THE ROLE OF RESOURCE PARTITIONING AND SIZE STRUCTURE IN THE COEXISTENCE OF NILE PERCH (*Lates niloticus* Linnaeus 1758) AND HAPLOCHROMINE SPP., IN LAKE SARE, WESTERN KENYA

BY

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ABSTRACT

The disappearance of haplochromines in Lake Victoria has been attributed to, among other factors, predation by the introduced Nile perch, *Lates niloticus* (Linnaeus, 1758). Lake Sare a satellite lake with an open direct dispersal corridor to Lake Victoria exhibits a unique phenomenon of coexistence of Nile perch and haplochromines. Other satellite lakes: Kanyaboli and Namboyo of Lake Victoria are home to several endemic haplochromines but are free from Nile perch invasion. This study has investigated the current size structure of Lake Sare Nile perch to establish their impact on the haplochromine population and the role of resource partitioning between the two fishes in order to determine the factors that control their co-existence. Surveys were conducted and a total of 1317 fish specimens obtained including 375 haplochromines, 315 Nile perch and 627 specimens comprising mainly of *Brycinus* spp., Mormyrids, Synodontis spp., *Gambusia* sp. and tilapiines. Species diversity Shannon-Wiener Index (H'= 1.8429), species richness (d =1.2529) and evenness (J =0.8004) were relatively low. The Nile perch population was predominantly immature (85.7%); in contrast, the haplochromine population comprised about 60% mature stages. There was minimal dietary overlap between Nile perch and haplochromines as shown by similarity index of shared food categories; plant materials (0.6090) where intake in Nile perch was of insignificant quantity and probably resulted from incidental intake rather than deliberate feeding, insects (0.2102) and Molluscs (0.1238). Although haplochromines of Lake Sare do not have an absolute size refuge from Nile perch, most of the haplochromines' body depth measurements fall within the same range as most mouth gape measurements of Nile perch (range 12 mm to 45 mm) thus according partial size refuge to the former, leading to their coexistence. Generally, the physico-chemical parameters were uniform throughout the lake. However, secchi disc transparency was highest in the open water portion of the lake, whereas turbidity was highest where River Yala enters the lake. Lake Sare haplochromines could potentially be a source of seeds of resurgence in Lake Victoria as there is an open direct dispersal corridor between the two lakes.

CHAPTER ONE

INTRODUCTION

1.1 Background information

Lake Victoria with a surface area of 69,000 km^2, the largest tropical freshwater lake in the world, because of its economic importance and extremely high endemism, has aroused much interest in the scientific community. Lake Victoria was home to over 500 haplochromine cichlid species of which about 99% were endemic (Greenwood, 1974; 1981; Witte *et al.*, 1992). In 1970 haplochromine cichlids contributed 83% of fish biomass (Kudhongania and Cordone, 1974) but this decreased to less than 1% by mid 1980s (Ogutu-Ohwayo, 1990).

The haplochromines belong to the class Teleostei, order Perciformes, family Cichlidae with many genera. The adult haplochromine has a size range of between 5-25 cm standard length. They have one nostril on each side of the head, a continuous dorsal fin comprising of a spinous and a soft rayed part, possession of three or more spines on the anal fin, a lateral line consisting of two parts and are distinguished from the tilapiine cichlids by the scales on the flanks and caudal peduncle which are ctenoid and feel rough to the touch in contrast to that of tilapiines which are cycloid. Adult males, have brightly coloured egg dummies on the anal fin and lack the 'tilapia mark' (black spot) at the base of the dorsal fin which characterizes most juveniles tilapiine cichlids (Scully, 1975). Haplochromines have exceptional trophic diversity viz. detritivores, algae-grazers, plant eaters, molluscivores, zooplanktivores, insectivores, crab-eaters, piscivores, scale-eaters, parasite-eaters, and phytoplanktivores. The haplochromines occupy habitats from less than 1m to depths of 50 m.

The disappearance of haplochromines in Lake Victoria has been attributed to, among other factors, predation by Nile perch, *Lates niloticus* (Linnaeus, 1758), a piscivorous fish introduced into Lake Victoria in the 1950s (Ogutu-Ohwayo, 1990; Witte and van Oijen, 1990; Witte *et al.*, 1992).

