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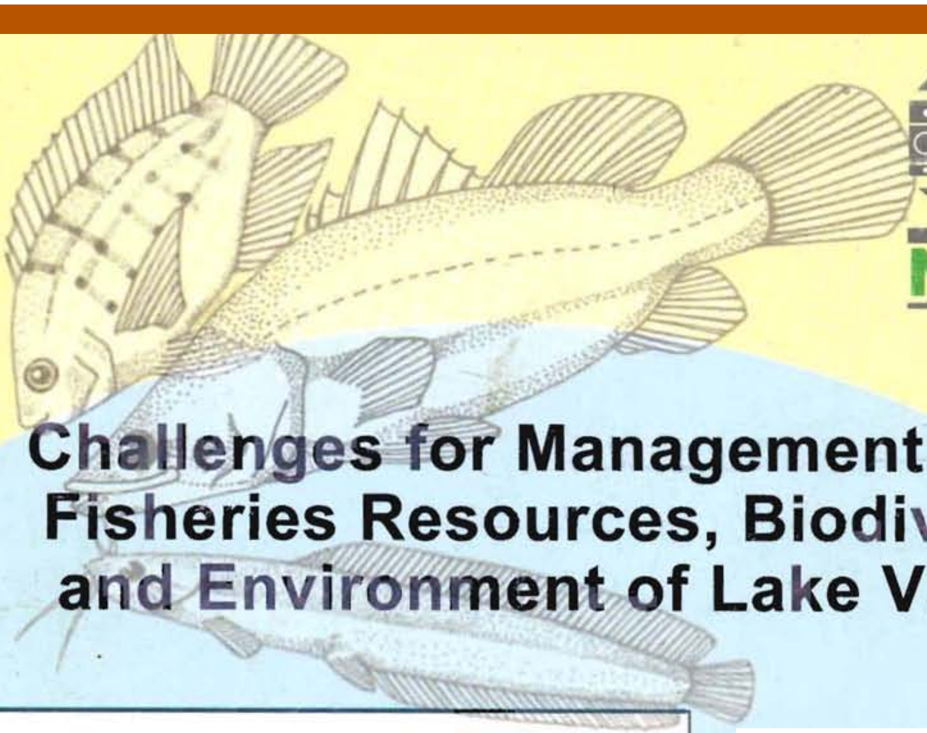
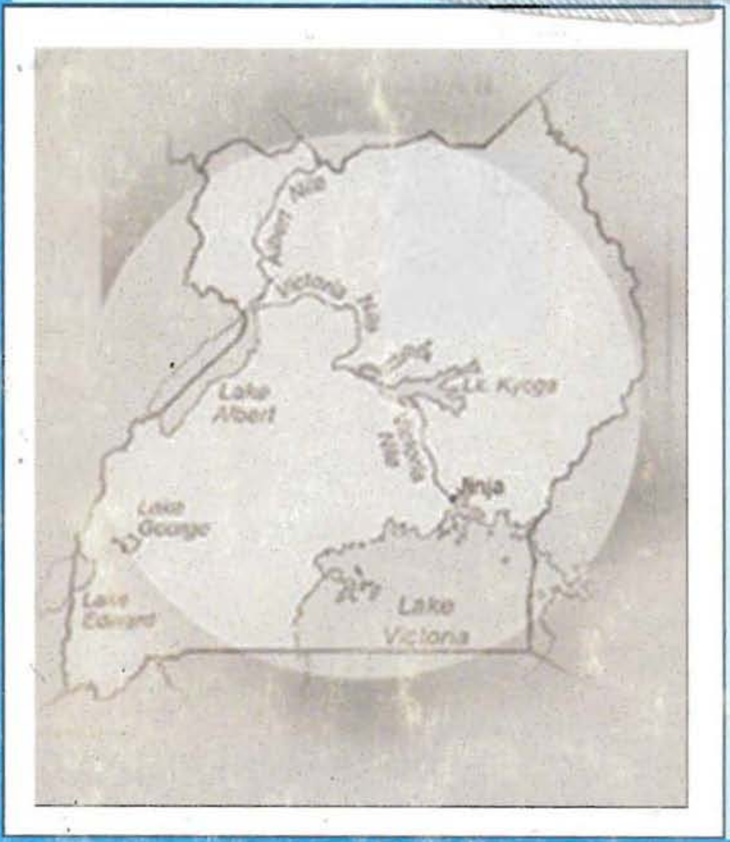


