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Fish species and trophic diversity of haplochromine cichlids in the Kyoga satellite lakes (Uganda)

Dismas Mbabazi[1], R. Ogutu-Ohwayo[2], S. B. Wandera[1] and Y. Kiziito[3]

[1]*National Agricultural Research Organisation, Fisheries Resources Research Institute, P.O. Box 343, Jinja, Uganda,* [2]*Lake Victoria Fisheries Organization, P.O. Box 1625, Jinja, Uganda and* [3]*Zoology Department, Makerere University, P.O. Box 7062, Kampala, Uganda*

Abstract

Prior to the 1980s, lakes Kyoga and Victoria previously supported an exceptionally diverse haplochromine fish fauna comprising at least 11 trophic groups. The species and trophic diversity in these lakes decreased when the introduced Nile perch depleted haplochromine stocks. From December 1996 to October 1998, we studied species and trophic diversity of haplochromine fishes in six satellite lakes without Nile perch in the Kyoga basin and compared them with the Kyoga main lake against historical data from Lake Victoria where Nile perch were introduced. Forty-one species were found in the study area, of which, the Kyoga satellite lakes contributed 37 species in comparison to only 14 from the Kyoga main lake. Analysis of trophic diversity based on 24 species that contained food material revealed seven haplochromine trophic groups (insectivores, peadophages, piscivores, algal eaters, higher plant eaters, molluscivores and detritivores) in the Kyoga satellite lakes in comparison to two trophic groups (insectivores and molluscivores) in the Kyoga main lake. Many of the species and trophic groups of haplochromines depleted by the introduced Nile perch in lakes Kyoga and Victoria still survive in the Kyoga satellite lakes. This is attributed to the absence of Nile perch in those lakes. Nile perch has been prevented from spreading into the satellite lakes by swamp vegetation that separate them from the main lakes. If these swamps prevent Nile perch from spreading into the lakes, it is possible to conserve fish species, especially haplochromines, which are threatened by introduction of Nile perch in the main lakes.

Correspondence: Dismas Mbabazi, National Agricultural Research Organisation, Fisheries Resources Research Institute, P.O. Box 343, Jinja, Uganda. E-mail: mbabazidismas@yahoo.com/mbabazi@firi.go.ug

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Résumé

Avant les années 1980, les lacs Kyoga et Victoria renfermaient une variété exceptionnelle de poissons du genre Haplochromis, qui comptait au moins 11 groupes trophiques. La variété des espèces et des groupes trophiques de ces lacs a diminué après que l'introduction de la perche du Nil a dévasté les stocks d' Haplochromis. De décembre 1996 à octobre 1998, nous avons étudié la diversité des espèces et des groupes trophiques d'Haplochromis dans six lacs satellites du bassin du Kyoga qui ne contenaient pas de perches du Nil et nous l'avons comparée à celle qui existe dans le lac Kyoga principal, en regard des données antérieures sur le lac Victoria, où l'on a aussi introduit la perche du Nil. On a découvert quarante et une espèces dans la zone étudiée, dont 37 sont présentes dans les lacs satellites pour seulement quatorze dans le lac Kyoga lui-même. L'analyse de la diversité trophique basée sur 24 espèces qui contenaient du matériel alimentaire a révélé sept groupes trophiques chez les Haplochromis (insectivores, pédophages, piscivores, mangeurs d'algues, de plantes supérieures, de mollusques, et détritivores) dans les lacs satellites du Kyoga, pour deux groupes trophiques seulement (insectivores et mangeurs de mollusques) dans le lac Kyoga lui-même. Nombreux sont les groupes trophiques et les espèces d'Haplochromis qui ont été décimés par l'introduction de la perche du Nil dans les lacs Kyoga et Victoria et qui survivent dans les lacs satellites du Kyoga. On attribue cet état de fait à l'absence de perches du Nil dans ces lacs. La dispersion de la perche du Nil vers les lacs satellites a été empêchée par la végétation des marécages qui les séparent des lacs principaux. Si ces marécages réussissent à empêcher la perche du Nil de se répandre dans les lacs satellites, il est possible

de préserver des espèces de poissons, et spécialement des Haplochromis, qui sont menacées par l'introduction de la perche du Nil dans les lacs principaux.