Nile perch, a freshwater fish, which is native to many African lakes and rivers but introduced in Lake Victoria, belongs to the class Actinopterygii, order Perciformes, suborder Percoidei, family Latidae, genus *Lates* and species *niloticus*. A typical Nile perch is silver in colour with a blue tinge. It has a black eye with a bright yellow outer ring, two nostrils on each side of the head, a continuous lateral line, a large spine on the free edge of the operculum, a dorsal fin almost completely divided into two parts, an enlarged third dorsal spine and small ctenoid scales (Howells, 1992; Froese and Pauly, 2005). It grows to nearly 2 m in length and occupies habitats to depths of 60 m with sufficient oxygen (Witte *et al*., 1992; Ogutu-Ohwayo, 1994). A fierce predator that dominates its surroundings, Nile perch undergoes ontogenetic dietary shift during its juvenile period feeding on invertebrates at young stages and turning piscivorous as adult (Ogutu-Ohwayo, 1990; 1994; Mkumbo and Ligtvoet, 1992; Schofield and Chapman, 1999).Co-existence is the occurrence of more than one species in a community at the same time and place. In a seminal paper, The Paradox of the Plankton, Hutchinson (1961) observed that many different species of plankton co-exist on a relatively homogenous resource. This observation contrasts the classical competition theory (Hardin, 1960) which suggests that there is at most one consumer for every resource. Because of this paradox, Hutchinson's paper has been one of the major stimuli provoking research on co-existence.

Co-existence has been observed in many organisms both aquatic and terrestrial with as many varied mechanisms that promote it (Wilson, 1990; Siepielski and McPeek, 2010).

Determining the mechanisms that allow species to co-exist is important in understanding community ecology and for conserving biodiversity (Cameron *et al*., 2007). Understanding how each mechanism contributes to co-existence in a community allows for predictions on both the long term persistence of community members and the process that leads to extirpation of a given species (Chesson, 2000). The mechanisms that promote co-existence are widely varied and include habitat segregation, resource partitioning, non-linear competition, age structure, size structure and density-dependent biological interactions. Species can, therefore, co-exist in variable environments if they respond differently to differing conditions and can persist through unfavourable periods. For a fish community to persist over time, all species must be able, on average, to replace each other on a one-for- one basis over their lifetime, otherwise populations will be gradually lost and eventually the community will only consist of a few but most successful species (Gislason *et al.*, 2008). Periods of decline or increase are common in fish populations and stabilizing and equalizing mechanisms are important for long term persistence.

Biologists have long recognized that introduced species may have major effects on native communities. If an invading species occupies the same niche as a native species, strong interactions are likely to occur (Njiru *et al.*, 2005). The introduced species often causes imbalance in ecological systems as they lack natural enemies in these systems and as a result exhibit ecological release leading to increase in population (Cox and Ricklefs, 1977). However, in some habitats of Lake Victoria, especially in sub littoral waters, some of the haplochromines have survived, recovered, or co-existed with the Nile perch (Witte *et al.*, 2000; Ojwang *et al.*, 2010). The phenomenon of co-existence of Nile perch and the haplochromines seems to be exhibited in Lake Sare, a satellite lake that has a direct connection to Lake Victoria (Aloo, 2003). Many of the satellite lakes of Lake Victoria, which are known to harbour haplochromines, have not yet been invaded by Nile perch (Sibylle, 1994), as is the case in Lake Sare. The Lake Sare situation therefore raises the question as to how this predator and its known preferred prey (Ogutu-Ohwayo, 1990) have been able to inhabit this small satellite lake seemingly without adverse species diversity effects that occurred in Lake Victoria. There is, therefore, need to determine the factors that control the co-existence of Nile perch and haplochromines in Lake Sare. This study investigated the co-existence of Nile perch and the haplochromine species in Lake Sare, in order to determine the mechanisms for their co-existence.

1.2 Statement of the problem

The depletion of haplochromines and loss of biodiversity, which coincided with the Nile perch boom, is one of the negative ecological impacts that occurred in Lake Victoria. The reduction of species, trophic groups and alterations in food webs among other factors have resulted in increasing algal blooms and deoxygenation of the deeper waters of Lake Victoria and mass fish kills (Ochumba, 1990). Nile perch on the other hand has become an important commercial species in Lake Victoria and therefore need for its fishery to be sustained. Lake Sare, a satellite of Lake Victoria, however exhibits coexistence of Nile perch and haplochromines. Size structure as one axis that influences coexistence of species, knowledge of the size structure of a piscivorous fish in an ecosystem is essential in determining the vulnerability of its prey. A detailed size structure study on Lake Sare Nile perch with a view to determine their impact on the haplochromine population has not been undertaken in the recent times. The current size structure of Nile perch in Lake Sare therefore needs to be established and the diet of the two fishes in the lake re-examined to establish whether dietary overlap vis a vis resource partitioning are part of the many mechanisms facilitating species co-existence in Lake Sare. Food resource partitioning is a key factor in promoting fish co-existence because competition is reduced when diet overlap is low (Merona and Merona, 2004).