Challenges for Management of the Fisheries Resources, Biodiversity and Environment of Lake Victoria



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Fisheries Resources Research Institute

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LAKE VICTORIA ENVIRONMENT MANAGEMENT PROJECT
LAVEMP
FOR MAXIMUM SUSTAINABLE BENEFITS

Challenges for Management of the Fisheries Resources, Biodiversity and Environment of Lake Victoria

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5.2 Implications of changes in trophic diversity and food webs on fisheries and the environment

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Introduction

Most of the earth's ecosystems are experiencing slight to catastrophic losses of biodiversity, caused by habitat destruction, alien species introduction, climate change and pollution (Wilcove *et al.,* 1998). These human effects have led to the extinction of native fish species, the collapse of their populations and the loss of ecological integrity and ecosystem functioning (Ogutu-Ohwayo & Hecky, 1991; Witte *et al.,* 1992a; Mills *et al.,* 1994; Vitousek *et al., 1996).* Food webs are macro-descriptors of community feeding interactions that can be used to map the flow of materials and nutrients in ecosystems (Jepsen & Winemiller, 2002). Comparative food web studies have been used to address theoretical questions such as 'does greater trophic connectivity increase stability?' (Cohen *et al., 1990),* and 'does the number of trophic levels increase with productivity?' (Briand & Cohen, 1987). Answers to such questions have obvious applications for natural resources management. From a multi-species fisheries standpoint, there is a need to understand consumer-resource dynamics within complex trophic networks.

Trophic interactions playa major role in aquatic ecosystems (Carpenter *et al., 1985;* Vander Zanden & Rasmussen 1999), and the trophic habits of fish have consequences for other aspects of their biology, including contaminant accumulation (Kidd *et al.,* 1995; Vander Zanden & Rasmussen 1996; Kidd *et al.,* 2001) as well as patterns of life history and growth (Martin, 1966). Fish are important consumers in aquatic food webs (Bax 1991). At the whole system scale, predation by fishes alters community structure and nutrient cycling, thus, both direct and indirect predation effects are expressed in population structure, community composition and productive processes at all trophic levels (Kitchell *et al.,* 1994). Fishers and related fishing activities can alter food web interactions because they target certain species that have important trophic effects on the entire food webs.

Like in any other African Great lakes, Lake Victoria has experienced dramatic changes in recent times, including eutrophication and deoxygenation (Hecky 1993; Hecky *et a/.,* 1994), the extirpation of native cichlid species (Witte *et a/.,* 1992b) an increase in Nile perch *(Lates niloticus),* Nile tilapia *(Oreochromis niloticus),* and *Rastrineobo/a argentea* fisheries (SEDAWOG 1999), intensive fishery exploitation (Kitchell *et a/.,* 1997) and the increase and subsequent decline of water hyacinth, *Eichhornia crassipes* (Twongo 1996). Equally dramatic shifts have been observed in food web structure and trophic relationships in Lake Victoria. This chapter reviews the original food web structure prior to the Nile perch introduction and other environmental shifts and compares this against the current food web structure.