Introduction

Exotic fish species are spreading throughout the world at an unprecedented rate, and the spread is considered to be one of the major threats to native fish fauna (Moyle, 1990; Allan & Flecker, 1993). For example, during the 1950s and 1960s, prior to fish species introductions in lakes Kyoga and Victoria (East Africa), Lake Victoria contained more than 500 species of haplochromine cichlids, of which about 99% were endemic (Greenwood, 1981; Witte *et al.*, 1992a,b; Kaufman & Ochumba, 1993; Seehausen, 1996, 2000; Seehausen, van Alphen & Witte, 1997; Witte *et al.*, 2000). Haplochromines occupied different trophic levels and included detritivores, phytoplanktivores, zooplanktivores, insectivores, molluscivores and piscivores (Witte *et al.*, 1992a,b). In the Mwanza Gulf of Lake Victoria, 54.5% of the biomass of the demersel haplochromine community in the sublittoral area comprised detritivores, followed by the zooplanktivores (27%) and the rest (5%) being insectivores (Goldschmidt, Witte & Wanink, 1993). The number of pelagic phytoplanktivorous haplochromine species was low (only three species; Witte & Van Oijen, 1990). The haplochromine cichlids were important not only as food for people, but also for having medicinal, scientific and ecological value.

The Kyoga satellite lakes are separated from the main lake by swamps, and most of them had no exotic species introduction. These lakes share water via the papyrus swamps, but fish movement across the swamps is limited to hypoxia-tolerant species (Chapman & Chapman, 1998; Schofield & Chapman, 2000). Nile perch requires high concentrations of oxygen (Fish, 1956), while some haplochromines can tolerate oxygen as low as 2–3 mg L^{-1} for extended periods (Van Oijen, Witte & Witte-Maas, 1981). The swamps are thus effective barriers to the dispersal of Nile perch (Kaufman, Chapman & Chapman, 1997). These satellite lakes harbour some haplochromine species and trophic groups depleted from the Kyoga and Victoria main lakes (Ogutu-Ohwayo *et al.*, 1999) and have been described as possible refugia for the Lake Victoria fish species and trophic diversity (Kaufman, 1997; Kaufman *et al.*, 1997) and a significant fishery resource (Kudhongania, Twongo & Ogutu-Ohwayo, 1992; Ogutu-Ohwayo, 1995; Schwartz, 2002).

Human exploitation and predation by the Nile perch (*Lates niloticus*; Linneaus, 1758) is thought to have depleted the various trophic groups of haplochromines in Lake Victoria (Witte *et al.*, 1992a,b) and most likely in Lake Kyoga. The haplochromines played a major role in energy flow and overall ecological efficiency of these lake systems and were important in maintaining the ecosystem that supported other food fishes, as well as the high biodiversity associated with the lake basins.

Nile perch and four tilapiine species were introduced into the Kyoga and Victoria basin lakes in the late 1950s and early 1960s (Gee, 1969; Ogutu-Ohwayo, 1990) to improve the stocks of declining fishery. As stocks of introduced species increased, those of the native species declined rapidly or disappeared altogether. The contribution of haplochromines dropped from about 80% of the fish biomass in Lake Victoria in the 1970s (Kudhongania & Cordone, 1974) to less than 1% in the 1980s (Ogutu-Ohwayo, 1990). The disappearance of the phytoplanktivores may partially explain the recent blooms of blue-green algae and deoxygenation of the hypolimnion that followed their disappearance, and were associated with mass fish kills in Lake Victoria (Ochumba & Kibara, 1989; Hecky *et al.*, 1994).

The overall objective of this study was to find out if the Kyoga satellite lakes without Nile perch contain haplochromine species and trophic groups depleted by Nile perch from the main lakes Victoria and Kyoga and whether the satellite lakes can be useful in conserving the lost species and trophic diversity from the main lakes following the Nile perch boom.

Materials and methods

The study area comprised of the main Lake Kyoga and six small satellite lakes of the Kyoga basin (Fig. 1). For the Kyoga main lake, where Nile perch is established, Iyingo landing site was the base of sampling. All the six satellite lakes (Nawampasa, Gigati, Nyaguo, Agu, Kawi and Lemwa) sampled have no Nile perch and are at different levels of human exploitation.

