THE BIOLOGY AND ECOLOGY OF LAKE VICTORIA FISHES:

THEIR DEVELOPMENT AND MANAGEMENT

(UGANDAN VERSION)

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CHAPTERS

The Trophic Structure and Diversity of Haplochromines among the Kyoga Minor Lakes

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Abstract

Before the introduction and establishment of the Nile perch, *Lates nilolicus* (L). Lakes Victoria and Kyoga had a diverse fish fauna, dominated by haplochromine cichlids. The haplochromines had evolved into many trophic groups which occupied virtually all trophic levels and contributed to the ecological efficiency of the lakes. Establishment of Nile perch in the main lakes was followed by a decline and in some cases complete disappearance of many haplochromine trophic groups. This is thought to have affected the efficiency of the ecosystem. This study examined the species composition and trophic diversity among haplochromines in Kyoga Minor lakes where Nile perch was not introduced and compared this with historical data from lakes Victoria.

Six Kyoga Minor lakes and the main Lake Kyoga (Iyingo) were sampled. Forty one haplochromine species were recorded in the Kyoga lake basin and only fourteen species were recorded from the main Lake Kyoga. Species and trophic diversity of haplochromines were highest in the Kyoga Minor lakes as compared to Lake Kyoga.

The food materials ingested by haplochromines were algae (blue-green algae, green algae and yellow-green algae), fish eggs, detritus, fish remains, higher plant material, insects *(Odonata,* mayfly, Dipteran larvae and pupae), insect eggs, molluscs(gastropods and bivalves) and fish scales. Six trophic groups were recorded from the Kyoga Minor lakes as compared to only two trophic groups in the main lake.

Most of the trophic groups of haplochromines which existed in the lakes Victoria and Kyoga prior to the Nile perch introductions and which are now believed to be depleted from these main lakes are present in the Kyoga Minor lakes. This provides a picture about the trophic structure of haplochromines from the Lake Kyoga before the Nile perch upsurge.

Some Kyoga Minor lakes like Nawampasa, Gigati, Kawi and Agu should be designated as conservation areas of haplochromines and other species threatened by introduction of exotics. Clearing of swamps and vegetation that separate Kyoga Minor lakes from the main lake should be avoided to prevent the spread of Nile perch into these lakes.

Back ground

The Victoria and Kyoga lake basins had a high fish species diversity with many endemic fish species. Two Tilapiine species, *Oreochromis esculentus* and *Oreochromis variabilis* were the most important commercial species in lakes Victoria and Kyoga. and did not exist elsewhere on earth (Graham 1929, Worthington 1929). Other species such as *Protopterus aethiopicus, Bagrus docmac, Clarias gariepinus, Barbus* spp, mormyrids, *Synodontis* spp, *Schilbe intermedius* and *Rastrineobola argentea,* were also abundant (Graham 1929, Worthington

1929, 1932a, Kudhongania & Cordone 1974). Rivers in the Victoria basin had a number of riverine species of which *Labeo victorianus* and *Barbus altianalis* were the commercially important. Lake Victoria contained more than 300 species of haplochromine cichlids about 99% of which were endemic (Witte et al. 1992 a, b). Lakes Kyoga and Nabugabo also had endemic haplochromine species (Worthington 1929, Trewavas 1933, Greenwood 1965, 1966). These haplochromines were important as food and were of medical, scientific and ecological value. They occupied many trophic levels thus playing a major role in energy flow and overall ecological efficiency of these lake systems. They were crucial in maintaining the ecosystem that supported other food fishes, as well as the high biodiversity associated with the lake basin. Studies of haplochromines played a major role in illustrating how organisms undergo adaptive radiation to produce new species, and how a trophically diverse assemblage can efficiently utilize an ecosystem (Lowe- Mc Connell, 1987).

By the 1960s, stocks of the native tilapiines and other large species of Lake Victoria had been reduced by overfishing (Jackson 1971, Ogutu-Ohwayo 1990a). Nile perch and four tilapiine species were introduced into many of the lakes in the basin, including lakes Victoria and Kyoga in 1950's and early 1960's to improve stocks of the declining fishery. As stocks of introduced species increased, stocks of most of the native species declined rapidly or disappeared altogether. Of the more than 300 native species, only *Rastrineobola argentea* (Mukene) remained abundant (Ogutu-Ohwayo 1990c). Haplochromines dropped from about 80% of the fish biomass in Lake Victoria in 1970s to less than 1% in 1980s, and about 200 species are feared to have become extinct.

As a result of overfishing and introduction of exotic fishes, populations of most of the native species declined and many species became extinct (Witte *et al*. 1992 a, b). Unlike the original decline in fish stocks which was due to overfishing (Jackson 1971, Ogutu - Ohwayo 1990 a), the recent and more drastic decline has been attributed to predation by the introduced Nile perch and overall environmental degradation (Ogari & Dadzie 1988, Ligtvoet & Mkumbo 1990, Ogutu - Ohwayo 1990 b, Witte *et al.* 1992 a, b).

The loss of species and trophic diversity, and associated alterations in food webs have been accompanied by more frequent algal blooms and deoxygenation of the hypolimnion, which sometimes have been associated with mass fish kills in Lake Victoria (Ochumba & Kibara 1989). The accumulation of excess organic matter is an indication that much of the organic matter produced in the lake is not being channelled efficiently through the food web. The haplochromines had occupied virtually all trophic levels, including phytoplanktivores, zooplanktivores, insectivores, molluscivores, detritivores, piscivores and maintained an efficient flow of organic matter in the system. The decline in stocks of this trophically diverse fish community seems to have reduced grazing pressure and the overall ecological efficiency of the lake systems.

Experimental fishing on Lake Kyoga has shown that, since 1991, stocks of haplochromines started to increase (Ogutu-Ohwayo, 1994; 1999). These initially consisted of a few species of *Astatotilapia*. This recovery of haplochromines started just after the invasion of the lake by the water hyacinth. The floating weeds seem to have provided cover from the Nile perch predation. Moving hyacinth mats also seem to have assisted in dispersing the haplochromines from their refugia. Some of the haplochromines could have recolonised the lake from the Kyoga minor lakes. High fishing pressure and use of destructive fishing gears and methods which has caused reduction in Nile perch stocks, has also contributed to recovery of haplochrornines (Ogutu-

Ohwayo,1994).

