Uganda Journal of Agricultural Sciences, 2004, 9: 348-359
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ISSN 1026-091

Trophic structure and energy flow in fish communities of two lakes of the Lake Victoria basin

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Abstract

Successful management of target fishery species often hinges on the ability to effectively manage prey resources; and knowledge of trophic relationships among fishes and their prey can help guide management efforts aimed at increasing and sustaining fish production. This study characterized the trophic structure and energy flow in the fish communities of two minor lakes in Uganda: lakes Kachera and Mburo. Stable isotope ratios of carbon (ä^{13}C) and nitrogen (ä^{15}N) were measured in fishes and their potential food sources (primary producers and aquatic invertebrates). These data were augmented with results obtained from stomach content analysis. The study indicated values of ä^{15}N that were often considerably lower than 3.4‰ per trophic transfer typically assumed in stable isotope studies. The low ^{15}N trophic fractionation indicted a high degree of omnivory as well as dietary overlap among the examined consumers. Hierarchical agglomerative clustering and Detrended Correspondence Analysis (DCA) indicated a degree of similarity in the diets of fish species between the two lakes, and in lakes, algae/ phytoplankton, benthic, and terrestrial material were important energy sources. However, organisms from Lake Kachera were generally more ^{13}C depleted compared with Lake Mburo indicating the importance of algal production to the upper food web in Kachera while in Mburo the ä^{13}C of the dense phytoplankton is similar to terrestrial grass material that would be contributed by the large hippopotamus population.

Key words Fishes, phytoplanktons, trophic, Uganda

Introduction

In most fisheries management the main global crisis has been overexploitation of the predator and prey stocks which has resulted in calls for multi-species and (or) "ecosystems based" assessment and management of the fish stocks and assemblages (Jennings and Kaiser, 1998; National Research Council, 1999) to avoid problems associated with fishing down the food web (Pauly *et al.*, 1998).

Food webs are macro-descriptors of community feeding interactions that can be used to map the flow of energy, materials and nutrients in ecosystems (Jepsen and Winemiller, 2002). In recent years several theoretical and empirical studies have emphasized the importance of trophic interactions for structuring lacustrine, mainly pelagic food webs and the available information from shallow lakes indicates that there are far more complex food web structures (Diehl and Kornijüw, 1998). Implementation of multi-species approaches will require improved understanding of the community ecology of fish assemblages that has rarely been explicitly incorporated into fisheries management practices.

Trophic structure has traditionally been characterized using stomach content analyses (SCA), direct observations or collection of prey remains (Balirwa, 1984, 1998; Beaudoin *et al.*, 1999; Mbabazi *et al.*, 2004).

Nowadays, the combined use of stable isotopes of carbon and nitrogen contributes to identifying the original organic nutrient sources in complex food webs (Jennings *et al.*, 1997; Magnussson *et al.*, 1999; Maneta *et al.*, 2003), assessing energy flow and trophic structure in aquatic systems (Kling *et al.*, 1992; Hesslein *et al.*, 1993; Gu *et al.*, 1994; Hecky and Hesslein, 1995; France *et al.*, 1996; Campbell *et al.*, 2003) however, the diversity of systems to which it has been applied is primarily pelagic food webs. Specifically the ä^{13}C ratio of a consumer reflects (usually within 1‰) the ä^{13}C signature of its diet (Peterson and Fry, 1987, France 1995; Vander Zanden and Rasmussen, 2001) and the ä^{15}N ratio of a consumer reflects its trophic position because there is an average enrichment of 3.4‰ per trophic transfer (Cabana and Rasmussen, 1996; Post, 2002).

Most limnologists always consider feeding pathways derived from phytoplankton to be most important for secondary consumers and fish growth or production in lakes (Yoshioka *et al*., Gu *et al*. 1996). There has been a growing appreciation that benthic primary producers and allochthonous organic matter from riparian vegetation are also important food resources for invertebrate consumers and fish growth (Hecky and Hesslein, 1995; France, 1997; Vadeboncoeur *et al*, 2003). Macrophytes and periphytic algae, a conspicuous and abundant source of fixed carbon in wetlands and shallow lakes, can supply carbon to these food webs (Bunn and Boon, 1993). Several stable isotope studies have however indicated that macrophysics carbon contribution to aquatic food webs is very little even when macrophytes are very abundant (Bunn and Boon, 1993; Hecky and Hesslein, 1995; Keough *et al*., 1996). Terrestrial organic carbon also has the potential to contribute energy to aquatic food webs (Planas *et al*. 2000) especially in streams. Terrestrial plants and macrophytes can either be C_3 or C_4 plants and have relatively fixed isotopic signatures because they use atmospheric carbon with constant isotopic signature while, algae are C_3 plants and in water can have a variable signature as isotopic signature of CO_2 varies.

Further, anthropogenic disturbance in lake catchments can change the balance of allochthonous (external) and autochthonous (internal) organic carbon sources (Holopainen *et al*., 1991) as well as affecting community structure through habitat change.

We used stable isotope and stomach content analyses to examine feeding relationships among consumers at higher trophic levels to determine the ultimate sources (producers) from which fish consumers derive their energy.