Fish samples were collected using monofilament gill nets with multiple mesh sizes ranging from 25.4 to 101.6 mm, with increments at 25.4-mm intervals in a fleet 45 m long. The nets were set at dusk and were retrieved the following morning. Fishes were sorted into

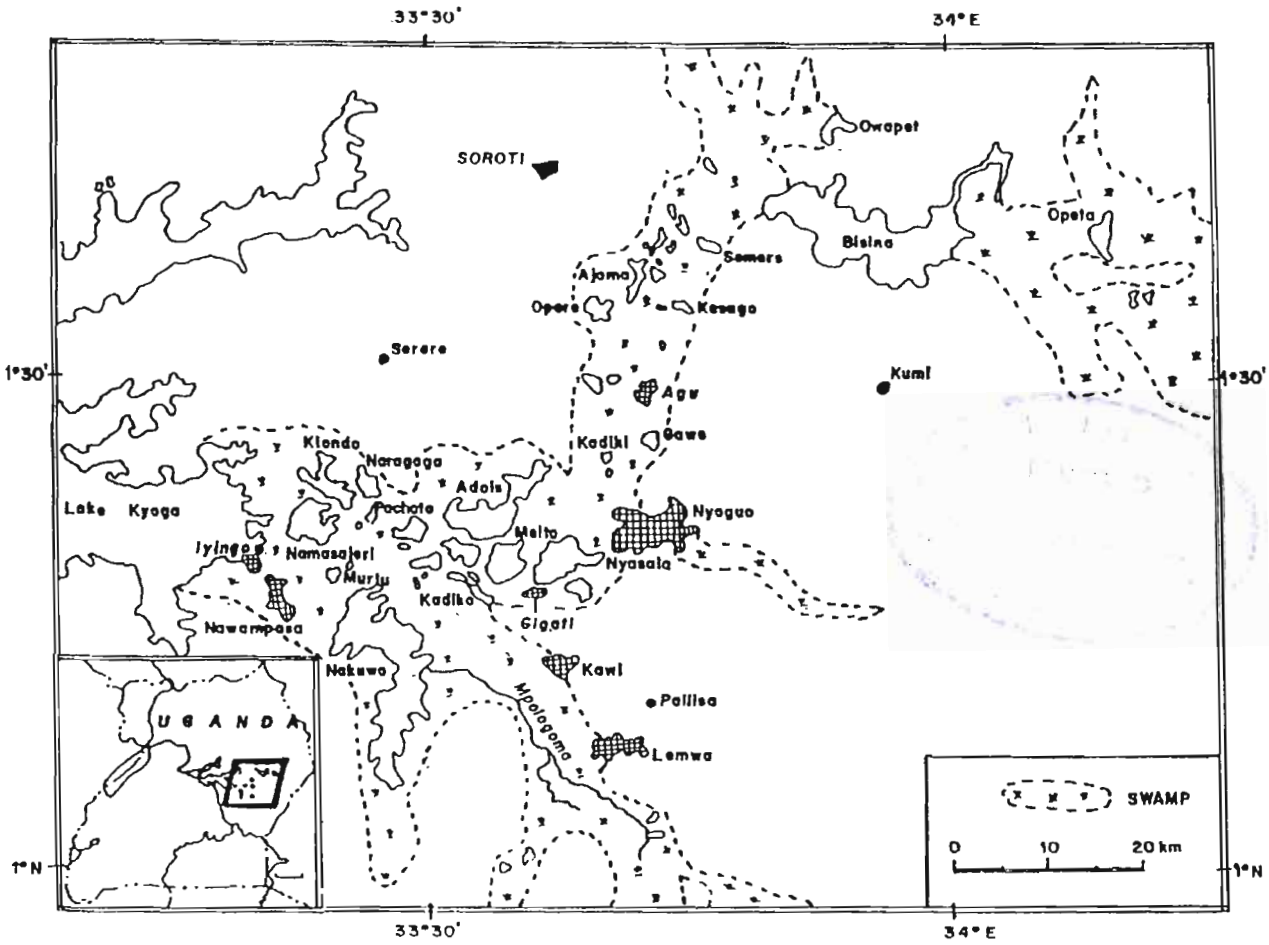

Fig 1 A map of part of the Kyoga main lake and the satellite lakes with an inset map of Uganda showing sampled lakes, which are shaded.

their taxonomic groups to species level, whenever possible, and the number and weight of each taxon were recorded. Haplochromine fishes were preserved in 10% formaldehyde solution.

In the laboratory, haplochromines were sorted into taxonomic groups (genera or species) based on morphometric and meristic procedures described by Greenwood (1981). Where a fish specimen was not exactly defined, it was assigned a 'chieronym' (working name). The different haplochromine taxa that were preserved separately for food studies were dissected and the stomach contents were examined under binocular and compound microscopes for the food items, following earlier studies (Balirwa, 1984; Winemiller, 1990). The relative importance of food items was determined by the point method as described by Hynes (1950). Each haplochromine taxon was assigned to one of the trophic groups: detritivores, phytoplanktivores, higher plant eaters, zooplanktivores, molluscivores, parasite eaters, insectivores, peadophages, prawn eaters, crab eaters and piscivores, depending on the dominant material ingested.