Only a few trophic groups of haplochromines are still surviving in inshore and offshore areas of lake Victoria (Namulemo, 1997; Tumwebaze, 1997; Ebong 1999). The inshore haplochromine community is dominated by insectivores with a few molluscivores, prawn eaters, phytoplanktivores and detritivores and in offshore waters, zooplanktivorous *Yssichromis sp.* Other trophic groups especially phytoplanktivores and detritivores are rare. Fish species diversity is higher in shallow inshore areas than in offshore areas especially in those areas with macrophyte cover and rocky out-crops (Namulemo, 1997).

Some of the haplochromines depleted from lakes Victoria and Kyoga are present in satellite lakes in the Victoria and Kyoga lake basins (Wandera *el ai,* 1999). The fish communities of most of these lakes are composed of native species. This study examined the trophic structure and diversity of haplochromines among the satellite lakes of the Kyoga lake basin to see if any of the trophic groups that have been decimated from lakes Victoria and Kyoga still existed in these lakes and to evaluate their current trophic status.

The Global Environmental Facility (GEF) is currently supporting the East African countries to try to restore the health of Lake Victoria especially the diversity of haplochromines. This includes providing the knowledge on trophic diversity and interrelationships between species. This study could contribute to this effort by showing the trophic status of haplochromines in those lakes where the group still survives.

Study Objectives

The overall objective of this study was to rectify the serious lack of knowledge on trophic ecology in the Victoria and Kyoga lake basins by examining species composition, food, trophic relationships and diversity of the haplochromines in the Kyoga satellite lakes. This was achieved by specifically examining the following;

a) The species composition and diversity ofhaplochromines in the Kyoga Minor lakes.

b) The food and trophic diversity of haplochromines in the Kyoga Minor lakes and how this compares between the Minor lakes and with lakes Victoria and Kyoga.

Study Area, Materials and Methods

Choice of the Study Area

This study focused on the Victoria and Kyoga lake basins (Figure 2.1). The Victoria and Kyoga lake basins had a similar native fish fauna (Graham 1929, Worthington 1929). The two main lakes have also had similar history with Nile perch being introduced and having similar impacts in the two lakes. For ichtyogeographical purposes, the two lakes can be considered to be similar. Lake Kyoga basin, however has many minor lakes which are separated from the main lake by swamp and many of which have had human impacts. It was therefore considered that understanding of these lakes would contribute to the knowledge base required to solve some of the problems experienced in Lake Victoria and Kyoga especially the loss in trophic diversity which seems to have enhanced trophic inefficiency.

Study Area

The study was carried out on lakes Kyoga (lyingo), Nawampasa, Gigati, Nyaguo, Agu, Kawi and Lemwa Figs 1 & 2.

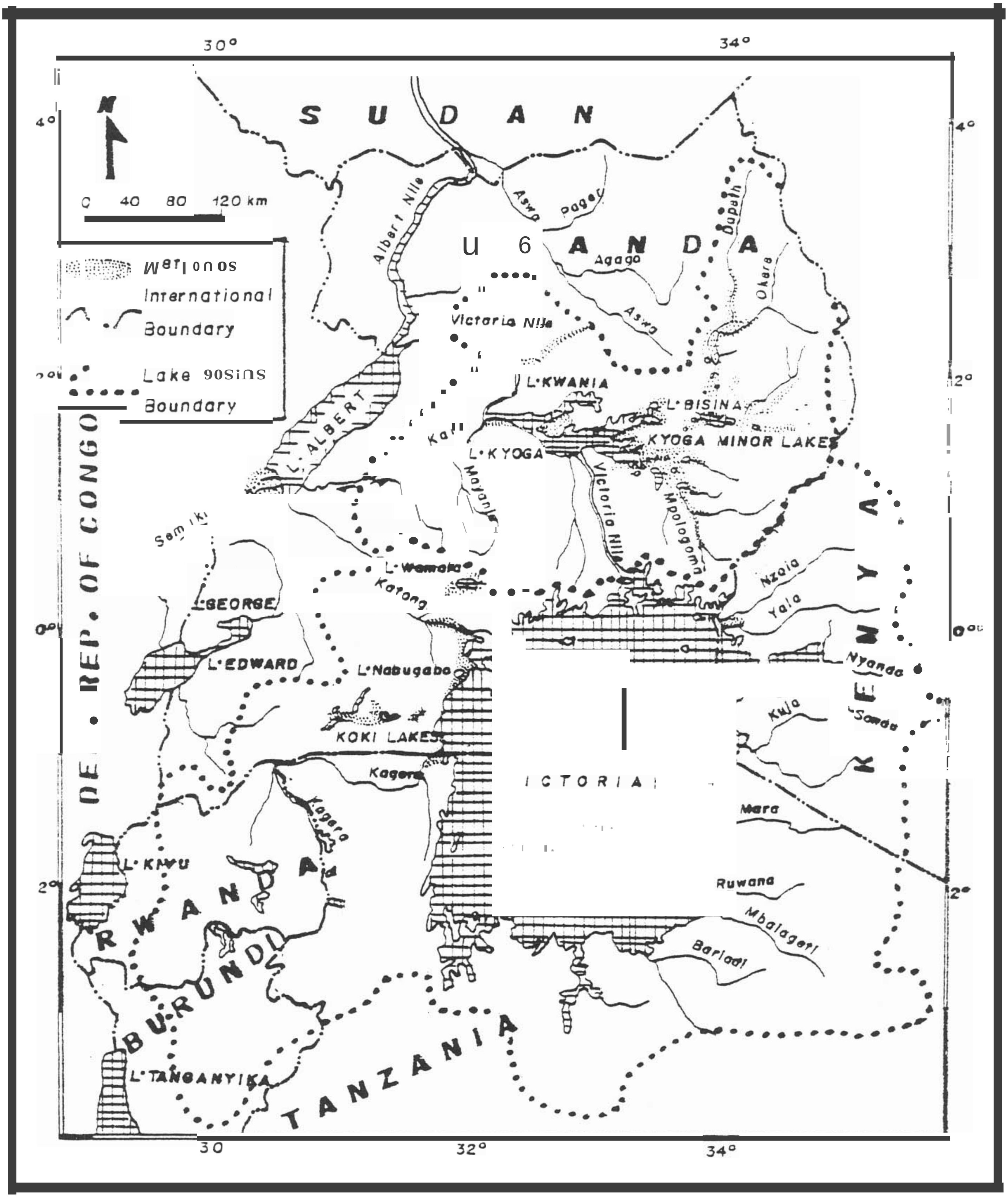


Fig. 1. Map of Uganda showing the Victoria and Kyoga Lake Basins.