The Original food web structure prior to transformation

Prior to the stockings of exotic fish species (Nile perch and four tilapiines (0. *niloticus, Oreochromis leucostictus, Tilapia zillii* and *Tilapia rendalll)* , Lakes Victoria and Kyoga had a high fish species and trophic diversity with many fish species that were found only in these lakes. The Victoria food web and fishery contained an ecologically and phylogenically diverse group of fishes. The fish fauna was dominated by a diversified, presumably monophyletic species flock of haplochromine cichlids (Meyer *et af., 1990).* The most recent estimates of Lake Victoria's pre-Nile perch species flock comprised of over 500 species that occupied a spectacular variety of niches in the lake (Greenwood 1974; Seehausen 1997). Prior to Nile perch introduction in Lake Victoria, the predators on adult haplochromines were: the catfishes such as *Bagrus docmac, C/arias gariepinus, Schilbe intermedius* and the lungfish, *Protopterus aethiopicus* (Olowo & Chapman, 1999), fish eating birds *(Pha/acrocorax africanus, Pha/acrocorax carbo, Ceryle rudis)* and otters (Goldschmidt, *et a/.,* 1990, Goudswaard & Wanink, 1993). A direct chain existed from phytoplankton to tilapiine species (Ligtvoet & Witte 1991). Lake Kyoga, downstream of L. Victoria and Lake Nabugabo, formerly connected to Victoria also had endemic haplochromine species (Worthington, 1929; Trewavas 1933; Greenwood 1965; 1966; Kendal! 1969). The fishes especially the haplochromines occupied most trophic levels and played an important role in the flow of energy in the ecosystem of these lakes. The haplochromines converted numerous protein sources such as detritus, algae, zooplankton, insect larvae, molluscs and many others into fish protein for consumption by higher trophic levels (Christian, 1995). The major food web started from detritus and phytoplankton run via the various trophic groups to the piscivores and other top predators such as crocodiles and humans (Fig. 5.2.1). Haplochromines were crucial in maintaining the ecosystem which supported other 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.