Species composition and relative abundance of haplochromines were estimated from percentage contribution by the number of each species. Analysis of trophic diversity was based on 24 haplochromine species that contained food material. Species and trophic diversity were calculated using the Shannon–Weaver Index H′ (Pielou, 1969), biodiversity values and number of species. The biodiversity values in the different lakes were assessed using the method given by Fuller *et al.* (1998). The recognized trophic levels were classified as: (i) primary consumers (i.e. haplochromines that fed on detritus, algae and higher plant material), (ii) secondary consumers (insects and molluscs) and (iii) tertiary consumers (fish

eggs and fishes). The categories were used to construct a pyramid of numbers.

Results

Species composition and diversity

Forty haplochromine species belonging to 11 genera were recorded in the seven lakes sampled, of which, the Kyoga satellite lakes contributed 37 species compared with only 15 from the Kyoga main lake. Within the Kyoga satellite lakes, the highest and lowest number of haplochromine species were recorded in lakes Nawampasa and Lemwa, respectively (Table 1). The three most abundant haplochromine fish species by number in the Kyoga satellite lakes that were absent or less abundant in the Kyoga main lake were *Astatotilapia* and *"fattooth"* (37%), *Haplochromis lividus* (32%) and *Xystichromis phytophagous* (11%), while the remaining 36 species contributed 20%. Similarly, the three most abundant haplochromines in the Kyoga main lake, *Paralabidochromis* and *"blackpara"* (41%), *Astatotilapia nubila* (Boulenger, 1906; 26%) and *Prognathochromis* and *"shovelmouth"* (19%), were the least abundant in the Kyoga satellite lakes. Species diversity of haplochromines was generally higher in the Kyoga satellite lakes than in the main lake (Fig. 2a,b). Based on biodiversity values, the diversity of haplochromines was rated as high in lakes Nawampasa (10) and Gigati (7), medium in lakes Kawi (4), Kyoga (4) and Nyaguo (3) and lowest in lakes Agu (2) and Lemwa (0). Lakes that had one or more unique fish species were noted and considered special lake(s), e.g. Lake Agu.

Food and trophic diversity

A wide range of food organisms occurred in stomachs of analysed fish samples. The major items ingested included algae (e.g. blue-green, green, diatoms and yellow-green), higher plant material (e.g. leaves and seeds), insects (e.g. Choaborus larvae/pupae, Chironomid larvae/pupae, mayfly, Odonata, insect eggs and unidentified insects), Molluscs (e.g. gastropods and bivalves), fish eggs and fishes (fish, embryo, scales and eyes; Fig. 3). According to the dominant feeding habits, the seven trophic groups were insectivores (8), peadophages (6), piscivores (4), algal eaters (4), higher plant eaters (1), molluscivores (1) and detritivores (1). In the Kyoga main lake, there were two trophic groups, namely insectivores (7) and molluscivores (1). From all the Kyoga basin lakes examined, all the seven species of the genus *Lipochromis* were trophically grouped as peadophages. Of the eight species of genus *Prognathochromis*, only two (*P. pellegrini* (Regan, 1922) and *P. stilleto*) were classified as insectivores in lakes Nawampasa and Kawi, respectively; the rest were primarily piscivores. The only species of genus *Pyxichromis* (*P. orthostoma*) was also classified as a piscivore. Out of the 10 encountered species of genus *Astatotilapia*, only one species (*Astatotilapia* and *"fattooth"*) was an insectivore in lakes Kawi, Lemwa and Nyaguo, one (*Astatotilapia "miniblack"*) was a detritivore in Lake Agu;

Table 1 Species composition by number of haplochromine genera recorded from Kyoga lake basins (December 1996-October 1998)

Genera	Lemwa	Kawi	Agu	Nyaguo	Gigati	Nawampasa	Kyoga (main)	All satellite lakes	Overall (all lakes)
Astatoreochromis	1	1	1	1	1	1	1	1	1
Astatotilapia	4	3	4	4	7	9	2	10	10
Gaurochromis	–	–	–	–	–	1	1	–	1
Haplochromis	1	1	1	1	–	2	1	2	2
Lipochromis	1	7	5	3	6	5	2	7	7
Paralabidochromis	2	2	1	1	3	2	2	5	5
Prognathochromis	1	3	4	4	3	5	2	7	8
Ptyochromis	–	–	–	1	1	1	–	1	1
Pyxichromis	1	1	–	1	1	1	1	1	1
Xystichromis	–	1	1	–	1	1	2	2	2
Yssichromis	1	1	–	–	–	–	1	1	2
Grand total	12	20	17	16	23	28	15	37	40