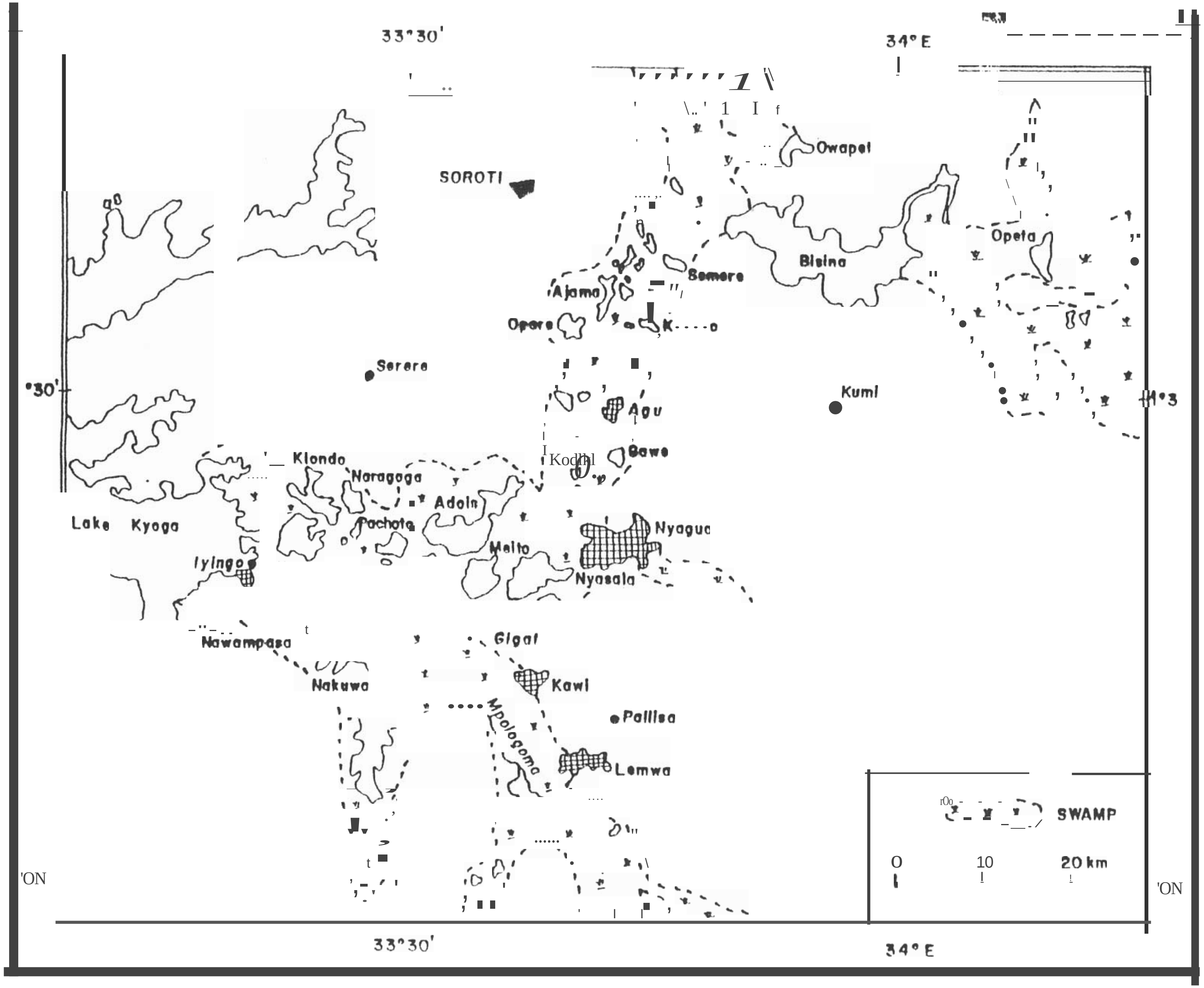


fig. 2.3 ^ map of Lake Kyoga complex. Sampled' . cs are shaded.

Materials and Methods

Fish specimen were collected using three fleets of monofilament gill nets of mesh sizes ranging from 25.4 mm to 101.6 mm increasing by 12.7 mm and locally constructed basket traps. The first fleet was set along the shoreline, the second within aquatic macrophytes whenever present or 20 m from the shoreline and the third in open water ≥100 m from shoreline. On Lake Kyoga a second set of three fleets was set offshore in the open water. The nets were set at dusk, and retrieved the following morning. Fish were sorted into their taxonomic groups to species level whenever possible and the number and weight of each taxa recorded. The specimen that could not be identified in the field were tagged with numbers and photographed. Haplochromines were preserved in 10% formaldehyde solution, labelled with date and habitat of capture and to the laboratory.

In the laboratory haplochromines were sorted into taxonomic groups to genus or species level where possible. Species were identified using morphometric and meristic procedure as in Greenwood (1981). If a fish could not exactly fit the described characters it was assigned an "chieronym". The different haplochromine taxa were then preserved separately for food analysis.

The preserved haplochromines were given serial numbers, cut open, the stomach of each fish dissected out and its degree of fullness determined as empty (0), <1/4, 1/4, 1/2, 3/4 or full (1). The stomach was opened and the contents emptied on to a petri dish, flooded with water and examined under a binocular microscope. A sample was then taken and examined under a compound microscope. The food items were sorted, identified as far as possible and as percentages through judgement by eye. The percentages were then allotted points 0, 1, 2, 4, 8 and 16 depending on the relative importance of the food item in the stomach according to Hynes (1950). Each haplochromine was assigned to one of the trophic groups previously described for Lake Victoria haplochromines

Species composition of haplochromines was estimated from the total number of each species encountered. The percentage contribution by number of each species was calculated.

Shannon-Weaver Index H' (Pielou, 1969) and number of species were used to estimate the diversity of haplochromines. The diversity Index H' was computed using the formula;

$$H' = -\sum_{i=1}^{s} p_i \log_e p_i$$

where s is the number of species and pi is the proportion by number, of each taxon in the sample.