Materials and Methods

Study sites

The study focused on two minor lakes in the Lake Victoria basin namely Mburo and Kachera (Figure 1) that are at different levels of anthropogenic interference. The sizes and shapes of these lakes vary from time to time due to floating islands. The two lakes comprise of similar fish assemblages (Namulemo and Mbabazi, 2004).

Lake Mburo is within a National park. It is characterized by controlled fishing but is intensively used for watering wild game and supports high populations of hippopotamuses during the day hours. Lake Kachera unlike Lake Mburo is shared by two districts of Mbarara and Rakai besides being not protected (i.e outside the National park). Lake Kachera is therefore exposed to more human interference and management problems than Lake Mburo. Overfishing, high populations of domesticated animals, and agricultural activities characterize Lake Kachera with most of the communities practicing mixed farming to varying degrees (Kamugisha *et al*. 1997; Namara and Infield, 1998; Emerton, 1999).

Field Sampling

The representative dominant taxa (fish, macro-different trophic levels and potential carbon sources were collected between August 2001 and January 2003. Sampling for fish was done using experimental multifilament gillnets with mesh sizes ranging from 25.4 mm to 203.2 mm with stretched mesh in 12.7 and 25.5 mm increments from 25.4 to 139.7 mm and 152.4 mm to 203.2 mm respectively fished overnight for approximately 12 hours. Some fishes were also obtained or purchased from local fishers. Upon retrieval, fish were sorted into their taxonomic groups, to species level whenever possible. For each captured fish the total and standard lengths were recorded and stomach removed. The stomachs were preserved in 10% formaldehyde for later stomach content analysis. Dorsal skinless muscles were removed from the anterior part of each fish from a maximum of three individuals per species and dried and dried samples were kept in scintillation vials and transported to the Environmental Isotope Laboratory (University of Waterloo, Canada) for analysis.

Aquatic macro-invertebrates were collected as potential prey from same sites as for fish within each lake (two sweeps per site). Additional samples of mollusks and other epiphytic invertebrates were hand picked. Benthic invertebrates in the profundal zone were sampled with a Ponar grab (Beaudoin *et al*., 2001; Zah *et al*., 2001; Jones and Waldron, 2003. For invertebrates, samples from the different sites were pooled to raise enough biomass for stable isotope analysis and were sun dried and treated as for fish.above. Dominant macrophytes were hand picked and thoroughly washed to obtain clean samples (Jones and Waldron, 2003).

Phytoplankton samples were obtained from vertical hauls of a 10 ìm mesh plankton net beginning from about 1.5 m below the water surface of the sampled lake. Samples from the different sites were pooled to ensure sufficient biomass for stable isotope analysis. Phytoplankton was filtered from lake water by use of a pre-combusted GF/F (1.2 ìm) filter paper that was immediately treated as above for invertebrates and fish.

Laboratory analyses

Stomach contents were identified and the percentage volume of each food item in the diet was assessed by visually estimating how much it contributed to the total contents using either a binocular or compound microscope depending on the diet of the fish species in question (Balirwa, 1984; Winemiller, 1990; Nakamura *et al*., 2003). Subsequently every other dietary component was awarded 16, 8, 4, 1 or 0 points depending on the relative importance of the food item in the stomach (Hynes, 1950; Genner *et al*., 1999).

For fish and invertebrates about 1 mg (± 0.005 mg) and a slightly larger quantity for macrophytes 2 mg (± 0.005 mg) were packed into tin capsules of 5 X 3.5 mm and immediately sealed for isotopic analyses. Stable carbon and nitrogen isotope analyses were performed on the same sample using a continuous VG Micromass 903E isotope ratio mass Spectrometer at the Environmental Isotope Laboratory, University of Waterloo, Ontario, Canada. Stable isotope data are presented as the relative difference between ratios of the sample and standard gases.

Table 1 Fish species list of the fish communities of the studied lakes

Family/group	Species	Author	ID CODE
Cichlidae	*Oreochromis esculentus*	Graham, 1928	O.e
	Oreochromis niloticus	Linneus, 1758	O.n
	Oreochromis leucosticus	Trewavas, 1933	O.l
	Tilapia zilli	Gervais, 1848	T.z
	Astatoreochromis alluaudii		A.a
	Astatotilapia aneocolor	Greenwood, 1973	A.c
	Harpagochromis squamipinus	Regan, 1922	H.s
Claridae	*Clarias gariepinus*	Burchell, 1822	C.g
	Clarias liocephalus	Boulenger, 1912	C.l
Protopteridae	*Protopterus aethiopicus*	Heckel, 1851	P.a
Food sources			
Detritus			Dt
Phytoplankton (C_3)			Pk
Vascular plants			Vp
Water fern (C_3)	*Cyclosorus sp*		Cs
Water cabbage (C_3)	*Pistia stratiotes*		Pi
Papyrus (C_4)	*Cyperus papyrus*		Cp
Ambachi tree (C_3)	*Aeschynomene eraphroxyon*		Ae
C_3 tree	*Euclea schemperi*		Es
Hippo grass (C3)	*Vossia cuspidata*		Vc
Protozoa (Ciliates)			Pz
Crustacean			Cr
Ephemeroptera			Ea
Coloeoptera			Ca
Nematocera			Na
Hemiptera			Ha
Isoptera			Is
Diptera			Da
Chironomid			Cd
Chaoborus			Cb
Odonata			Od
Trichoptera			Ta
Oligochaeta			Oa
Molluscs			Ml
Fish eggs (embryo)			Fe
Fish			Fs

ä $X= (R_{sample}/R_{standard} -1)\ X\ 10^3$

Where X is the isotope of interest (either ^{15}N or ^{13}C) and R is the ratio of this isotope to the most abundant isotope (^{14}N or ^{12}C). ä is the measure of heavy to light isotope in the sample.