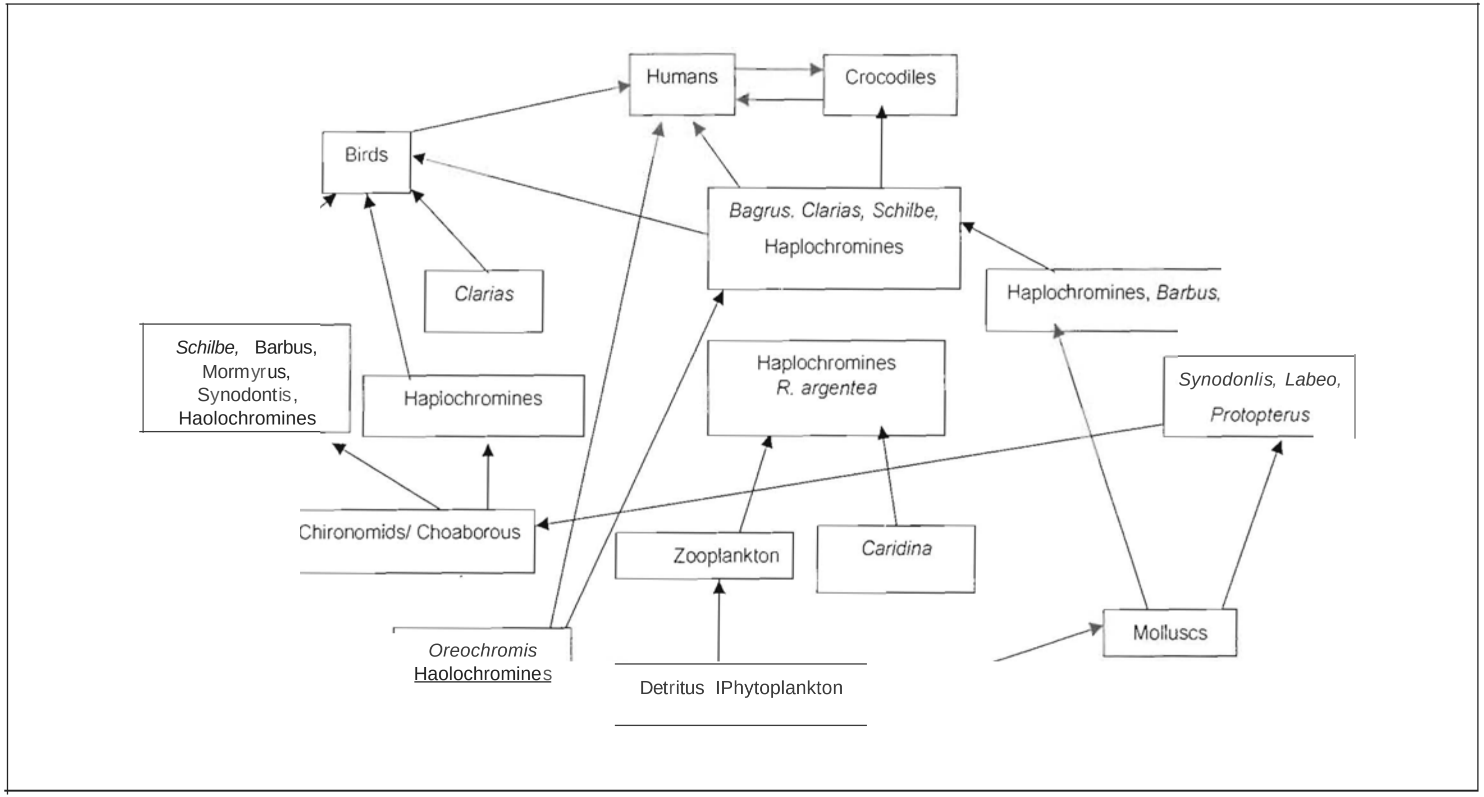

Fig. 5.2,1. A simplified food web of the pelagic Lake Victoria before **Nile** Perch introduction (Modified from Worthington, 1933; Ligtvoet and Witte, 1991, Witte and van Densen, 1995). Note the number of ecological niches that haplochromine species occupy.

Current food web structure from dietary gut content and stable isotope analyses

Changes in the food web of Lake Victoria during the last 40 years are among the most dramatic known to ecology (Kaufman 1992; Lowe-McConnell 1994). By the 1960's, stocks of the native tilapiines and other large species of Lake Victoria had been reduced byoverfishing (Jackson 1971; Ogutu-Ohwayo 1990a;b).

With the establishment of introduced species in Lake Victoria, the trophic ecology of the system changed, both through predator-prey and competitive interactions, and through the removal of various trophic groups from the food web (Reinthal & Kling, 1994). The detritivore/phytoplanktivore group, which constituted 40% and 16% respectively of the total dermersal fish biomass, disappeared in the early 1980's, with the explosive :ncrease of the introduced Nile perch. Only after the haplochromines densities had declined to near zero did the Nile Perch switch to other prey, such as the atyid prawn *Caridina nilotica* (Goldschmidt *et al.,* 1993), native cyprinid R. *argentea* and its own young (Witte *et al.,* 1992a). In the presentfood web of Lake Victoria, the Nile perch is the top predator, replacing all the original piscivores. The detritivorous/ phytoplanktivorous'haplochromines have been replaced by the prawn C. *nilotica* while the indigenous tilapiine species have been replaced by the introduced Nile tilapia. Nile tilapia particularly the young ones, live in the littoral and sub-littoral regions of the lake'and have rninimal overlap with the Nile perch (Lowe-McConnell 1997; Welcomme 1988; Ogutu-Ohwayo 1990a) and the two species also co-exist in lakes Albert and Turkana. An important feature of the present system is the extensive cannibalism within the Nile perch population, which starts at very young stages (Crul1998). The introduced Nile perch severely disrupted the ecosystem with the simplification of the food web through virtual eradication of haplochromines from many interactions and the development of short food chains to the Nile perch. Whereas the haplochromines converted numerous protein sources into fish protein for consumption by higher trophic levels, Nile perch now eats quite a lot of its own juveniles, which feed on the same food items as the haplochromines did previously (Christian, 1995). Other changes were also observed at the top of the food pyramid. The pied Kingfisher (C. *rudis)*, shifted from the diet of mainly haplochromines to exclusively R. *argentea.* A similar shift in diet was also found for the Great Cormorant P *carbo* and the long-tailed Cormorant P *africanus* (Goudswaard *et al.,* 1993). Currently humans are a dominant component of the Lake Victoria food web, and the fisheries have the potential to further alter community structure and dynamics (Kitchell *et al., 1997).*

The loss of species and trophic diversity, and associated alterations in food webs have been accompanied by more frequent algal blooms (Ochumba & Kibara 1989; Hecky & Bugenyi 1992; Mugidde 1993) and deoxygenation of the deeper water of the lake, which sometimes has been associated with mass fish kills in Lake Victoria (Hecky *et al.,* 1994). The accumulation of the excess organic matter is an indication that much of the organic matter produced in the lake is not being channeled efficiently through the food web. Originally the native fishes occupied virtually all trophic levels, including phytoplanktivores, zooplanktivores, insectivores, molluscivores, detritivores, and piscivores and maintained an efficient flow of organic matter in the system. The depletion in stocks of this trophically diverse fish community by Nile perch changed the food web of the lake and seems to have reduced grazing pressure and the overall ecological efficiency of the ecosystem in the lakes.