The biodiversity values of haplochromines in the different lakes were assessed using the method given by Fuller *et al.*, (1998). Species richness and species rarity for uniqueness were used in determination of biodiversity ratings.

The food items were classified into related groups and the dominant food category was taken as decisive of the trophic classification (Witte, 1981). A trophic group consists of species using the same food category. Shannon-Weaver Index H' (Pielou, 1969) and number of trophic groups were used to estimate the trophic diversity of haplochromines between the lakes. The diversity Index H' was computed using the formula;

$$H' = -\sum_{i=1}^{s} p_i \log_e p_i$$

where s is the number of trophic groups and pi is the proportion by number of species of each trophic group.

The transfer of energy by haplochromines in the different lakes was assessed through the primary, secondary and tertiary levels. The haplochromines feeding on detritus, algae and higher plant material were regarded as primary consumers, those feeding on insects and molluscs were regarded as secondary consumers and those feeding on fish eggs and fish were regarded as tertiary consumers.

Results

Forty one haplochromine species were recorded in the six lakes sampled in the Kyoga lake basin (Table I). Haplochromine species diversity within the different lakes basing on number of species and Shanon Weaver Index of Diversity is illustrated in Figure 3. Basing on number of species the diversity was highest in Lake Nawampasa (29), followed by lakes Gigati (26), Kawi (20), Agu (17), Nyaguo (16), Kyoga (15) and was lowest in Lake Lemwa (12). Basing on Shannon-Weaver index the diversity ofhaplochromines was highest in Lake Agu (1.68), followed by lakes Nawampasa (1.60), Kawi (1.27), Nyaguo (1.22), Gigati (1.17), Kyoga (1.08) and was lowest in Lake Lemwa (1.07). Overall, the species diversity ofhaplochromines in the minor lakes was higher than that in the main lake.

The biodiversity values of the different lakes is given (Table 2). The biodiversity values were high in lakes Nawampasa and Gigati, medium in lakes Kawi, Kyoga Nyaguo and was low in lakes Agu and Lemwa. Lake Agu was however considered a special lake / site.

Table 1 The overall percentage composition of haplochromines by number from the Kyoga lake basin.

	Lakes								
Species	Lemwa	Kawi	Agu	Nyaguo	Gigati	Nawampasa	Kyoga	Kyoga minor	Overall
Astatoreochromis alluaudi	0.72	1.19	3.19	0.50	0.87	0.\5	0.27	0.77	0.74
Astatotilapia I0lifascialQ	0.00	0.00	0.64	0.00	0.69	\.41	0.00	0.70	0.66
Astatotilapia martini	0.10	0.00	0.00	0.74	0.04	0.00	0.00	0.05	0.05
ASlatali/apia nubila	22.98	8.7\	3\9	25.81	0.43	0.30	25.97	4.24	5.56
AS1QlOtilapia "miniblack"	0.10	0.00	7.99	0.00	0.74	5.90	0.00	2.0\	1.89
AstalOtiiapia 'fattoh"	54.66	64.37	17.57	49.13	26.22	39.03	0.00	36.56	34.34
Aslatoti/apia "macrops"	0.00	0.\6	0.00	1.49	0.28	0.07	0.00	0.23	0.22
AstolOtiiapia "thick/ipped"	0.00	0.00	0.00	0.00	0.07	0.04	0.00	0.04	0.04
Astaslolilapia "kyogaastato "	0.00	0.00	0.00	0.00	0.00	0.\5	6.97	0.04	0.46
Gaurochromis sp	0.00	0.00	0.00	0.00	0.00	0.15	0.05	0.04	0.04
Haplochromis lividus	\3.04	0.63	43.13	0.50	43.74	32.27	0.\4	31.98	30.04
Lipochromis "blackcryptodon"	0.21	3.48	0.64	0.74	0.39	0.82	0.\4	0.84	0.80
Lipochromis cryptodon	0.00	0.40	0.00	0.50	0.05	0.00	0.00	0.09	0.08
Lipochromis microdon	0.00	0.24	0.64	0.00	0.44	0.41	0.00	0.36	0.34
Lipochromis obesus	0.00	2.69	4.79	0.50	0.97	067	0.00	1.10	1.03
Lipochromis parvidens	0.00	0.16	1.92	0.00	1.22	0.97	0.\4	0.91	0.87
Lipochromis "while"	0.00	0.\6	0.00	0.00	0.00	0.00	0.00	0.02	0.02
Lipochromis maxillaris	0.00	0.32	0.64	0.00	0.05	0.52	0.00	0.20	0.\9
Paralabidochromis "blackpara "	6.83	1.43	0.00	0.00	0.02	0.00	40.73	0.75	3.\9
Paralabidochromis "redfin"	0.\0	0.63	0.00	0.00	0.25	0.59	0.00	0.35	0.32
Paralabidochromis "deep body"	0.00	0.00	0.00	0.00	0.04	0.00	0.00	0.02	0.02
Prognathochromis argen/us	0.62	2.38	5.\1	0.00	0.60	4.79	0.00	1.9\	1.79
PrognQ/hochromis "long lower jaw piscivore"	0.00	0.00	0.00	0.50	0.04	0.00	0.00	0.04	0.03
Prognalhochromis pellegrini	0.00	000	2.56	0.00	0.00	3.79	0.00	0.98	0.92
Prognathochromis "silvermale"	0.00	0.00	0.00	1.99	0.00	0.00	0.00	0.07	0.07
Prognathochromis "black red rail piscivore"	0.00	0.00	0.00	0.74	0.00	0.07	0.00	0.04	0.04
Prognathochromis "stilleto"	0.00	0.08	0.32	0.00	0.00	1.89	0.00	0.47	0.44
Prognathochromis "shove/mouth"	0.00	8.31	2.24	13.90	1.60	2.90	19.27	2.98	3.97
Ptyochromis "gigatisheller"	0.00	0.00	0.00	0.25	0.04	0.04	0.00	0.04	0.03
Pyxichromis orthostoma	0.4\	4.35	0.00	1.99	0.34	0.4\	0.27	0.86	0.82
Paralabidochromis ';victoriae"	0.00	0.00	0.32	0.74	0.00	0.00	0.00	0.04	0.03
Xystichromis phytophangus	0.00	0.\6	5.11	0.00	20.81	2.34	0.27	11.13	10.47
Yssichromis "lemwa zooplanktivore"	0.2\	0.\6	0.00	0.00	0.00	0.00	0.00	0.04	0.03
Yssichromis "kyoga zooplanktivore"	0.00	0.00	0.00	0.00	0.00	0.00	0.36	0.00	0.02
Paralabidochromis "earthquake"	0.00	0.00	0.00	0.00	0.00	0.00	2.32	0.00	0.14
Prognathochromis guiarli	0.00	0.00	0.00	0.00	0.00	0.00	0.68	0.00	0.04
Xyslichromis "flame back"	0.00	000	0.00	0.00	0.00	0.00	2.4\	0.00	0.15
Paralabidochromis "silverpara"	0.00	0.00	0.00	0.00	0.07	0.00	0.00	0.04	0.03
Haplochromis "unicuspid"	0.00	0.00	0.00	0.00	0.00	0.07	0.00	0.02	0.02
Astoloti!apia "redtai/fattooth"	0.00	0.00	0.00	0.00	0.00	0.04	0.00	0.01	0.0\
Astatotilapia "pseudomartini"	0.00	0.00	0.00	0.00	0.00	0.22	0.00	0.05	0.05
Grand total	100	lOa	lOa	100	\00	\00	\00	100	100