Data analysis

Resource use by the individual fish species was expressed as percentage composition by points of the food item and was presented in tabular form. Specimens with less than three stomachs with food were noted but excluded from further analysis. Data were pooled for each species and lake for the entire sampling period since the aim was to determine the time-averaged trophic structure and energy sources of the fish communities. Hierarchical agglomerative cluster analysis (Pielou, 1984) and Detrended Correspondence Analysis DCA (Hill and Gauch, 1980; Gauch, 1982) were applied to diet data in order to classify the different consumers into distinct trophic groups by using Community Analysis Package -CAP version 2 (Pisces Conservation Ltd, 2002).

Results

Stomach dietary analyses

In the two Koki lakes nine fish species examined resulted into 23 prey or food resources (Table 2). In the both lakes studied insects formed the most important primary prey (50%) in most fishes with the exception of *Oreochromis esculentus* and *Oreochromis niloticus* whose main primary prey was algae, however these fishes still included at least (10%) insects in their diet (Tables 2).

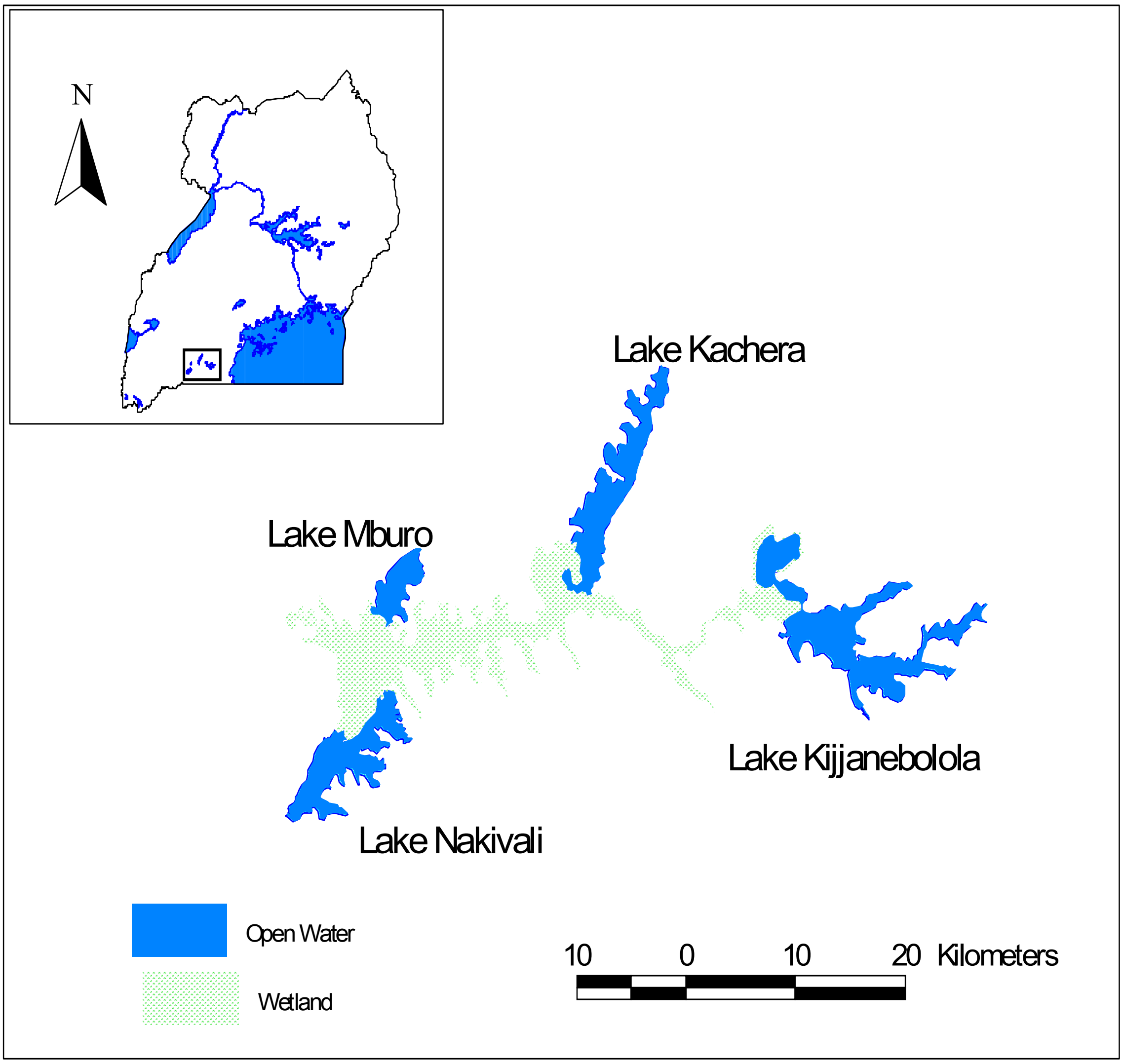

Figure. 1 A map showing the study area (lakes Mburo and Kachera) with the other associated Koki lakes, and their location in Uganda (National Biomass, 1995)

