African Journal of Environmental Science and Technology Vol. 5(6), pp. 457-463, June 2011
Available online at http://www.academicjournals.org/AJEST
DOI: 10.5897/AJEST10.311
ISSN 1996-0786 ©2011 Academic Journals

Full Length Research Paper

Preliminary gut content and dentition analysis reveal subtle resource partitioning and feeding adaptations within a haplochromine cichlid community of Lake Victoria satellite lake

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Accepted 30 May, 2011

The trophic relationships between six haplochromine cichlids of Lake Kanyaboli, a satellite lake of Lake Victoria that has not been infested by the Nile perch (*Lates niloticus*), were studied as a first step towards understanding the cichlid community structure in this threatened wetland ecosystem. Co-efficient of similarity analysis of diet revealed subtle trophic resource partitioning within this haplochromine community. Trophic specializations are further revealed by differences in dentition structures. Of the six haplochromine species examined, *Astatotilapia nubila* and *Astatoreochromis alluadi* had the highest coefficient of similarity (0.5256±0.300), indicating highest diet overlap, while *Astatotilapia 'big eye'* and *Xistichromis phytophagus* were the most ecologically separated (0.0210±0.019). Resource partitioning is further enhanced by a diurnal spatial distribution of the six species within the lake. Overall, the haplochromine cichlid community of Lake Kanyaboli is characterized by a relatively high trophic diversity compared to Lake Victoria. Small water bodies (SWBs) thus present opportunities for conservation of trophic diversity threatened by introduction of exotics in the Lake Victoria basin.

Key words: Community structure, haplochromines, resource partitioning, satellite lakes, trophic ecology.

INTRODUCTION

Lake Victoria, the largest tropical lake in the world, once contained over 500 species of haplochromine cichlids of which about 99% of species were endemic and exploited virtually all food sources in the lake (Witte et al., 1992). However, this situation changed dramatically in the late 1970's and early 1980's. Population explosion of introduced Nile perch (*Lates niloticus*) in Lake Victoria, in combination with eutrophication and other environmental changes, coincided with dramatic changes in the trophic ecology of the system. Most notably, a simplification of the food web occurred due to the extirpation of up to 200 species of indigenous haplochromine cichlids (Witte et al., 1992; Goldschmidt et al., 1993; Seehausen et al., 1997a). By 1990, the haplochromines comprised less than 2% of the biomass and about half of the endemic species had either vanished or were threatened with extinction (Ogutu-Ohwayo, 1990a; Witte et al., 1992). Although the cichlid fauna in Lake Victoria seem to have partially recovered (Seehausen et al., 1997b; Witte et al., 2000), the eradication of haplochromines in Lake Victoria is possibly the largest extinction event of vertebrate species in modern human history (Goldschmidt et al., 1993).

The exceptional species diversity of the haplochromine cichlids in the Lake Victoria region has been attributed to – among other factors – trophic specializations, which promote co-existence of ecologically similar species (Fryer and Illes, 1972; Barel et al., 1977; Seehausen and Bouton, 1997). Feeding specializations have been instrumental in resource partitioning and therefore in shaping the cichlid community structure. Trophic differentiation (Salzburger, 2009) as well as asymmetric interspecific interactions (Maruyama et al., 2010) are some of the factors that have been hypothesized to have contributed to the evolution and adaptive radiation of cichlid fishes in the great lakes of East Africa. The trophic ecology of Lake Victoria haplochromines