Table 2 **The relative Biodiversity values of haplochromine species for different lakes.**

		Lakes						
Parameter	**Organisms**	Lemwa	**Kawi**	**Agu**	Nyaguo	Gigati	Nawampasa	Kyoga
Species richness (I)	Haplochromines	0	3	2	1	4	5	0
Species rarity (2)	Haplochromines	0	1	0	2	3	5	4
Overall total (I+2)		0	4	2	3	7	10	4
Ratings		L	M	L S	M	H	H	M

Modified from (Fuller *et ai, 1997)*

Biodiversity value	**Rating** (critical values are arbitrary)
High (H)	5-10
Medium (M)	3-5
Low (L)	<3

Special sites/lakes (S)

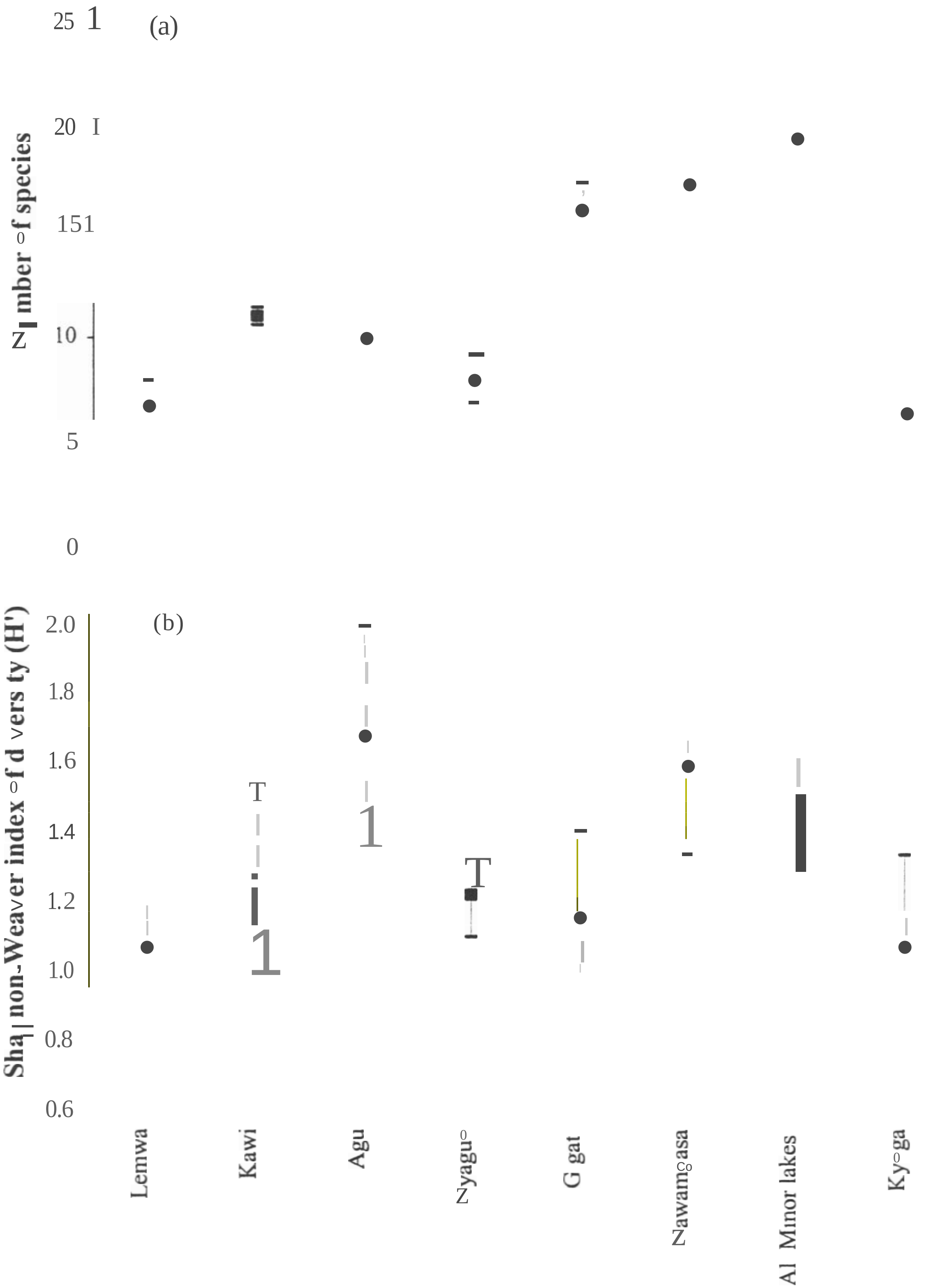


Fig. 3 Comparison by number of species (a) and Shannon-Weaver index of diversity(H')(b) of haplochromines between lakes. Vertical bars represent upper and lower critical limits (p <0.05)

Forty one haplochromine species from the sampled lakes were examined for food out of which 24 species contained food material. Overall, seven food categories were identified from the stomach contents. These included detritus, algae, higher plant material, insects, molluscs, fish eggs and fish remains. Kyoga basin haplochromines therefore comprised 7 trophic groups.The trophic groups in order of abundance by species were insectivores (8), peadophages (6), piscivores (4), algal eaters (4), higher plant eaters (I), molluscivore (I) and detritivores (I). The haplochromine species whose trophic groups were unknown were (17). In Lake Kyoga main trophic groups were insectivores (7) and molluscivores (I). The percentage contribution by number of species for different lakes is shown in Fig. 4. The haplochromines whose trophic groups were unknown were (5).