Fish also formed another important component of the diet for *H. squamipinus* (e"13%), C. *gariepinus* (e"13%) and *P. aethipopicus* (>8%). Molluscs formed an important component of diet in *P. aethiopicus* (e"10%) in both lakes and formed the largest component in the diet of *C. liocephalus* (e"35%) in Lake Kachera. Mollusks did not appear to contribute to the diet of *H. squamipinus* in Lake Kachera but contributed (e"10%) to the same fish in Lake Mburo (Table 2). Ephemeroptera contributed (e"10%) and (e"20%) in *A. alluaudii* and *A. aneocolor* respectively in Lake Mburo but was missing in the diet of the Lake Kachera fishes. Fish eggs/embryo formed another important dietary component of *A. aneocolor* (e" 34%) in lake Mburo but was not encountered in any of the fish diets for Lake Kachera. In both lakes there were generally a larger proportion of fishes with empty stomachs compared to those that contained food material, however this was morepronounced in lake Kachera than Lake Mburo (Table 2). The high percentage of fish with empty stomachs in Lake Kachera compared to Mburo may reflect higher feeding intensity of fishes in lakes with little anthropogenic interference.

Bray-Curtis average linkage cluster analysis illustrated that based on 17 prey groups or food sources in the overall Koki lakes, the nine fish species could be grouped into two different trophic groups or clusters (at distance or dissimilarity d" 0.40 and $P<0.05$), with all two trophic groups present in both lakes (Figure 2A). Trophic clusters were generally similar for fish species in the two but varied between their taxonomic prey (Figures. 2 B)

The DCA factor scores coded from cluster analysis above explained 26.7% variation in these data and were plotted along with the factor scores of the prey groups or food sources (Figure 3.1B). The fishes with high scores on DCA 1 were carnivorous and depended on such benthic food sources as fish eggs (Fe), ephemeroptera (Ea), coleoptera (Ca), millipedes (Md crustaceans- crabs (Cr), odonata (Od), fish (Fs) and hemiptera (Ha) (Figure 2B and Table 2).

Table 2. Fish stomach contents (% volume) in diets of fishes pooled from all sites within the individual Koki lakes from August 2001 to January 2003. Total sample size and and number of fish with food in stomach are also indicated.

Fish species	Lake	Detritus	Green algae	Blue green algae	Diatoms	Other algae		Ciliate	Crabs	Un identified insects	Ephemeroptera	Coleoptera	Nematocera	Hemiptera	Isoptera	Chironomids	Chaoborus	Odonata	Oligochaeta	Sandgrains	Molluscs	Fish eggs/embryo	Millipedes	Un identified fish	Sample size (food)	Sample size (total)
A. alluaudi	Mburo	-	-	-	-	-	-	-	-	0.35	0.11	0.22	-	-	-	0.14	-	0.18	-	-	-	-	-	-	19	71
A. aneocolor	Kachera	0.09	-	-	-	-	0.15	-	-	0.05	-	-	-	-	-	0.12	0.24	-	-	-	0.03	-	-	0.31	27	233
	Mburo	-	-	-	-	-	0.14	-	-	0.06	0.24	-	-	-	-	0.12	0.02	-	-	-	-	0.34	-	0.06	26	501
C. gariepinus	Kachera	-	-	-	-	-	0.03	-	0.05	-	-	-	-	-	-	0.13	0.20	0.04	-	-	0.01	-	0.40	0.08	22	113
	Mburo	-	-	-	-	-	-	-	-	0.09	-	-	-	0.52	-	0.16	0.04	-	0.04	-	0.02	-	-	0.13	26	119
C. liocephalus	Kachera	-	-	-	-	-	0.11	-	-	-	-	-	0.28	-	-	0.22	0.04	-	-	-	0.35	-	-	-	6	24
H. squamipinnis	Kachera	-	-	-	-	-	-	-	-	-	-	-	-	-	-	0.33	-	0.33	-	-	-	-	-	0.33	3	44
	Mburo	-	-	-	-	-	0.12	-	-	0.30	-	-	-	-	-	0.15	0.02	-	0.03	-	0.12	-	-	0.25	39	285
O. esculentus	Kachera	0.19	0.13	0.17	0.07	0.02	0.15	0.15	-	-	-	-	-	-	-	0.13	-	-	-	-	-	-	-	-	55	213
	Mburo	0.10	0.09	0.14	0.05	0.02	0.27	0.08	-	-	-	-	-	-	-	0.11	0.15	-	-	-	-	-	-	-	138	435
O. leucostictus	Kachera	0.04	0.01	0.02	0.01	-	0.30	-	-	-	-	-	-	-	-	0.53	0.09	-	-	-	-	-	-	-	24	203
	Mburo	0.17	0.01	0.02	0.01	-	0.05	-	-	0.46	-	-	-	-	-	0.16	0.12	-	-	0.01	-	-	-	-	26	104
O. niloticus	Kachera	0.08	0.08	0.13	0.04	0.01	0.28	-	-	-	-	-	-	-	-	0.28	0.10	-	-	-	-	-	-	-	65	139
	Mburo	0.12	0.12	0.17	0.06	0.02	0.13	0.02	-	0.02	-	-	-	-	-	0.11	0.06	-	-	0.17	-	-	-	-	90	185
P. aethiopicus	Kachera	0.09	-	-	-	-	0.12	-	-	0.03	-	-	-	-	0.07	0.14	-	0.33	-	0.01	0.13	-	-	0.08	54	131
	Mburo	0.02	-	-	-	-	0.16	-	-	0.14	0.05	-	-	-	-	0.08	-	0.27	-	-	0.10	-	-	0.18	34	72