Use of Stable nitrogen and carbon isotope ratios in food web studies

Trophic interactions in fresh water food webs have traditionally been defined using dietary analyses of fish stomachs or gut contents or from the presence of organisms within a system (Balirwa 1984; Balirwa 1998; Mbabazi 1999). The Lake Victoria food web structure is shifting, based on information on the volume and composition of the fish catch in the lake, as well as on the stomach contents of fish (Balirwa 1998; Ogutu-Ohwayo 1995; Wanink 1998).

While dietary analysis provides valuable taxonomic information on fish diets, they can be complemented by the analyses of stable nitrogen (d 15N) and carbon ($d^{13}C$) isotope ratios of biota to characterise food web structure and trophic interactions (Peterson & Fry 1987). Stable isotopes integrate a longer temporal scale of feeding, assimilation, and growth (Kling *et al.,* 1992; Yoshioka *et al., 1994,* Harvey & Kitchell 2000). Globally, stable isotope analysis has been used successfully to describe aquatic food webs and their measurements have been used to estimate feeding patterns and food web structure in several African lakes, including Lake Kyoga in Uganda (Hecky & Hesslein, 1995); Lake Malawi in southern Africa (Bootsma *et al.,* 1996; Genner *et al.* 1999; Hecky & Hesslein 1995; Kidd *et al.,* 2001) and in Napoleon and Winam Gulfs of Lake Victoria in East Africa (Campbell 2003.).

Nitrogen isotopes consistently fractionate in organisms. 14N is selectively eliminated while 15N is incorporated into body tissues. At every successive trophic transfer, $d^{15}N$ values in the tissue of biota increase. Many studies find the average $d^{15}N$ difference between an animal and its food source is approximately 3 to 4 $^{01}{}_{00}$ (Peterson & Fry 1987; Vander Zanden & Rasmussen 2001; Post 2002). This consistent change provides a powerful analytical tool to quantify relative trophic position or dietary changes in fish (Cabana & Rasmussen 1994).

In contrast carbon isotopes fractionate very little in biota, with 1 0/00 enrichment in d^{13}C per trophic level (Peterson & Fry, 1987; Vander Zanden & Rasmussen, 2001 ; Post 2002). Because of these low fractionation rates, the stable carbon isotope values of organisms reflect the average d^{13}C of their diets. d^{13}C values can vary at the base of the food web due to differences in photosynthetic enzymatic fixation, growth rates, CO$_2$ and pH levels and these differences are passed up in the food chain, indicating the origin of organic carbon in organisms at higher trophic levels (Hecky and Hesslein, 1995). In lakes, d^{13}C is useful for differentiating between two major sources of available energy, littoral (near shore) production from attached algae and detritus, and pelagic (open water) production from phytoplankton, because the d^{13}C of the base of the littoral food web tends to be enriched in 13C (less negative d^{13}C) relative to the base of the pelagic food web (France 1995; Post 2002).