Comparison of diversity by number of species and trophic diversity by Shannon Weaver index (H') between different lakes is illustrated in figure 5. Basing on number of species, highest in Lake Nawampasa (29), followed by lakes Gigati (26), Kawi (20), Agu (17), Nyaguo (16), Kyoga (15) and was lowest in Lake Lemwa (12). Basing on Shannon Weaver index (H'), trophic diversity was highest in Lake Nawampasa (1.28), followed by lakes Gigati (1.25), Kawi (Li8), Agu (0.89), Lemwa (0.81), Nyaguo (0.35) and was lowest in Lake Kyoga (0.13). Overall, the minor lakes (1.49), had higher trophic diversity than the main lake (0.13).

Trophic diversity by number of trophic groups was highest in lakes Nawampasa, Gigati, Agu, and Kawi (5), followed by Nyaguo and Lemwa (3) and the lowest number was recorded in Lake Kyoga main (2).

Transfer of energy by haplochromines basing on the proportion by number of primary, secondary and tertiary consumers among haplochromines in each lake is illustrated (Figure 6). Lake Lemwa was dominated by secondary consumers followed by primary consumers and very few tertiary consumers. Lake Kawi had no primary consumers and was, like Lake Lemwa dominated by secondary consumers. Lake Agu had no secondary consumers was dominated by primary consumers. Lake Nyaguo had no primary consumers but had almost equal proportions of secondary and tertiary consumers. Lake Gigati was dominated by primary consumers, Lake Nawampasa had almost equal proportions of secondary and primary consumers. Overall, Kyoga Minor lakes were dominated by primary consumers followed by almost equal proportions of secondary and tertiary consumers. Lake Kyoga had only secondary consumers.

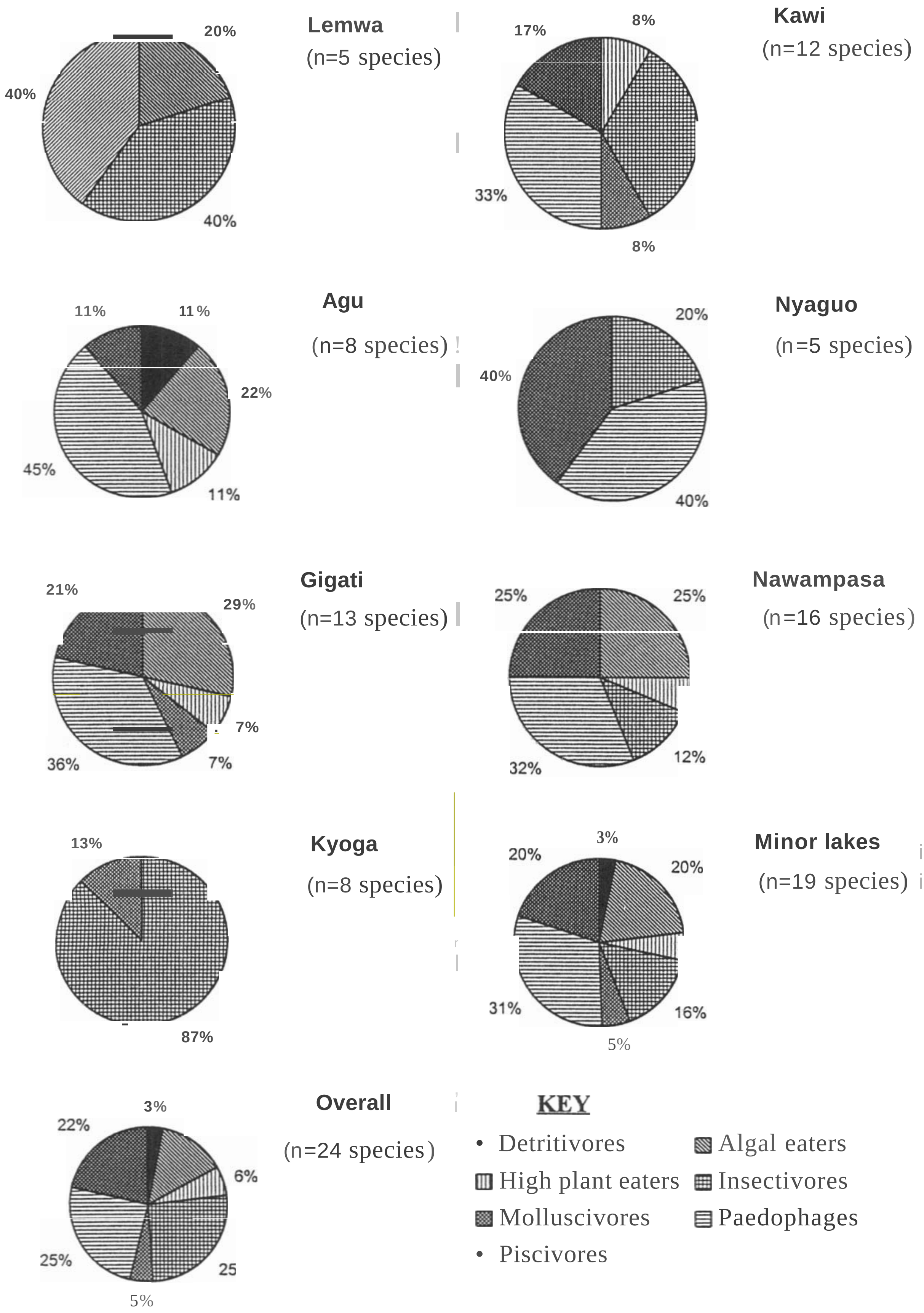


Fig. 4 Overall percentage contribution of trophic groups by species of haplochromines from Kyoga lake basin