1.3 Justification

Lake Sare has been reported to support diverse fish species including Nile perch and the haplochromines that once inhabited Lake Victoria (Aloo, 2003; Abila *et al.*, 2008). Restoration of the haplochromines, which formed a complex community with incredible ecosystem functions or roles viz., grazing on organic matter and thereby reducing decomposition and oxygen depletion in the system, would contribute immensely towards efforts to improve the well being of the lake as well as the welfare of the riparian communities. The fact that Lake Sare, home to several relict population of Lake Victoria haplochromine species, has open corridor, allows the possibility of restocking Lake Victoria, with Lake Sare as the source of species resurgence. This is ostensibly possible through an integrated ecosystem approach aimed at reducing the amount of pollutants in Lake Victoria thus improving the environment and the hypothetical view that less perturbed ecosystem as in Lake Sare is fundamental to the co-existence of Nile perch and haplochromine species. There is, therefore, need to study the mechanisms responsible for the co-existence of Nile perch and haplochromines in Lake Sare as a means of gathering the necessary information for the sustainable management of Lake Victoria and its wetlands both for conservation and for sustainable fishery resources. The understanding of the scenario in Lake Sare would provide necessary empirical basis for formulation of ecosystem management and practices policy aimed at improving the biodiversity status of the greater Lake Victoria basin wetlands. Information gathered in this study may also make it possible to use Lake Sare as an *in-situ* conservation model and a natural laboratory for learning evolutionary processes, thereby providing tools for addressing biodiversity concerns within ecosystems.

1.4 Assumptions

This study was conducted with the following assumptions:

1. That the size structure of Nile perch influences its coexistence with the haplochromine species in Lake Sare..

2. That there is resource partitioning between Nile perch and the haplochromine species in Lake Sare that allows their coexistence.

3. That there is high species diversity in Lake Sare

1.5 Objectives

1.5.1 Overall objective

To determine the role of resource partitioning and size structure in the coexistence of Nile perch and the haplochromine species in Lake Sare.

1.5.2 Specific objectives

1. To determine the size structure of Nile perch and the haplochromines in Lake Sare
2. To determine the food habits and diet overlaps between Nile perch and the haplochromines in Lake Sare.
3. To determine species diversity and relative abundance in Lake Sare, as a way of establishing the prevailing fish biodiversity status of the lake.

CHAPTER TWO

LITERATURE REVIEW

2.1 Resource partitioning

One of the many mechanisms facilitating species co-existence is food resource partitioning, whereby co-existing consumer species reduce shared prey to avoid deleterious effects of competition (Zahorcsak *et al*., 2000). The food resource is partitioned in such a way that each species has sufficient access to ensure its survival and reproduction. Thus, co-existence is possible among species which use the same resources (Tilman, 1977). Resource partitioning is, therefore, a key factor in promoting fish co-existence because competition is reduced when diet overlap is low (Merona and Merona, 2004). Studies on sympatric species like the skates, *Psammobatis normani* and *P. rudis,* along the Argentine continental shelf have shown co-existence with no notable morphological differences between the species but rather diet segregation in terms of proportion (Mabragana and Giberto, 2007). Mabragana and Giberto (2007) have also suggested that greater availability of prey and the use of different prey proportions may reduce interspecific competition and thus promote co-existence. Generally, partial spatial segregation, differences in feeding behavior and good prey availability are reported to facilitate the co-existence of sympatric species (Platell *et a*l., 1998). Species that exhibit low dietary overlap have a better chance of co-existing in the same community (Merona and Merona, 2004), whereas specialist feeders that exhibit a low flexibility in their diet compared to generalists, tend to reduce their food intake rather than increase the niche breadth for co-existence. For example Carvalho and Goulding (1985) reported high consistency of, and reduction in the diets of *Hypophthalmus fimbriatus* and *H.perporosus* specialists planktivorous fish, under low plankton availability.