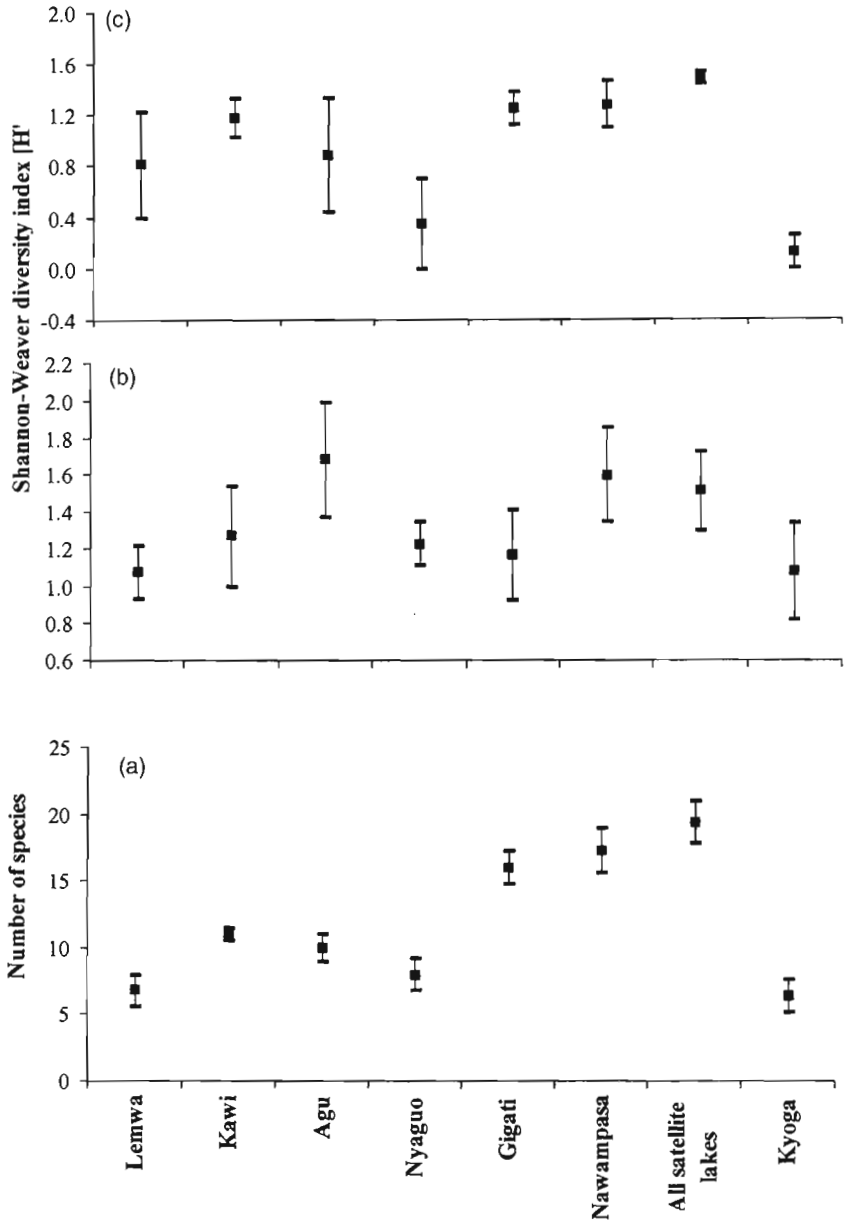

Fig 2 Comparison by number of haplochromine species (a), Shannon--Weaver indices of diversity (H') of species (b) and trophic groups (c) for different lakes. Vertical bars represent upper and lower critical limits ($P < 0.05$).

the rest being primarily algal eaters. *Prognathochromis* and *"shovelmouth"* was classified as an insectivore and piscivore in lakes Gigati and Nyaguo, respectively. *X. phytophagus* was grouped as a higher plant feeder, whereas all *Paralabidochromis* spp. were grouped as insectivores and *Astatoreochromis alluaudi* was grouped as a molluscivore. The Kyoga satellite lakes showed higher trophic diversity than the main lake (Fig. 2c). In terms of numbers of fish, haplochromines in the Kyoga satellite lakes played an important role in energy transfer at primary, secondary and tertiary consumer, trophic levels, compared with the Kyoga main lake where haplochromines only played the role of secondary consumers (Fig. 4). Lakes Lemwa and Kawi lacked primary consumer haplochromines, while Lake Agu had no secondary consumers.