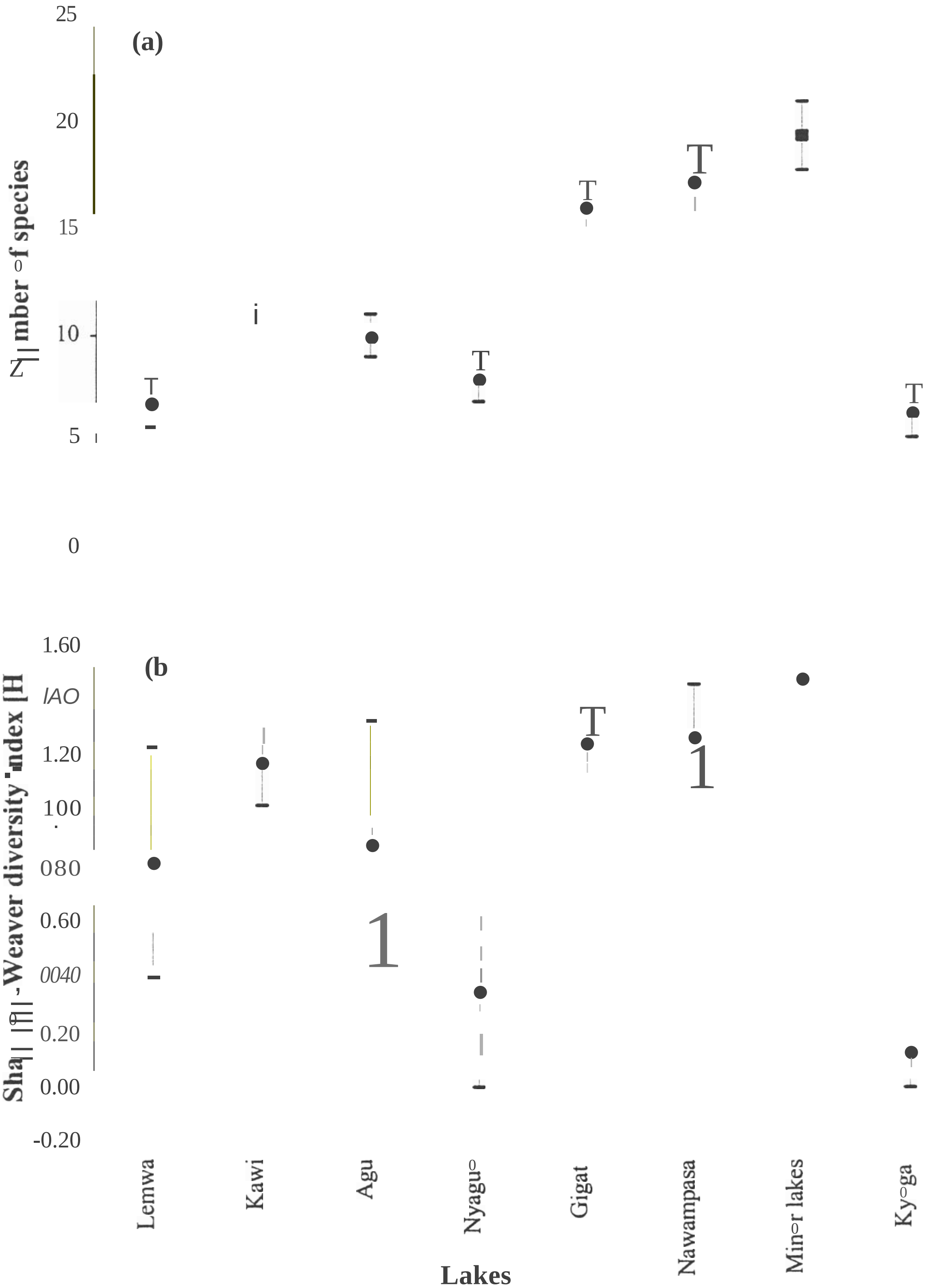
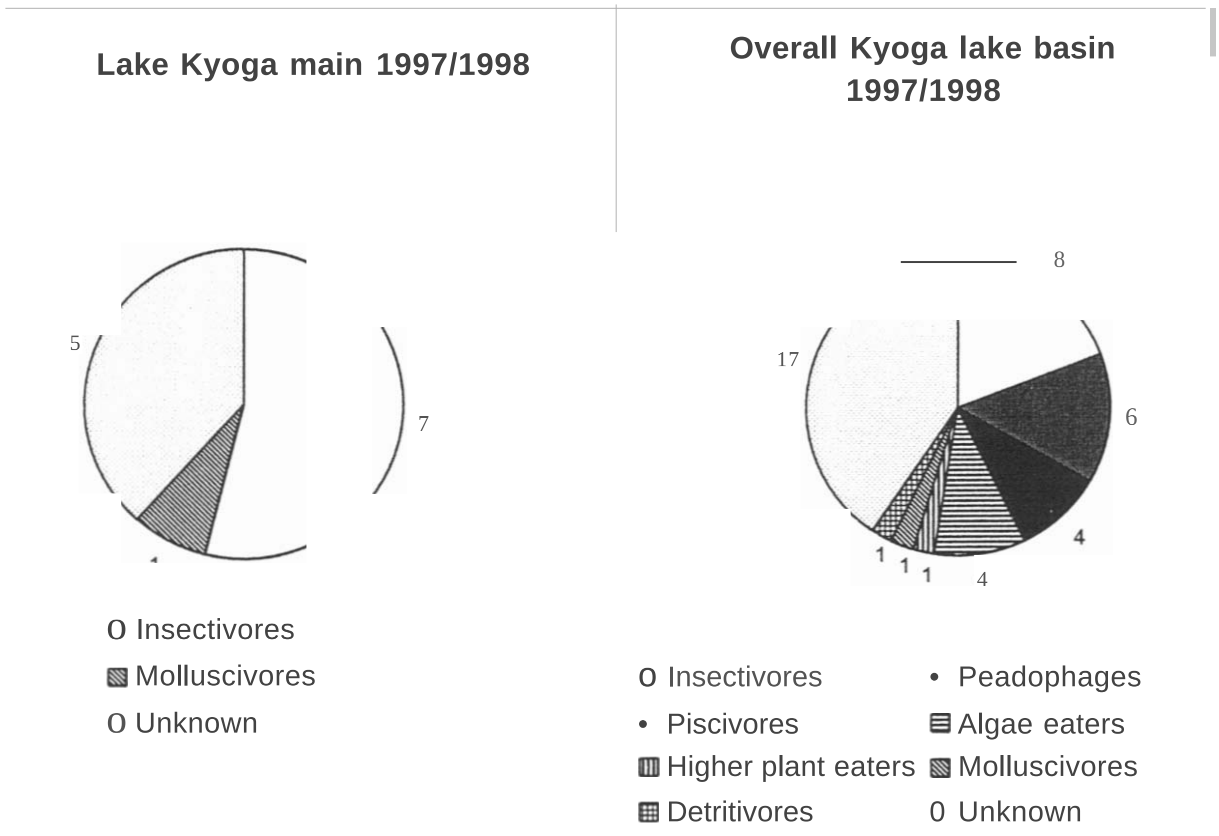
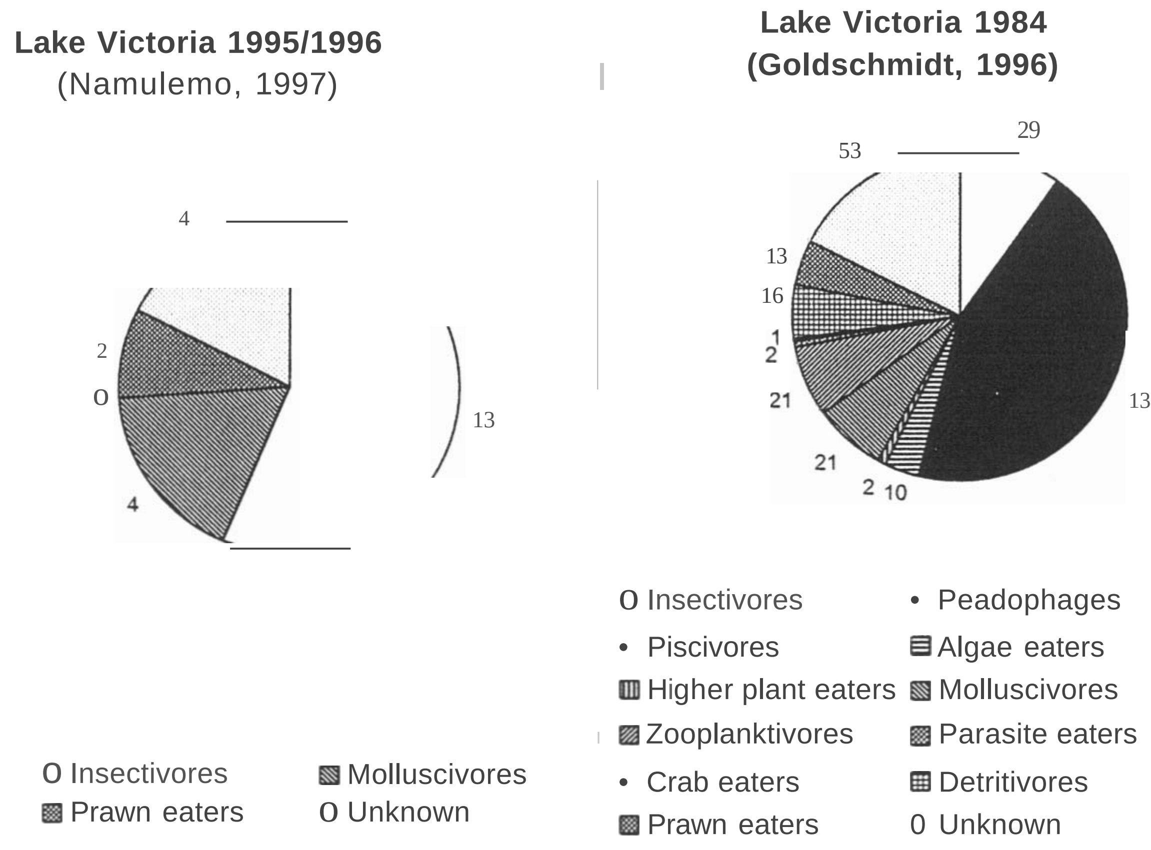