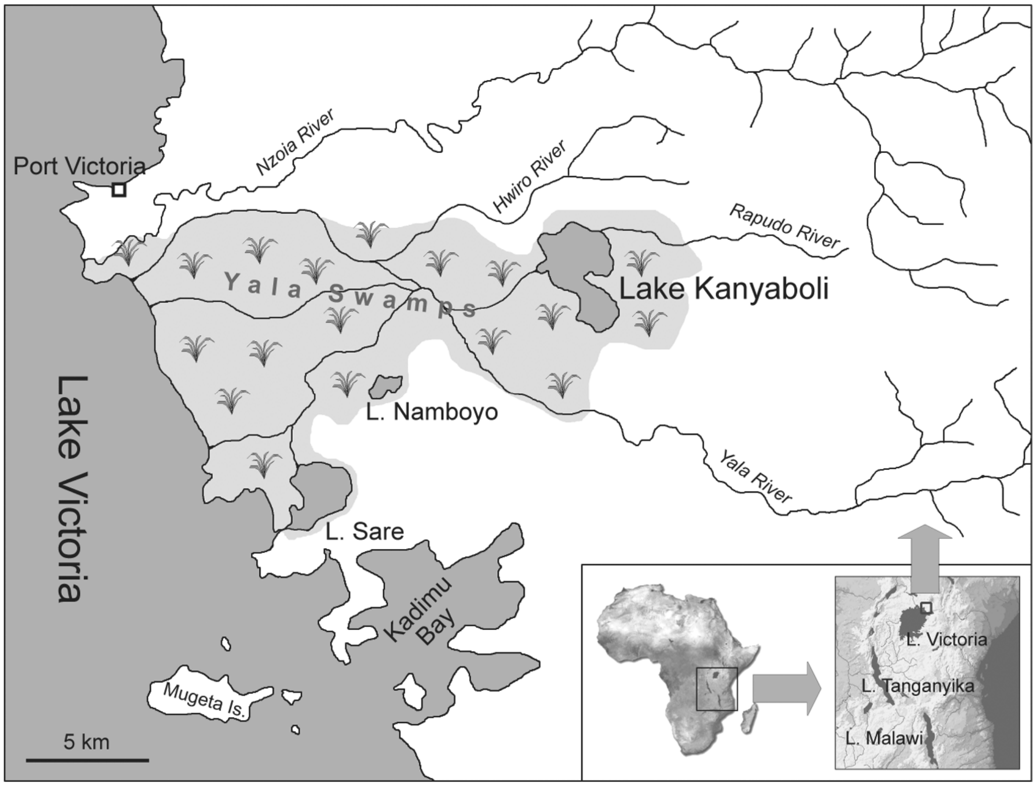

Figure 1. Map of the Yala swamp, Kenya's largest wetland, and associated lakes (Abila et al., 2004).

have been extensively studied by among others van Oijen (1982), Lowe-McConnell (1993) and Goldschmidt et al. (1990). Overall, these studies indicate that the haplochromine cichlids of Lake Victoria exhibited high levels of feeding specializations which likely minimizes competition and promotes co-existence of ecologically similar species. These studies further demonstrated the existence of trophic specialization among the Lake Victoria haplochromines with regards to their food and habitat (Seehausen and Bouton, 1997). It has also been shown that morphological and dentition characters are correlated with the trophic habits of the species (Seehausen and Bouton, 1997). Feeding interactions have also been used to map the flow of energy, materials and nutrients in ecosystems (Jepsen and Winemiller, 2002) and hence gain an insight into the dynamics of an ecosystem.

While previous studies focused on the haplochromine communities of Lake Victoria, there is a dearth of knowledge about the trophic ecology of the haplochromine communities of the smaller (satellite) lakes of Lake Victoria basin. Such satellite lakes have long been recognized as important functional refugia for endangered Lake Victoria haplochromines (Kaufman and Ochumba, 1993; Maithya, 1998). In a recent study, we identified eight major food items consumed by the six haplochromine species (Abila et al., 2008). Recent molecular studies on haplochromines and tilapiines have further demonstrated the significance of the satellite lakes in the conservation of the genetic diversity of Lake Victoria cichlids (Angienda et al., 2011; Abila et al., 2004). Most of these haplochromine cichlids disappeared from the main Lake Victoria before their ecology was documented so that satellite lakes, which have not been invaded by the Nile Perch, provide an opportunity of obtaining further insights into their ecology and the effects of Nile Perch introduction in shaping the haplochromine community structure. A recent analysis of the trophic diversity of 24 haplochromine species in six satellite lakes in the Lake Kyoga basin, Uganda, revealed seven trophic groups, namely insectivores, paedophages, piscivores, algal eaters, higher plant eaters, molluscivores and detritivores (Mbabazi et al., 2004). In contrast, only two trophic groups (insectivores and molluscivores) were found in the main Lake Kyoga that has been impacted by the Nile Perch.