Campbell *et al.,* 2003 found out that the food webs of the widely separated gulfs (Napoleon and Winam) of Lake Victoria with differing water qualities and anthropogenic effects are similar despite the different d^{15}N and d^{13}C values at the base of their food webs. In the current Lake Victoria, Nile perch depends on a variety of macro-invertebrates and it's own young for its growth through maturity and even into adulthood (Fig. 5.2.2). Young Nile perch and *Caridina* are isotopically consistent as prey items for larger adults and there is an increasing preference for piscivory with increasing size. Nile tilapia in Napoleon Gulf have isotopic signatures consistent with strong preference for detritus throughout its life history, while in Winam Gulf, there are indications of shifting dietary patterns. R. *argentea* and *Yssichromis /aparograma* cannot be contributing to somatic growth of Nile perch (Fig. 5.2.2) as the pelagic fish have d^{15}N signatures indistinguishable from Nile perch (and in Napoleon Gulf, significantly different d^{13}C values). Common fish species as *Schi/be intermedius* and *Synodontis afrofischeri,* which coexist with Nile perch in the modem lake, are trophically isolated from Nile perch. This suggests that only a narrow group of fishes is available to sustain growth of larger Nile perch and the stability of prey populations is crucial to the sustainabillity of Nile Perch.

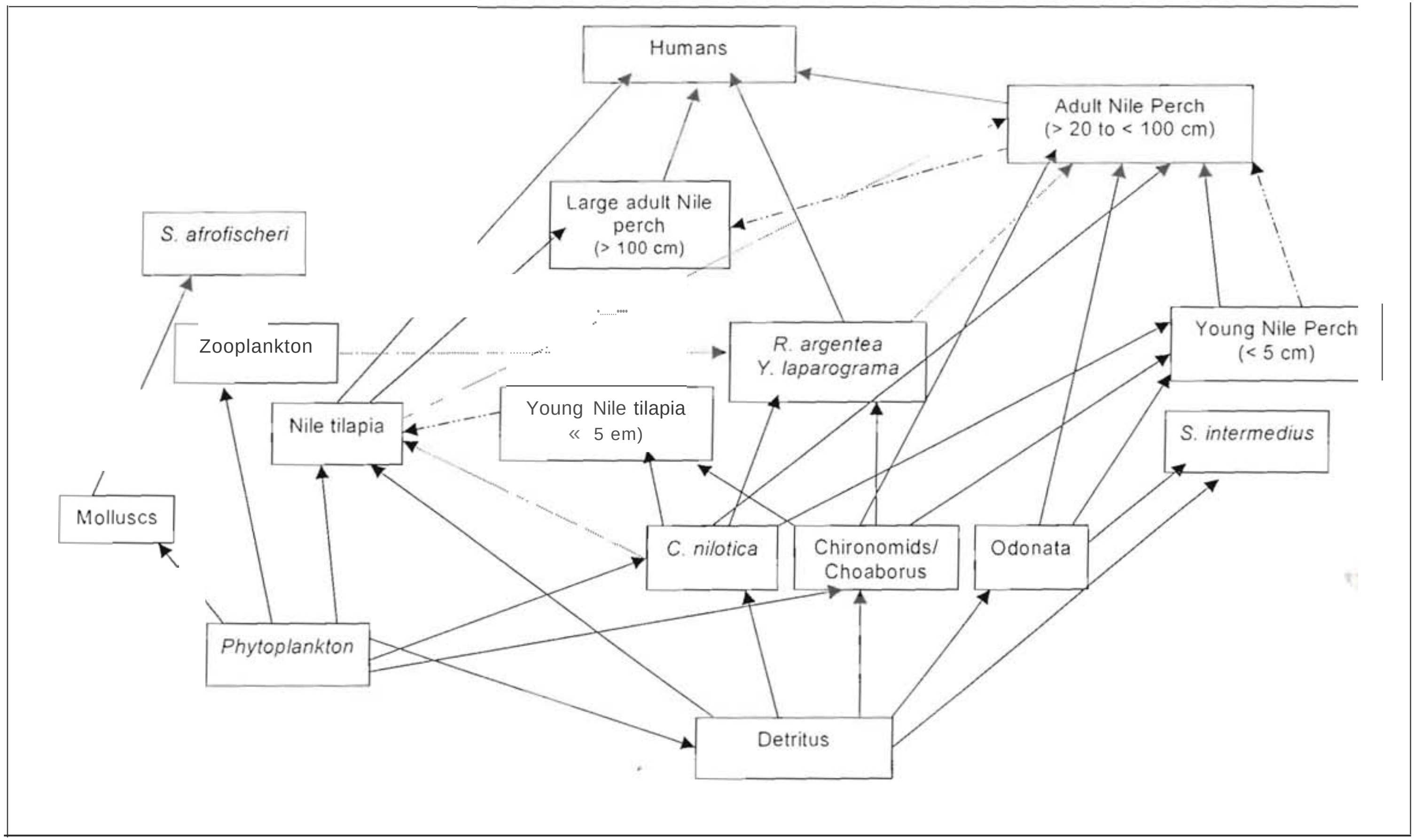

Fig. 5.2.2. A simplified food web of the pelagic Lake Victoria before Nile Perch introduction (Modified from Campbell *et al.* in *press).* Note the number of ecological niches that haplochromine species occupy. The dotted lines indicate that the fish occasionally includes that prey in its diet and the dot-dash lines indicate that the fish changes its diet as it grows.

Effects of fishing on trophic interactions and food webs

Currently humans make a dominant comp.onent of the Lake Victoria food web, and fisheries have the potential to further alter community structure and dynamics. The complex nature of fishing effects on ecosystems became entrenched in the environmental consciousness when it became clear that fishing could cause imbalances in the most basic of species interactions, predator/prey relationships. Like in many other aquatic bodies fishing down food webs occurs as the fishery concentrates on the top predators and subsequently more abundant prey species of these predators (Pauly *et al.,* 1998; Steele & Schumacher 2000). This decreases both structural and functional diversity of ecosystems, presumably also decreasing their resilience (Coleman & Williams 2002).