Fig. 5 Comparison of number of Species of haplochromines (a) and Shannon-Weaver indices of diversity[H') (b) of trophic groups between lakes. Vertical bars reperesent lower critical limits ($p<0.05$).



Lake Kyoga main 1997/1998

Overall Kyoga lake basin 1997/1998



Lake Victoria 1995/1996 (Namulemo, 1997)

Lake Victoria 1984 (Goldschmidt, 1996)

Fig. 7 Comparison of number of haplochromine trophic groups from Lake Victoria and Kyoga lake basins.

Haplochromines feed on a broad range of food items. This factor, more than any other, may have contributed to proliferation of these fish in lakes where they are found as it ensures maximum utilization of the food resources (Fryer, 1969). In Lake Victoria, haplochromines have undergone extensive adaptive radiation to produce about 300 species. Speciation is largely reflected in the feeding habits with adaptations for feeding on all possible foods. In Lake Victoria it is usual for more than one haplochromine species to occupy the same niche in the same habitat.

Conclusion

The present study has shown that many haplochromine trophic groups which existed in lakes Victoria and Kyoga prior to the Nile perch introductions and whose stocks were reduced these lakes are present in the Kyoga Minor lakes. The study may also provide a picture of the trophic structure of haplochromines that existed in Lake Kyoga before Nile perch upsurge. The presence of Nile perch in Lake Kyoga has simplified the trophic structure of haplochromines in the lake from seven trophic groups to two. The Kyoga Minor lakes therefore provide a great opportunity for conservation of fish species diversity threatened by introduction of exotics and other anthropogenic impacts in the Victoria and Kyoga lake basins.

It is therefore recommended that;

a) Some of the Kyoga minor lakes like Nawampasa, Gigati, Kawi and Agu be designated as conservation areas of haplochromines and other species threatened by introduction of exotics in lakes Victoria and main lake Kyoga.

b) Clearing of swamps and vegetation that separate Kyoga Minor lakes from the main lake be avoided to prevent the spread of Nile perch into these lakes. This is because presence of extensive swamps around these lakes is one of the factors that has prevented Nile perch from colonising minor lakes.

c) There is need for a more detailed study on the trophic ecology to include the other fishes in these lakes in order to answer the question of how energy is channelled through the different systems.

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