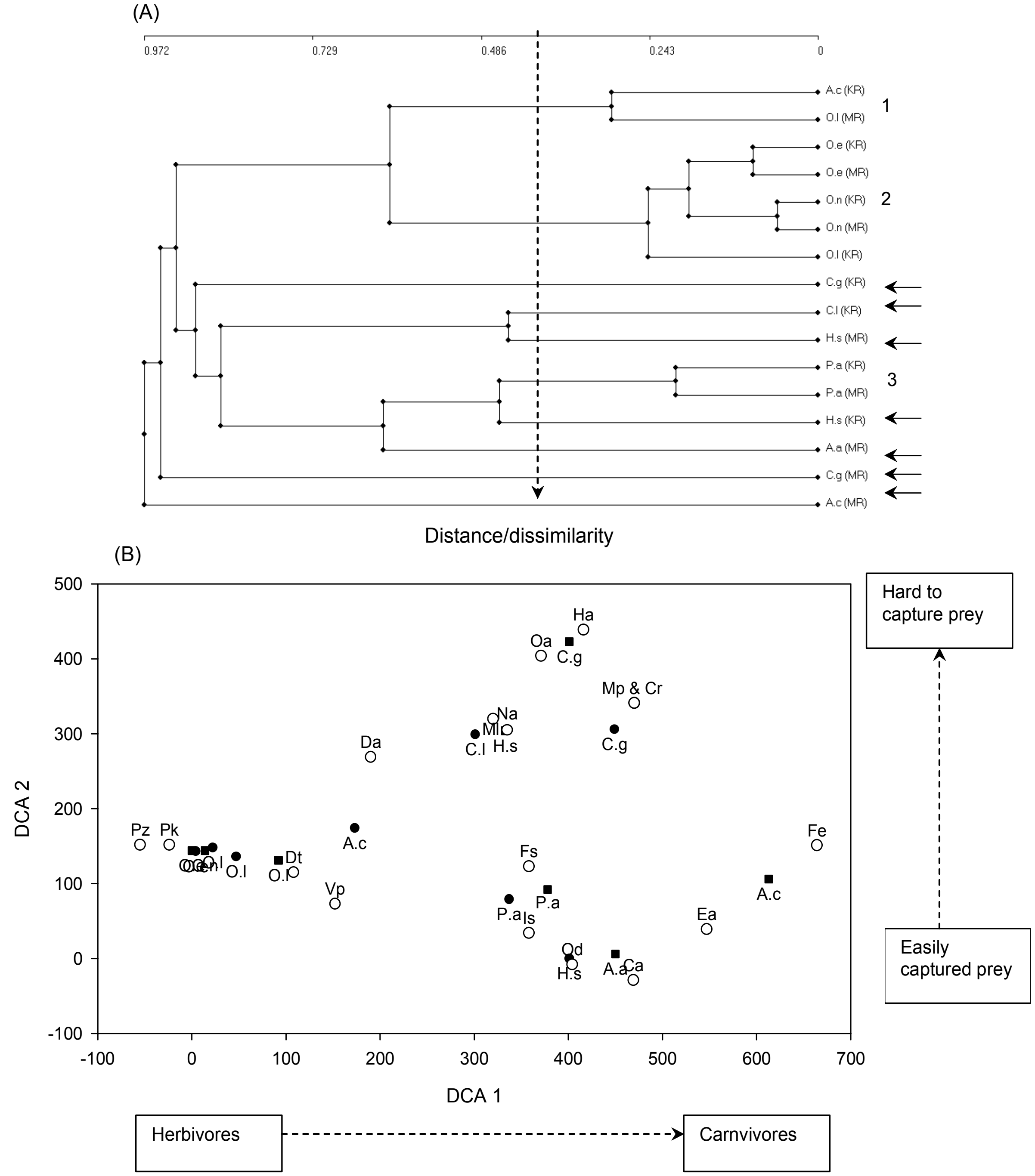

Figure 2 (A) Bray curtis average linkage cluster diagram showing the similarity in diets using the distance measure. At the ≤ 0.40 diet similarity indicates that 10 trophic groups are significant at $P<0.05$;arrows indicate un grouped species (B) A DCA scatter plot showing the spatial patterns between 17 food sources (○) and nine fish species from Koki lakes. DCA 1, grad. length =6.13; eigen value (E.V)= 0.90; DCA 2 grad. length =4.2; E.V= 0.73 (Lake Kachera (KR) or (●); Lake Mburo (MR) or (■) text codes for fish species and food sources Table 1)

These fishes were mainly the piscivores, The low scores on DCA 1 were associated with omnivores which mainly depended on planktonic diet (Pk) dominated, by phytoplankton, bacteria (Pz), detritus, vascular plants and diptera.