Discussion

Of the 40 haplochromine species recorded from the study area, 13 had been recorded in lakes Kyoga and

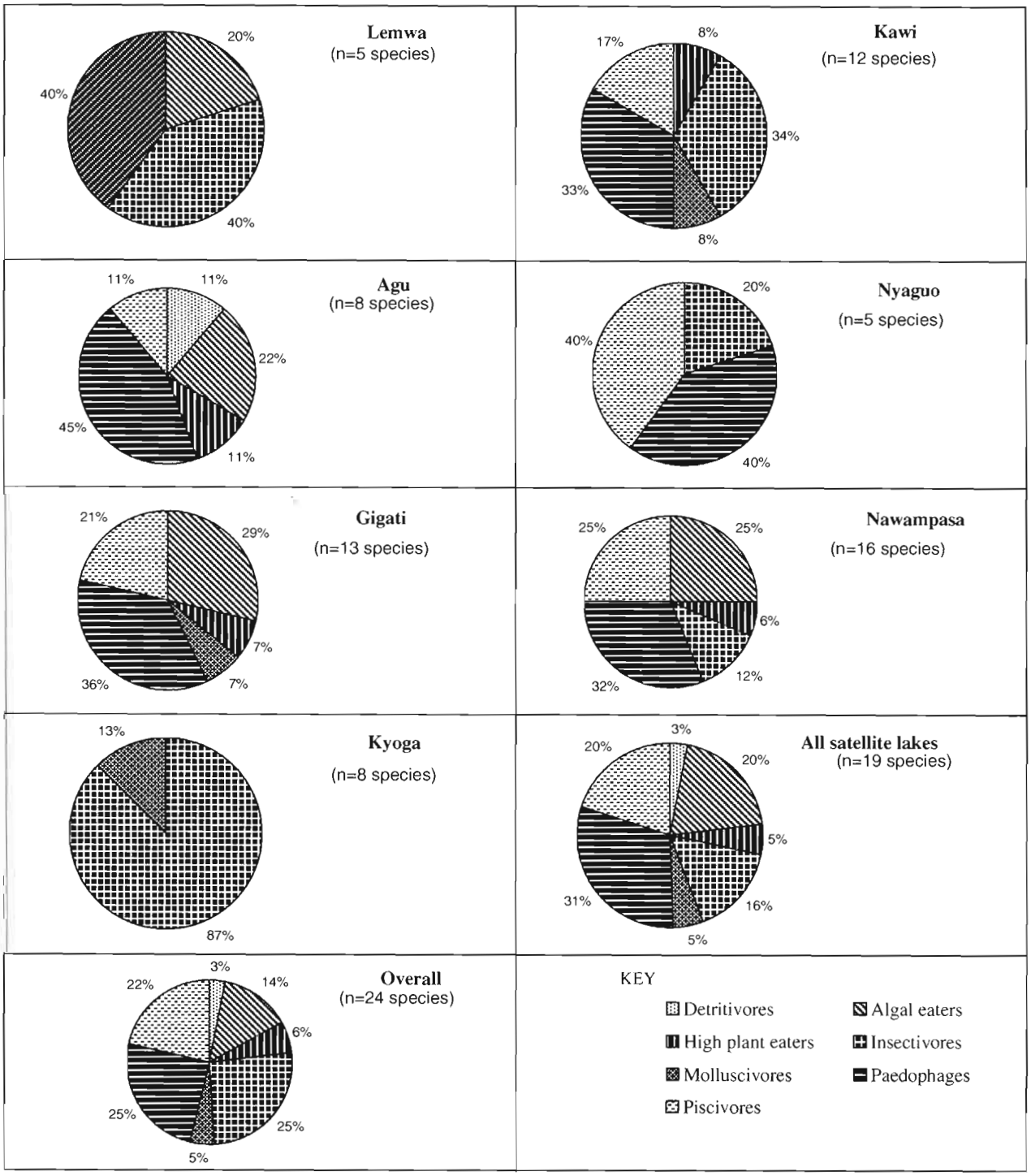

Fig 3 Overall percentage contribution of trophic groups by species of haplochromines from Kyoga lake basin.