This work presents the first attempt to determine niche differentiation and resource partitioning of the haplochromine fauna in Lake Kanyaboli, a small (10.5 km^2) and shallow freshwater lake (00°04”30”N; 34°09"36”E; average depth: 2.5 m; maximum depth: 4.5 m) situated in the Yala wetlands in Western Kenya (Figure 1). The Yala swamp is the largest freshwater wetland within the Lake Victoria basin and covers about 175 km^2. Three main lakes exist in the Yala wetlands (Kanyaboli, Namboyo and Sare), of which Lake Kanyaboli is the largest and most remote from Lake Victoria. Lake Kanyaboli is separated from Lake Victoria by massive papyrus swamps that inhibit faunal exchanges between the two lakes. Nile Perch does not occur in Lake Kanyaboli, suggesting that this lake has been isolated from Lake Victoria at least since the 1950's. The fish fauna of Lake Kanyaboli is dominated by cichlids: three species of tilapia, *Oreochromis esculentus*, *Oreochromis variabilis* and *Oreochromis leucostictus* and six haplochromine cichlid species *Astatoreochromis alluaudi, Astatotilapia nubila Astatotilapia sp.* 'dwarf big eye', *Lipochromis maxillaris,*, *Pseudocrenilabrus multicolor victoriae* and *Xystichromis phytophatus* (Kaufman and Ochumba, 1993; Odhiambo, 2002; Aloo, 2003; Abila et al., 2004). While *A. alluaudi* and *P. multicolor victoriae* are representatives of more ancestral haplochromine lineages, the remaining four species are part of the Lake Victoria region superflock (Verheyen et al., 2003; Salzburger et al., 2005).

Although the haplochromines form an important component of the fisheries of Lake Kanyaboli and are a crucial source of food and income to the local community (Abila, 2002; Mwakubo et al., 2007), lack of ecological knowledge on the fish stock may hamper implementation of fisheries management. Understanding the trophic interactions and community structure of the fish community is an essential requirement towards successful implementation of the ecosystem approach in fisheries management and conservation. The objective of this study was to characterize the trophic ecology of the Lake Kanyaboli haplochromines and to compare this with similar satellite lakes of the Lake Victoria region. This would, once more, demonstrate the importance of satellite lakes in wetlands around Lake Victoria as refugia for the genetic and ecological diversity of otherwise endangered Lake Victoria basin haplochroimines (Kaufman and Ochumba, 1993; Abila et al., 2004).

MATERIALS AND METHODS

Fish sampling

The following six haplochromine species were sampled from Lake Kanyaboli in Kenya (Figure 1): *X. phytophagus* (N=50), *L. maxillaris* (N=44), *A. nubila* (N=37), *A. alluaudi* (N=56)*, P. multicolor victoriae* (N=47) as well as the "dwarf big eyed" *Astatotilapia* (N=26). Samples were taken along the fringing papyrus at a depth of 1.0 to 1.5 m and at inshore depths of 3.0 to 4.0 m using experimental gill nets with stretched mesh sizes (25.4 to 203.2 mm) during both day and night hours every 2 weeks between April and August 2002 and in July to September 2003 (Abila et al., 2008). Gill nets were hauled every hour to reduce post harvest digestion. Angling was done to obtain fish from areas that could not be accessed by nets, for example the thick infringing papyrus. Upon collection, adult fish species were categorized into different species. Color photographs of the specimens were taken in the field and the fish were preserved in 90% ethanol.

Gut content analysis

Adult fish were dissected and the whole gut removed. Gut contents were mixed to form a homogenous mixture in a Petri dish. The gut contents comprising of fine particles were shaken in water and drops of the suspension were examined under a microscope (40 to 400 fold magnification). Ingested material was identified and placed into food categories that ranged from broad taxonomic or ecological groups to individual genera. A number of specimens with empty stomachs were caught but were not included in the analysis. Food items were identified using identification keys in Hyslop (1980). The contribution of each food item to the diet of every species was determined by calculating three important feeding habit parameters: relative abundance (percentage proportion), percentage of occurrence, and prominence value (Hyslop, 1980).

Relative abundance (RA)

Relative abundance was determined by comparing the area occupied by each food item in the field of view. Numbers from 1 to 10 were allocated to each food item representing the percentage fraction allocated to one food item (hence, 1 indicated that a certain food item was estimate to constitute about 10% of the total gut contents and 10 was allocated when the whole stomach content was made up of a single food type). The points counted to a food item were then expressed as the percentage of the total points for all food ingested by that species.

Percentage of occurrence (PO)

Percentage of occurrence was determined by counting the number of stomachs of each species in which a food item was present. These numbers were added up and expressed as the percentage of guts in which a certain food item occurred.