The first obvious trophic group in the DCA scatter plot comprised the omnivores and was associated with both low scores on both DCA1 and DCA2 plotting near plants and animal food sources (Figure 2B). The fishes in cluster 2 and 3, with similar DCA scores in the scatter plot, which comprised all tilapiine species from both lakes and *A. aneocolor* (A.c (KR) comprised this trophic group. These fishes dominantly fed on phytoplankton, detritus, vascular plants, bacteria and dipteran larvae and pupae (Figure 2B and Table 2). *A. aneocolor* (A.c (MR) not grouped at a distance of d"0.4 in cluster analysis was associated with diet of ephemeroptera (Ea) and fish eggs (Fe) and vascular plants (Table 2) was conveniently included in this trophic group. The last trophic group was the piscivorous, cluster 3 and the remaining fish species (*H. squamipinnis*, H.s, (KR and MR), *A. alluaudi,* A.a (MR), *C. gariepinus,* C.g, (KR and MR) and *C. liocephalus*, C.l, (KR)) not grouped at a distance of d" 0.4 in cluster analysis (Figure 2B).

These fishes had DCA 1 scores associated with the fish (Fs) food source. Some fishes in this group also consumed a wide range of food items such as odonata (Od), mollusks (Ml), nematocera (Na), oligochaetes (Oa), crustaceans and millipedes placing them near those food sources in the scatter plot. Finally hierarchical agglomerative cluster analysis and DCA finally established two trophic groups for the Koki lakes and were present in both sampled lakes.

Stable isotope analyses

Carbon Sources

Stable isotope ratios for primary producers generally showed a clear separation in the two studied lakes (Fig. 3). In lakes, plankton (Pk), *V. cuspidata* (Vp) and *C. papyrus* (Cp) showed similar isotopic signatures; being ^{13}C enriched compared to the other primary producers, however plankton were more ^{13}C depleted (e"5‰) in Lake Kachera relative to Lake Mburo. The stable isotope ratios for primary producers showed little separation with respect to ä^{15}N except for C3 tree *E. schemperi* (Es) in Lake Mburo and *C. papyrus* (Cp) in both lakes that exhibited exceptionally high ä^{15}N signatures.

In both lakes *O. esculentus* (O.e) and *O. niloticus* (O.n) occupied similar position in isotopic space but other fishes and plankton were more enriched in Lake Mburo than in Lake Kachera. This suggests that most of the food web in both lakes may be tracking plankton (Fig. 3), which is enriched in ^{13}C in Mburo relative to Kachera. Plankton and *C. pypyrus* (Cp) came out to be the major potential food source and contributed significantly to the diets of most consumers especially fish in the two lakes. In both lakes the fish had highly variable ä^{13}C ratios both within and among taxa, suggesting that these fishes had broad diets driving energy from a range of C_4 and C_3 plants, including phytoplankton whose ä^{13}C can vary in time if photosynthetic demand for CO_2 exceeds the supply of CO_2 and isotopic fractionation by photosynthesis is reduced (Hecky and Hesslein, 1995). In general as algal biomass increases, algae will become enriched in ^{13}C and have a heavier ä^{13}C. The ä^{13}C of the animal food web can become more similar to the C_4 higher plants (*V. cuspidata* (Vc) and *C. papyrus* (Cp)) and the C_3 phytoplankton. In Lake Mburo the nutrient enrichment provided by the hippopotamuses would cause denser phytoplankton populations resulting in a heavier ä^{13}C as well as directly introducing enriched ä^{13}C undigested C_4 grass debris from hippo defecation directly into the lake.

Trophic relationships

Assigning fishes into specific obligate trophic levels basing on their ä^{15}N was not possible because the observed enrichment values for ä^{15}N were often considerably lower than 3.4‰ typically assumed in stable isotope studies. For example *C. papyrus* (Cp) and *E. schemperi* (Es) exhibited a higher ä^{15}N than all invertebrates sampled in both lakes and can be excluded as direct dietary inputs to those invertebrates, but a mixed diet of papyrus debris and plankton could account for the ä^{15}N signatures of all the fish. Omnivory seems to be the rule among the fishes with potentially high degree of dietary overlap among the fishes. Only habitat separation within the lakes would prevent strong trophic competition among these trophic generalists.

In both lakes ä^{15}N signatures placed fish at the top of the lakes' food webs, with the haplochromine cichlid *Harpagochromis squimipinus* being the most ä^{15}N enriched reflecting a stronger tendency to consume other fishes (Table 2). At the base of the food webs were possibly *V. cuspidata* (Vc) and more probably plankton for lakes Kachera and Mburo respectively as the upper food web appears to track the plankton as reported by Hecky and Hesslein (1995). In both lakes invertebrates had ä^{15}N that were intermediate between those of the fishes and papyrus and the plankton indicating their dependence on the plankton and their predation by fish. In both lakes the two *Oreochromis* spp. had non-overlapping isotopic signatures for the sampled fishes and were most similar to papyrus among the plants. Their isotopic signatures were the only ones among the fishes to be similar in both lakes further suggesting a dependence on papyrus detritus in both lakes.

