or odonates.

The model developed by Gu et al. (1996) to estimate functional overlap, indicated strong overlap among the three zooplanktivores, confirming that all three were feeding at a similar trophic level. This study therefore suggests that even though other food items are often encountered during gut content analysis (Ebong, 1998; Wanink, 1998), these species are mainly assimilating zooplankton into their bodies for growth and reproduction. In any event, it seems unlikely that food is a proximal limiting factor for the zooplanktivorous assemblage in Lake Victoria. This notion is consistent with the trend in trawl surveys data, which show strong reemergence of zooplanktivorous haplochromines (comprising

15% of acoustically estimated biomass in the water column) without a corresponding decrease in the numbers of *R. argentea* in Winam Gulf (23% of water column biomass) (Getabu et al., 2003). According to Wanink et al. (1991), most adults of *R. argentea* dwell close to the water surface at night, and deeper by day. Witte (1984) and Goldschmidt et al. (1990) reported other species of zooplanktivorous haplochromines in Lake Victoria to behave similarly, occupying the lower half of the water column and taking zooplankton – by day, and the upper half-switching to insects larvae and pupae – at night.

However, due to limited number of invertebrate samples included in our study, more work is suggested to sort and discern roles of predatory, herbivorous insects and the rest of the microinvertebrates in the diets of reemerging zooplanktivores (Katunzi et al., 2003) and other fish species, considering the dynamics within the lakes ecosystem. The exact foraging time of these species is still a mystery, especially in the Kenyan waters. A 24-h sampling strategy to determine spatial and temporal distribution pattern and qualitative gut content analysis is called for so that patterns of diurnal habitat segregation and utilization can be determined. This would shed light on other ecological interactions between zooplanktivorous haplochromines and *R. argentea*.

Fortuitously, we have been able to compare our values to those obtained by Campbell et al. in a very recent paper of theirs examining stable isotopic signatures for some fishes and fish prey in Winam and Napoleon Gulf (Campbell et al., in press). In general, our values are in accord with those of Campbell et al. for Winam Gulf, with some interesting exceptions. Campbell et al. concluded that *Rastrineobola* and *Yssichromis* were not solely dependent upon zooplankton, and were likely to have been feeding largely upon lake flies. Our data differ. A slightly lower mean value for zooplankton, and substantially higher values for *Rastrineobola* and two species of *Yssichromis*, makes it likely that the pelagic fish specimens that we sampled were feeding substantially on zooplankton, or on a mix of zooplankton and lake flies. Even with our limited non-fish samples, there are two possible explanations for this, both of interest. One is that our values differ because our samples were taken in different seasons or different

years, ours during May–August of 2002, and those of Campbell et al. in the lattermost months of 1998. Time of sampling relative to seasons or the arrival of biomass pulses from a particular source (such as upwelling) can greatly influence the patterns apparent in stable isotopic studies (O'Reilly et al., 2002). There can also be temporal shifts in the proportion of predatory to herbivorous lake microinvertebrates in the samples, something that if not carefully sorted prior to analysis, could cause discrepancies particularly in zooplankton signals. Changes in prey base or species composition are also likely suspects in differences between our ^{15}N enrichment values and those of Campbell et al. for odonate larvae (means of 11.2 here, vs. 6.0 in Campbell et al.).

Lastly, heavy nitrogen enrichment in the three species of macrophytes that we examined in Winam Gulf (*Cyperus papyrus* and *Vossia cuspidata*, and *Eichhornia crassipes*) were on the order of 1.5 orders of magnitude greater than that observed by Campbell et al. in Napoleon Gulf (values were not provided for Winam Gulf). We postulate that this was due to a combination of the generally more enriched food base in Winam Gulf. Gichuki et al. (2001) attributed the high enrichment of ^{15}N in *Eichhornia crassipes* to uptake of residual nitrate enriched in ^{15}N . Indeed, approximately 70% of the surface water input to all of Lake Victoria comes from Kenya, emptying first into the strongly bottlenecked embayment of Winam Gulf. We are equally surprised by the extremity of this difference, as we are by the fact that the open water phytoplankton and zooplankton do not seem to be greatly influenced by this very strong estuarine signal.

Although the three zooplanktivorous fishes examined here occupy similar positions in the food web of Winam Gulf, they do not represent equivalent value in terms of biomass transfer to the Nile perch fishery. Evidence suggests that Nile perch feed preferentially, and grow fastest, on haplochromines as prey (Ogutu-Ohwayo, 1990; Kaufman & Schwartz, 2002). If this proves to be generally true, then management might wish to further circumstances that maximize energy flow from haplochromines to Nile perch. Conservation of the surviving haplochromines, or at least the zooplanktivorous species, would be in the interest of the fishery (Kaufman & Schwartz, 2002; see also

Balirwa et al., 2003). Currently, only two of what may have been up to a dozen zooplanktivorous haplochromine species are regularly found in Kenyan waters.

Our results also afford clear testimony that the present fisheries management objectives of the Lake Victoria Environmental Management Project (LVEMP): i.e., to conserve and rehabilitate some of the threatened species, should be strongly encouraged. Several studies have raised the question of niche overlap and functional redundancy especially when considering the role of rare species like some of the zooplanktivorous haplochromines. In Lake Victoria, these species are already showing signs of resilience (ability of a population to recover from different magnitudes of stress, according to Holling (1973)) and could eventually provide a measure of ecosystem stability by spreading Nile perch across a broader food base, encompassing species with differing vulnerabilities to environmental vicissitudes.

Conclusion

Stable isotope and stomach contents analyses supplied us with somewhat different but complementary information on the diets of *Y. laparogramma*, *Y. fusiformis* and *R. argentea*. The $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values obtained demonstrated the linkages between primary carbon sources and the fish species' trophic history for Kenyan waters of Lake Victoria. This study not only establishes some baseline carbon and nitrogen isotope data for the Lake Victoria ecosystem, but is also one of the few studies in the region to use stable isotope analyses, a relatively new ecological technique to help in studying and understanding trophic dynamics in this perturbed ecosystem.

The livelihood of more than 30 million people in the Lake Victoria region revolves around the lake's fishery and its other resources. Fish provide the main protein source and a substantial commercial income for the people in most of the basin. An understanding of factors responsible for fisheries production is of crucial importance. Fish production can be viewed as the final step in the series of carbon (or energy) transformations beginning with carbon dioxide fixation by plants. These plants are the primary producers that form the energy base

supporting fisheries production. Stable isotope analysis may therefore provide a simple way of determining the relative contribution of alternative energetic pathways, each with distinct management outcomes. Stable isotope analysis thus appears to have great potential as a discrete, measurable trigger for ecosystem-based fisheries management in this system. It provides a means by which the energy basis of secondary production can be determined. This is especially important for an ecosystem like Lake Victoria that is very much in flux, as the lake continues to respond to increasing population pressures, large-scale watershed disturbances, and global climate change.

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