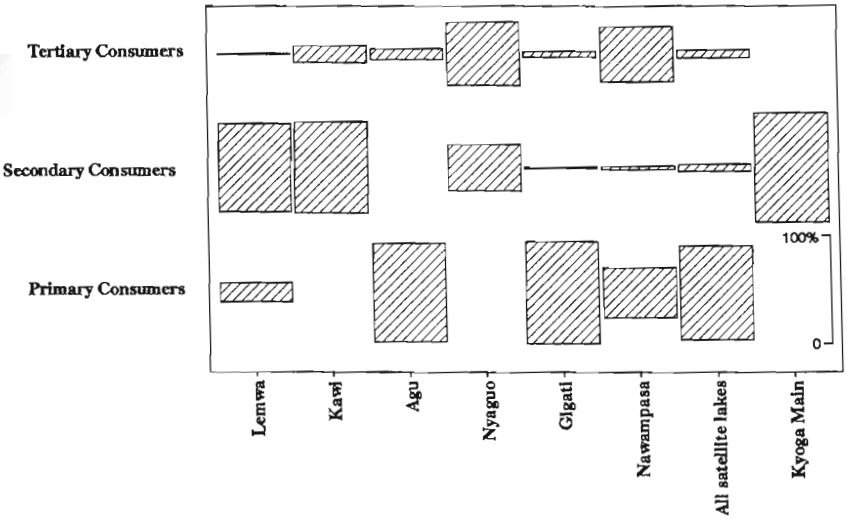

Fig 4 The percentage contribution by number of haplochromines at different trophic levels in different lakes of Kyoga lake basin.

Victoria prior to the Nile perch upsurge (Worthington, 1932; Greenwood, 1981). However, only two species (*A. alluaudi* and *A. nubila)* were recently recorded in Lake Victoria (Namulemo, 1998). These two species are widely distributed in Uganda and may not be considered threatened. In Lake Kyoga, the six species documented by Worthington (1932) before Nile perch introduction (*A. latifasciata, A. nubila, L. microdon, P. pellegrin. P. argenteus* and *P. orthostoma*) were encountered in the sampled part of Kyoga main lake during this survey. The recovery was probably because of the reduction of predation rates on haplochromines as a result of intense fishing pressure on Nile perch (Ogutu-Ohwayo, 1994; Kitchell *et al.*, 1997; Schindler *et al.*, 1998) and the increase in cover from predation provided by the expansion of the water hyacinth (*Eichornia crassipes*; Ogutu-Ohwayo, 1994). Still, the overall species and trophic diversity of haplochromines in the Kyoga satellite lakes was higher than that found in the sampled Kyoga main lake. This was attributed to the absence of Nile perch from the satellite lakes examined. Nile perch has probably been prevented from entering the Kyoga satellite lakes from the main lake by swamps separating these lakes.

The species and trophic diversity of haplochromines varied between the Kyoga satellite lakes. Generally, lakes Nawampasa, Gigati and Agu had higher species and trophic diversity compared with lakes Lemwa and Kawi. The above observation is probably because of high habitat diversity, a phenomenon associated with high species and trophic diversity as observed in other aquatic ecosystems (Tonn & Magnuson, 1982; Eadie & Keast, 1984; Randall & Minns, 2002). Submerged and floating weeds in lakes Nawampasa, Gigati and Agu provide a wide ecological niche compared to lakes Lemwa and Kawi, which are dominated by papyrus swamps along the shoreline with only open waters. However, Lake Kawi had higher species and trophic diversity than Lake Nyaguo, which is close to one of the highly diversified lakes, Lake Agu, because Lake Nyaguo is characterized by a narrow ecological niche of open waters compared with Lake Kawi that is located between the highly diversified lakes (Nawampasa, Gigati and Agu) and the low diversified one (Lemwa) and probably shares some of the characteristics of both the systems. Lake Agu had low number of species and its biodiversity value was also rated low, despite the high Shannon–Weaver index of diversity because it exhibited high evenness of relative abundances; however, this lake had one species (*Paralabidochromis victoriae*) that was absent in those lakes with high species diversity and was therefore considered a special lake. Lake Agu has low fishing pressure and can be gazetted for conservation purposes with minimum socio-economic consequences. Lake Nyaguo, which is very close to Lake Agu and is rich in the relatively larger non-haplochromine species (Ogutu-Ohwayo *et al.*, 1999), would then provide the alternative source of fish protein to the communities that are dependent on Lake Agu. Lake Nawampasa had a high number of species evenness of relative abundance, and its biodiversity value was rated high, thus making it suitable for conservation purposes. The lake is dominated by the small