Discussion

Analysis of trophic groups may show differences in trophic structure and ecosystem dynamics and therefore have implications for the management of fisheries (Koslow, 1997). For the same energy input of organic matter at the base of the web different trophic structures will yield different levels of secondary production and different fish

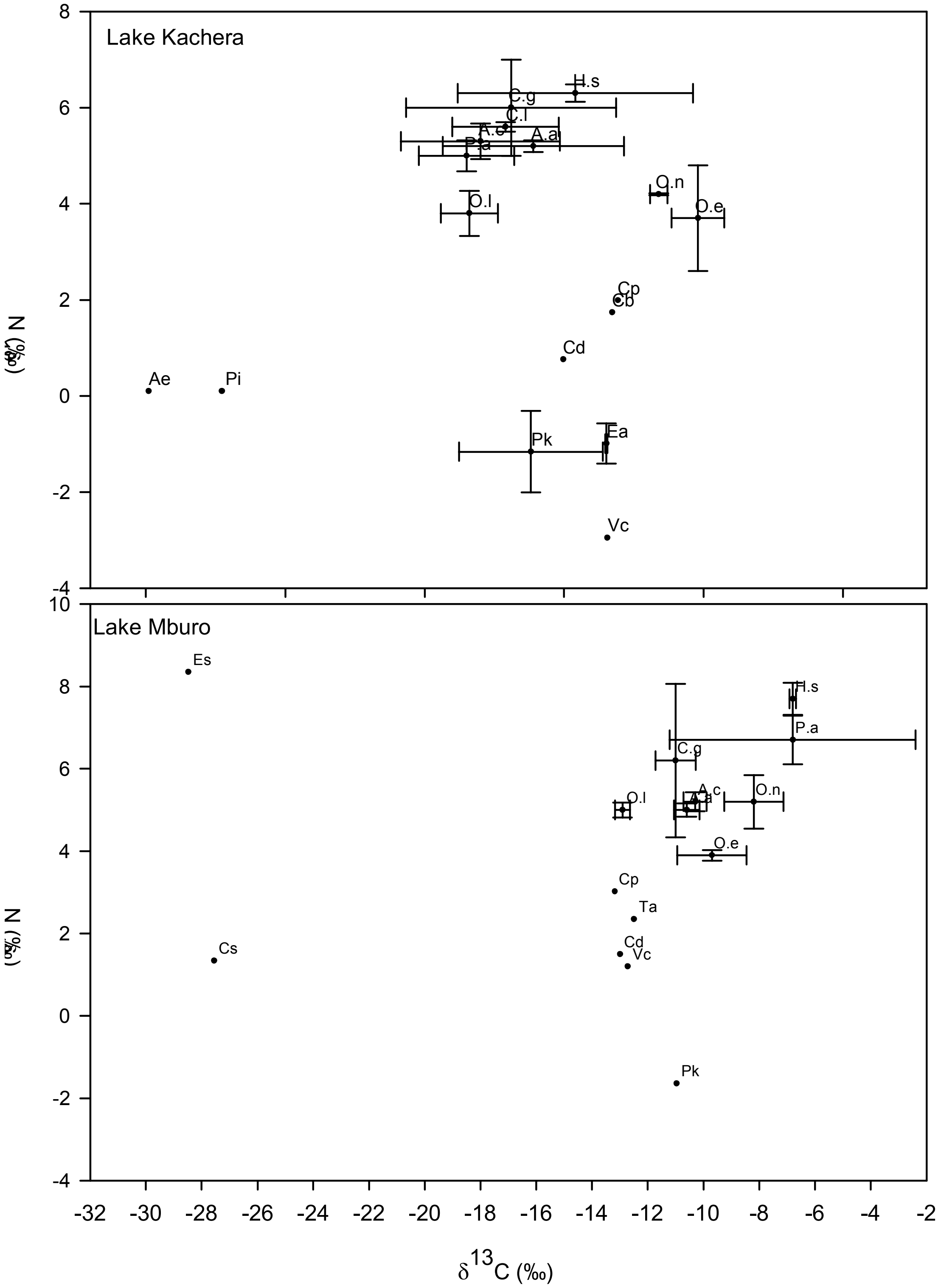

Figure 3. The Mean ± S.D of ä^{15}N and ä^{13}C for nine fish species fishes and 10 potential food sources from Koki lakes. Note the lighter and high variation in ä^{13}C of food web structure of Lake Kachera to Lake Mburo (text codes Table 1).

species composition that can determine the economic value of the fishery.

The trophic relationships between two species can also change through ontogeny and the degree of niche overlap between two species may also vary ontogenetically (Polis, 1984; Piet *et al.*, 1999). Therefore our fishes may not represent the feeding behavior of the juvenile and immature fishes not captured by our nets. These in turn will be missing in our analyses as food resources for the piscivorous fishes. Therefore our sampling methods can limit the interpretations possible, but our stomach analyses indicate that we have sampled most elements of the biota that occur in fish stomachs.

In general, fish species in the two studied lakes had similar diets. However, there were some few exceptions. For example in Lake Mburo *H. squamipinus* included mollucs and vascular plants that were not fed on at all by the same fish in Lake Kachera. In both lakes *A. alluaudii* were classified as insectivorous in contrast to molluscivores by earlier studies on Kyoga basin lakes (Mbabazi *et al.*, 2004). Such differences may be partly related to habitat differences or geographic variations, such as differences in food availability at different localities (Nakamura *et al.*, 2003). Shallow lakes are complex heterogeneous environments with a variety of sources of primary production available for exploitation (Jeppesen *et al.*, 1998).