In Lake Victoria today, the dominant components of the fish community are Nile perch, Nile tilapia, and the pelagic *R. argentea* (Ogutu-Ohwayo 1994). The life history strategies of Nile tilapia and *R. argentea* allow their persistence. Nile tilapia is sympatric with the Nile Perch and appears resistant to predation due to its rapid growth and large adult size (>30 cm total length). From a socioeconomic perspective, the Lake Victoria fisheries are in a highly desirable state due to the high fish exports. However from a fisheries mahagement perspective, the current state is problematic. This is because regulatory policies are difficult to define as they require international agreements however, fish populations change more rapidly than the policy-making process, and regulations are difficult to implement due to the dispersion of fishing effort and responsibility for regulatory enforcement (Kitchell *et al., 1997).*

From an ecological perspective, the trophic system is now relatively simple. Increased nutrient loading fuels algal blooms., increasing the detritus base consumed by the extraordinary abundant *C. nilotica.* This prawn is the main prey of juvenile Nile perch, which is the primary prey of adult Nile perch. *R. argentea* grows rapidly on the increased abundance of large zooplankton and emerging insects (Kaufman & Cohen 1993, Campbell *et al.*, 2003.). Based on experiences in great lakes else where, this much-simplified ecosystem is unlikely to remain in its current state (Kaufman & Cohen 1993).

The fisheries of Lake Victoria have undergone massive changes in the past and are likely to change in the future. Environmental conditions are in flux (Mugidde 1993; Hecky *et a/.,1994),* fish populations and predator-prey interactions are changing rapidly (Ogutu-Ohwayo 1990a; 1994), and humans continue to become more efficient top predators in this ecosystem and their effects extend beyond the lake shores (Riedmiller 1994). Conserving the remnant species flock of haplochromines depends in many ways on the success of the Nile Perch fishery (Ribbink 1987; Kitchell *et al., 1997).*

Although restoration of Lake Victoria's biodiversity and its historical food web could be impossible, fisheries management can control exploitation in ways that should benefit both the people that depend on the Nile Perch fishery for their livelihood and those that are concerned with conserving and sustaining a diverse fish community (Bruton 1.990; Kitchell *et a/.,* 1997; Schindler *et a/., 1998).*

Conclusion

Trophic interactions and food webs have crucial implications for both community and ecosystem patterns and processes, such as the regulation of species diversity, energetic efficiencies and the biomass of trophic levels, community stability, contaminant levels in the biota and biogeochemical fluxes from ecosystems. Understanding of trophic interactions and food weds of aquatic systems is long over due and can be enhanced through accurate quantification of these processes through the complementary use of stable isotopes and dietary gut content analyses.