Prominence value (PV)

The relative abundance and percentage of occurrence were used to estimate the relative importance of each food item consumed by calculating its prominence value using the equation:

$PV = RA \times PO$

Where;

PV = prominence value
RA = relative abundance
PO = percentage of occurrence

Using the PV's as a guide, species were classified into feeding groups by determining the coefficients of similarity of the food items:

$C = 2 \times PV\ (Low) / (PVN1 + PVN2)$

Where;

C = coefficient of similarity index
PV (Low) = the value of the lower prominence values calculated for each of the food items taken in common by any two species to be compared
PVN_1 and PVN_2 = the prominence values of each food item for species 1 and 2 respectively.
C (the co efficient of similarity) ranges between 0 and 1 where 0 shows no sharing of any food between the two species compared and 1 indicating total overlap in feeding. The coefficient of similarity reveals diet overlaps and is thus an indicator of potential competition for food.

In addition, the dentition structures including the number of teeth in oral jaws, the number of rows of teeth in oral jaws, as well as the

Table 1. Co-efficient of similarity (mean±S.D.) between six species of haplochromine cichlids in Lake Kanyaboli based on five food items ingested.

Species	*A. nubila*	*Astatotilapia* sp. (big eye)	*L. maxillaris*	*X. phytophagus*	*A. alluaudi*	*P. multicolor victoriae*
A. nubila	-	0.2228(±0.308)	0.2668 (±0.360)	0.1170 (±0.132)	0.5256(±0.300)	0.4526(0.332)
Astatotilapia sp. (big eye)	-	-	0.1934 (±0.335)	0.0210(±0.019)	0.2147(±0.306)	0.2982(±0.336)
L. maxillaris	-	-	-	*0.1142* (±0.185)	0.3106(±0.377)	0.2360(±0.295)
X. phytophagus	-	-	-	-	0.2278(±0.106)	0.0810(±0.117)
A. alluaudi	-	-	-	-	-	0.3650(±0.420)
P. multicolor victoriae	-	-	-	-	-	-

oral and pharyngeal jaw type were examined and quantified using the method of Seehausen (1996).

RESULTS

Food and feeding habits as determined by frequency of occurrence and relative abundance

Eight broad food items were found to consistently constitute the diet of haplochromine cichlids in Lake Kanyaboli. These food items were algae (both blue green algae and diatoms), chironomid and *Chaoborus* larvae, other unidentified insects, mollusks, fish embryos, fish eggs, plant remains and detritus (Abila et al., 2008).

Trophic relationships of the haplochromines as determined by coefficient of similarity of food items

The coefficient of similarity indicated that there were various degrees of dietary overlap between the six haplochromine species (Table 1). Diet comparison between *A. nubila* and *A. alluadi* had the highest coefficient of similarity (0.5256±0.300), indicating highest diet overlap while *Astatotilapia* sp. (big eye) and *X. phytophagus* were the most ecologically separated (0.0210±0.019). *L. maxillaris* had the widest dietary niches while *Astatotilapia* sp. (big eye) had the narrowest dietary niche.

Dentition structures and feeding adaptations

The dentition structures differed between the six haplochromine species investigated (Table 2). The algae eaters *P. multicolor victoriae* and *Astatotilapia* sp. 'big eye' had up to six rows of unicuspid oral and hypotrophic pharyngeal jaw teeth. *A. nubilia*, which mainly fed on insect larvae, had four to five rows of weakly bicuspid oral and hypotrophic pharyngeal jaw teeth; the insect and plant eater *X. phytophagus* had three to five rows of unicuspid and weakly bicuspid teeth in the oral jaws and hypotrophic ones on its pharyngeal jaws. The paedophagous *L. maxillaris* had three rows of unicuspid oral teeth and also hypotrophic pharyngeal jaw teeth, whereas the molluscivorous *A. alluaudi* showed three rows of unequal bicuspid teeth and hyptertrophic dentition on its pharyngeal jaws.

Feeding regimes and habitat distribution of the Lake Kanyaboli haplochromines

Chironomid and *Chaoborus* larvae exhibited a strong day – night distribution in the guts of the fishes. In all the species, over 60% of the insect larvae were taken at night. This is in line with the expected behavior of insect larvae: at night they move from the bottom sediments to the upper water layers. The haplochromines obviously utilize this briefly abundant food source. There were no strong differences in the other food items taken at night and day. The distribution of the haplochromines was restricted to the fringing papyrus swamps during the day at depths up to 1.5 m. *X. phytophagus*, *L. maxillaris* and *A. alluaudi* were caught inshore during the night when they feed proportionately on chironomid and *Chaoborus* larvae. The three species therefore exhibited lake-wide distribution at night.