Variation in stable isotope ratios of primary producers is often averaged out in consumers (Kirililk *et al.*, 1995) making it difficult to determine precisely which primary producers were carbon sources for a particular consumer. In these lakes overlapping carbon signatures of plankton and C_4 plants especially in Mburo made it impossible to determine quantitatively the relative importance of these different internal carbon sources (e.g Boudoin *et al.*, 2001) although when both lakes are considered, it is clear that the upper food web consisting of fishes demonstrates a dependence on the plankton as both the web and the plankton have heavier isotopic signatures in Mburo.

Fish had a varied diet, which in part was influenced by their species and size, but in general displayed a lack of specialization. Omnivory is common in freshwater food webs especially among freshwater fish assemblages (Vadas, 1990) and our results (Table 2) and stable isotope analysis (Figure 3) strongly support this observation in the two studied lakes. Fish ä^{13}C signatures were typically variable and intermediate among several different prey ä^{13}C signatures and had intermediate ä^{15}N values relative to predatory and non-predatory fish or invertebrates.

There was no clear segregation between pelagic and littoral habitat organisms because within in these lakes as has been observed in other similar small lakes (Jones and Waldron, 2003, Beaudoin *et al.*, 2001), because the littoral and profundal zones are less distinct than it is in deeper lakes. However, it was apparent that the food web of Lake Mburo was comprised of fish and plankton with more enriched carbon signatures than in Lake Kachera (e”5‰). This is likely due to nutrients that arise directly from the dung from large population of hippopotamuses with no major return pathways known (Laws, 1968, Grey and Harper, 2002). Hippopotamuses graze selectively on short grass species C_4 plants (Lock, 1972; Grey and Harper, 2002) with a daily intake of about 18Kg of dry matter (Law, 1963). The ingested grasses use the C_4 photosynthetic pathway and exhibit distinct highly ^{13}C enriched signatures compared to aquatic basal resources. As the beast grazes on land and usually defecates in the water, there is a drain of nutrients to the lakes, Similar studies indicated that fecal return by ungulates was positively and linearly linked to both production and consumption (Douglas and McNaughton, 1992). Ungulates excrete >90% and 65-95% of the phosphorus and nitrogen they ingest respectively (Ruess, 1987) and these nutrients are in forms readily available to plants and soil microbes (Floate, 1981; Douglas and McNaughton, 1992) and will enrich lakes. Our study indicates that the fish community is dependent on energy from phytoplankton and that enrichment of this food source should produce higher fish production and yields in Lake Mburo.

The observed trophic enrichments for ä^{15}N (Figure 3) were considerably lower than a typical assumed shift of (3.4‰) per trophic level predicted from a synthesis of previous stable isotope studies (DeNitro and Epstein, 1978, Post 2002). Results from other studies indicated that trophic enrichments for ä^{15}N can vary depending on the trophic level, animal diet system or ecosystem under consideration and lower than expected (i.e < 3.4‰) enrichments often occur (Pinnegar *et al.* 2001; Vander Zanden and Rasmussen, 2001; Zah *et al.*, 2001; Herwig *et al.*, 2004), although we cannot discount differences in fractionation (Adams and Sterner, 2000; Ben-David and Schell, 2001).

Stable isotope analysis is an important tool that can be used to understand feeding ecology, food web structures and ecosystems level processes but the method should be complemented by quantitative analysis of stomach content analysis and controlled field experiments rather than as a strict substitute (Rounick and Winterbourn, 1986) if detailed information is required for fish stock management. Despite these challenges, this study indicated that the food webs of these lakes are complex, characterized by omnivory and generalism. The determination of definite food sources for the different fish species was not possible because of dietary overlap integrating primary producers signatures; however, we were able to identify that the carbon sources to fishes from the two lakes were from different origins.

Trophic structure and ecosystem management

The slight spatial differences observed in trophic structure of two similar lakes located in the same watershed drainage system may reflect differences in species membership and biomass dominance among the fish assemblages. Associated with these patterns are differences in complexity of food webs, the strength of species interactions and the resulting energy and biomass flow especially for aquatic systems located in different watersheds. Development of ecosystem based fisheries management guidelines, should explicitly account for the spatial differences in community structure of aquatic systems located in the different watersheds. Stable isotope analysis is a rapid means of determining trophic specialization or generalization in fish stocks and can provide information on primary energy sources. Survey of isotopic food web structure can provide essential information for fisheries management.

Acknowledgements

The Lake Victoria Environmental Management Project, National Agricultural Research Organization and Uganda Government provided logistics and laboratory space. The staff and students of Biology Department, University of Waterloo provided office space, technical guidance and financial support for additional stable isotope analyzes. W. Mark assisted with stable isotope analyzes at the Environmental Isotope Laboratory, University of Waterloo and Prof. W. Taylor from the same University for guidance on multivariate statistics. The Uganda Wild life Authority permitted the research. This work was made possible with assistance from the support staff and scientists at the Fisheries Resources Research Institute, whom we sincerely acknowledge. We would end by acknowledging A. Katende without whose expertise the aquatic plants would not have been identified.

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