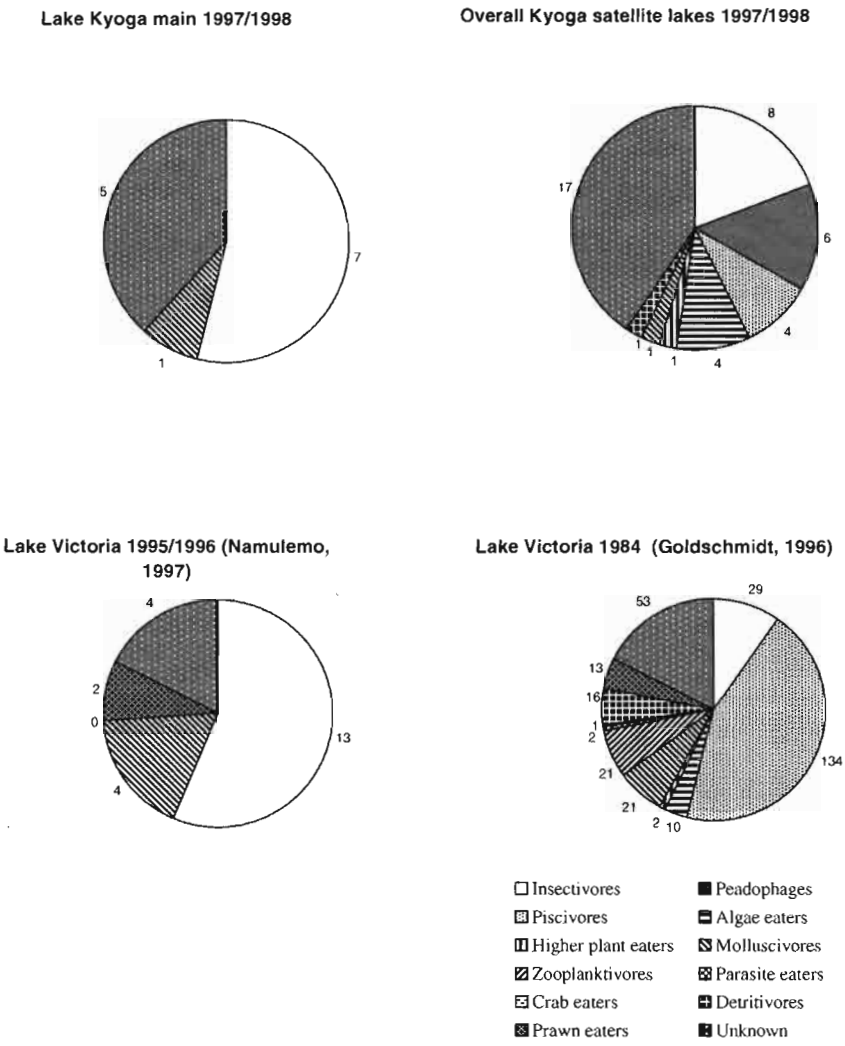

Fig 5 Comparison of number of haplochromine trophic groups from Lake Victoria and Kyoga lake basins.

haplochromine species and thus has a low fishing pressure because it is adjacent to the main Lake Kyoga, which has larger fishes (e.g. *L. niloticus, Oreochromis niloticus*), which provide an alternative source of fish protein. Lake Gigati had a high number of species with low evenness of relative abundance and a high biodiversity value. This lake has a very high fishing pressure to the extent that at any one time of the day, nets cover three quarters of the lake. This lake is very close to lakes Kawi and Nyasala, which would provide alternative sources of fish protein if it was gazetted for conservation purposes. Lake Kawi has a high fishing pressure, but the lake has sudds that naturally help in reducing this pressure through carrying away nets of fishermen. Lake Nyasala has already been invaded by Nile perch (Twongo, 1995) and may not be suitable for conservation of haplochromines but may rather be suitable for human exploitation.

No previous studies were carried out on the food of haplochromines from Lake Kyoga before the Nile perch upsurge and, therefore, most of the indigenous species disappeared before their trophic structure was studied. Historical data on trophic structure of haplochromines in Lake Victoria before Nile perch upsurge were therefore used for comparison with current observations in the lakes examined in the Lake Kyoga basin. A comparison of the current observations in the Kyoga basin lakes with information obtained from Lake Victoria before the Nile perch upsurge (Fig. 5) indicates that most

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