DISCUSSION

The Yala swamps are Kenya's largest wetland and cover an area of about 175 km^2 along the shore of Lake Victoria. The Yala swamps are an important refugium for endangered animals, such as the Sitatunga antelope (*Tragecephalus spekei* L.) as well as papyrus endemic birds. The lakes in the wetland are home to about a dozen of fish species indigenous to the Lake Victoria basin. At least one of the lakes, Lake Kanyaboli, is devoid of the Nile Perch that was introduced in the Lake

Table 2. Feeding specializations and adaptations in six Lake Kanyaboli haplochromines.

Species	Major food type	Oral jaw tooth type	No. of tooth rows	Pharyngeal jaw type	Adaptation
X. phytophagus	Other insects, plant remains	Unicuspid – Weakly bicuspid	3 – 5	Hypotrophic	Biting/Scrapping
P.m. victoriae	Algae	Unicuspid	3 – 6	Hypotrophic	Scrapping
L. maxillaris	Embryos, Eggs	Unicuspid (Deeply embended)	3	Hypotrophic	Sucking
A. alluaudi	Molluscs	Subequally – Unequally bicuspid	3	Hypertrophic	Crushing
A. nubila	Chironomid/*Chaoborus* larva	Weakly bicuspid	4 – 5	Hypotrophic	Biting/picking
A. 'Big eye'	Algae	Unicuspid	3 – 6	Hypotrophic	Scrapping

Victoria basin half a century ago, making this lake an important refugium, too (Kaufman and Ochumba, 1993; Abila et al., 2004). Unfortunately, past and current land use changes in the Yala swamp posses a great threat to the future ecological integrity of this wetland system. Understanding the community structure of cichlid fishes in this wetland ecosystem is therefore a first step towards its conservation.

Among the six species of haplochromine cichlids from Lake Kanyaboli studied here, there is a certain degree of overlap in diet. No species fed exclusively on a single food item (Abila et al., 2008). Insectivory, for example, is employed by all six species of haplochromines, and chironomid and C*haobarus* larvae represented the highest proportion of food items overall. Such a broad feeding spectrum is common among haplochromine cichlids inhabiting lakes where no strong competition for food occurs (van Oijen, 1982). However, for each species certain food items contributed to varying degrees to the fishes' diet and coefficients of similarity were typically around 0.2 (Table 1). Trophic resource partitioning therefore appears to be common in this haplochromine community, a factor that may contribute to continued co-existence and hence persistence of this haplochromine community. Future studies on trophic ecology should incorporate stable isotope analysis (SIA). Unlike gut contents that are more like a 'snap shot' of the trophic status, SIA gives a trophic history of the organism. The combined use of stable isotopes of carbon and nitrogen contributes to identifying the original organic nutrient sources in complex food webs and assessing energy flow and trophic structure in aquatic ecosystems (Herwig et al., 2004; Maneta et al., 2003; Hecky and Hesslein, 1995; Wetzel, 1995).

Food partitioning is further reflected in the dentition structure of the studied species (Table 2). The algal feeders *P. multicolor victoriae* and *Astatotilapia* sp. *'big eye'* both posses broad, densely spaced and equally sized unicuspid teeth on the outer oral jaw and a hypotrophied pharyngeal jaw. Their dentition is further characterized by higher number of teeth rows, an adaptation to scraping filamentous algae (Barel et al., 1977; Seehausen and Bouton, 1997; Ruber and Adams, 2001). The chisel-shaped weakly bicuspid nature of the *A. nubila* teeth and the hypotrophied pharyngeal jaw teeth is most probably an adaptation to biting and picking of mobile insect prey. Invertebrate picking in this insectivore may further be facilitated by the smaller interorbital width, which might increase the ability to visually select food items. The deeply embedded unicuspid oral jaw teeth of *L. maxillaris*, its long jaw relative to head and its thick lips seem to be an adaptation to sucking out eggs and embryos from the other mouthbrooding haplochromines while the fusiform body shape appears to allow for faster maneuvers. *A. alluaudi* exhibits very different ecomorphological adaptations. The species possess sub-equally- to unequally-sized bicuspid oral jaw teeth and highly hypertrophied pharyngeal jaw teeth. These are adaptations to crushing mollusk shells. Whether the hypertrophied nature of *A. alluaudi* pharyngeal jaw is adaptive (that is genetically induced) or whether it is environmentally induced has been hotly debated (Hoogerhood, 1986). *X. phytophagus* has both unicuspid and weakly bicuspid oral jaw teeth. This and the high number of teeth rows is an adaptation to macrophyte feeding (Barel et al., 1977; Seehausen and Bouton, 1997).

Fish feeding on the same food item often employ different feeding techniques. Therefore, species that exhibit overlap in diet may still be differentiated along food acquiring techniques. For example, *Astatotilapia* sp. *'big eye'* and *P. multicolor victoriae* are both algivorous, but showed differences in teeth structure and preferred habitat. While *Astatotilapia* sp. *'big eye'*, like the other haplochromines, was restricted to the papyrus littoral zones, *P. multicolor victoriae* occured mostly in small isolated water pools. There may therefore exist differences in methods of obtaining algae between these two species. Studies involving finer taxonomic resolution of diet and more robust data analysis techniques like principal component analysis as well as experiments on asymmetric interspecific interactions could identify more subtle resource partitioning among potential competitors. The six haplochromine cichlid species were restricted to the fringing papyrus swamp during the day and no species was caught inshore during the day. The fringing swamp is therefore the single most important habitat for the haplochromines.

The littoral zone of the lake has been found to harbour 98.3% of the lake's macroinvertebrate biomass consisting of ephemeropteran, odonata, chironomid and *Chaobarus* insect larvae as well as mollusks, hydracarina, hirudinea and oligochaetes, while the inshore accounted for only 1.7% of the lakes macroinvertebrate biomass made up only of oligochaetes, chironomids and *Chaobarus* (Abila, 1995). It is therefore not surprising that this habitat is the main feeding – and probably also breeding – ground for the haplochromines. *L. maxillaris*, *A. alluaudi* and *X. phytophagus* were caught inshore at night and therefore seem to have a lake wide distribution at night. Movement into deeper waters at night is probably to take advantage of the emerging chironomid and C*haobarus* larvae. Why the other species do not move inshore at night need to be investigated.

In employing relative abundance, percentage of occurrence and prominence values to quantify diet of the haplochromines, we are aware of their potential drawbacks (Nooton, 1992). The relative abundance technique tends to be subjective, for it is based on virtual assessment of food contributions. Percentage of occurrence only provides information on the presence or absence of food categories and not their relative numbers or importance; it does not show how much of each item has been eaten. However, it is a useful measurement for obtaining information on diet that does not occur in discrete numbers or of partially digested food. The prominence value combines these two indices to minimize their limitations. This approach has, for example, been successfully employed to quantify trophic relationships among fishes in the Sudd swamp (Hickley and Bailey, 1987), Tilapias in Lake Naivasha (Muchiri et al., 1991) and in the Nyanza Gulf of Lake Victoria (Njiru, 2003), as well as ploidy forms of the *Squalius alburnoides* complex in the Guadiana River basin, Portugal (Gomes-Ferreira et al., 2005).

Taken together, this study suggests that the haplochromine cichlids of Lake Kanyaboli are trophically diverse and occupy several trophic levels and niches. Although the six haplochromine cichlids exhibit dietary overlaps, feeding preferences can still be discerned within the haplochromine community and feeding may represent the most explicit axis of niche differentiation among these haplochromines hence promoting their co-existence. By supporting longer food chains, the haplochromine cichlids play an important role in energy flow and ecological efficiency of this wetland lake ecosystem. The present study also corroborates the role of Yala swamp wetlands and enclosed lakes as important refugia for conservation of not only species and genetic diversity (Angienda et al., 2011; Abila et al., 2004) but also of trophic diversity threatened by introduction of exotics and other anthropogenic impacts in the Lake Victoria basin. Just like in satellite lakes of Lake Kyoga in Uganda (Mbabazi et al., 2004), Lake Kanyaboli sustains all major trophic groups (only true piscivors are absent in Lake Kanyaboli). In contrast, Mbabazi et al. (2004) found only two trophic groups in Lake Kyoga, a lake heavily infested by the Nile perch. Baseline data as provided in this study may thus provide a framework upon which the ecological consequences of Nile perch introduction on community structure of Lake Victoria region haplochromines can be assessed and re-examined. The recent gazettement of Lake Kanyaboli into a national reserve by the Kenya Government thus offers an excellent opportunity for conservation of this biodiversity hotspot.

ACKNOWLEDGEMENTS

This study was funded by a German Academic Exchange Programme (DAAD) In-country Ph.D. Scholarship and the Institute of Research and Postgraduate Studies (IRPS), Maseno University. I would like to thank Drs. D.O. Owiti and M.F. Ndonga for providing guidance and support during the study and the anonymous reviewers for critically reading the manuscript. Charles Otundo, Stephen Onyango and Antony Omondi provided valuable field and laboratory assistance during the study.

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