2.2 Morphological characteristics related to feeding

Patterns in the morphology of co-occurring species have been a popular means to characterize community organization (Bowers and Brown, 1982; Stevens and Willig, 1999), an important assumption being that the ability to detect, handle and process food is dependent on feeding morphology. Substantial evidence adduced by Brown and Lieberman (1973) and Stevens and Willig (1999), indicate that this is generally true. Indeed, Gatz (1979), Wikramanayake (1990), Hugueny and Pouilly (1999), and Wyckmans *et al*. (2006) agree that morphological features, specifically those related to the capture and intake of prey, evolve to maximize feeding performances, and there is a strong relationship between these morphological features and the diet in this respect. Individual species are adapted not only to feed on a specific component of the broader resource base, but also on food particles of a particular size. Because of the direct relationship between mouth width and prey size, food acquisition is a major axis along which co-occurring fish species are segregated; differences in trophic adaptations among species having the effect of feeding segregation, while differences in the diet of coexisting species reflecting underlying morphological diversity (Ross, 1986). Therefore, variations in morphology lead to variations in feeding success, thereby influencing species diet (Wainwright and Richard, 1995). Thus, although many species may co-habit the same area, dietary overlap between species could be low, leading to successful ecological co-existence. Numerous studies also show that lengths of predators and prey are positively correlated (Wysujack and Mehner, 2005; Domer *et al.*, 2007). Such studies, carried out in natural ecosystems, demonstrate strong correlations between the morphological features associated with feeding and diet. For example, Campbell *et al.* (2005) demonstrated the positive variation of the average cross sectional area of prey with the mouth area of the predator fishes in five co-existing Thai fish species, *Rasbora* *caudimaculata, Schistura desmotes, Dermogenys pusillus, Xenentodon cancila* and *Monopterus albus.* Abdel-Tawwab (2005) also reported increased predation efficiency with increase in size and mouth gape of the Catfish, *Clarias gariepinus* preying on Nile tilapia, *Oreochromis niloticus.*

2.3 Size structure

Size-structured competitive interactions have always been of interest to ecologists as they have been shown to have important dynamical consequences for intra and interspecific population interactions (Juanes and Conover, 1995). Competitive interactions are pervasive in nature and represent a major structuring force in ecological communities (Brown *et al.,* 1975; Stevens and Willig, 1999). Most if not all species pass through different size stages as their development progresses and as such, competition occurs not only within species but also within and between stages of different species. The influence of competition and other drivers of community structures such as predation and other population dynamics will thus depend on the relative sensitivity of the participating life stages to resource access and predation risk (Schmitz *et al.*, 1997; Chase *et al.*, 2002; Manderson *et al.*, 2004; Dmitriew and Rowe, 2005). Many animals including fishes also undergo shifts in habitat or prey preference at pivotal points during development (Juanes and Conover, 1995). Juveniles often do not compete with adults for resources.

McCann (1998) suggested that ontogenetically driven stage structure promotes co-existence, a suggestion that is supported by observations made on the larvae of the Caddis fly (Trichoptera; *Hydropsychid* species). Since larvae of this genus have similar ecological requirements, interspecific competition within co-existing members of the family would be expected. However, the co-existence of several species of this caddis fly family in the same habitat seems to be facilitated by temporal segregation in their life cycle as was demonstrated by Hildrew and Edington (1979), who reported the presence of *Hydropsyche pellucidula* and *H. siltalai* in the same microhabitat but at different times of their life cycles. Life cycle asynchrony, along with different life cycle lengths thus acts to promote co-existence.

2.4 Ecology of Nile perch and the haplochromine species in Lake Victoria

2.4.1 Nile perch

Nile perch is a freshwater fish widespread throughout Africa and is native to several African lakes and rivers. It is one of the largest freshwater fishes, reaching lengths of nearly two metres and weighing up to 200 kg (Ogutu-Ohwayo, 1994). Nile perch lives at a depth range between 0 m to 60 m (Witte *et al.*, 1992). They reach sexual maturity at between 60 cm and 80 cm total length (TL) when they are three or four years old (Ogutu-Ohwayo, 1994). At young stages the Nile perch feeds on invertebrates but turns to piscivorous feeding as it grows larger, exhibiting ontogenetic dietary shift during their juvenile period (Ogutu-Ohwayo, 1990; 1994; Mkumbo and Ligtvoet, 1992; Schofield and Chapman, 1999). Nile perch was introduced into Lake Victoria in the 1950s to feed on haplochromines and convert the small bony non-commercial haplochromines into a larger fish (Nile perch) of higher commercial value (Pringle, 2005). The population of Nile perch in Lake Victoria increased steadily over the years reaching peak values in the 1980s (Balirwa *et al.*, 2003). The Nyanza Gulf was the first place to register Nile perch boom in Lake Victoria in 1979 (Balirwa *et al.*, 2003). Initially in Lake Victoria the main diet of Nile perch was haplochromines but after the depletion of haplochromines, Nile perch diet shifted to the benthic shrimp *Caridina nilotica*, the pelagic cyprinid, *Rastrineobola argentea*, and its own juveniles (Kaufman, 1992; Ojwang *et al.*, 2010).

2.4.2 Haplochromines of Lake Victoria

The haplochromines of Lake Victoria belong to many trophic levels including detritivores, algae-grazers, plant eaters, molluscivores, zooplanktivores, insectivores, crab-eaters, piscivores, scale-eaters, parasite-eaters, and phytoplanktivores. Adult haplochromines sizes usually range between 5-25 cm standard lengths and all species are female mouth brooders. They occupy various habitats with depth ranges varying for different trophic groups, ranging between less than 1 m and 50 m. When the haplochromines were abundant there was high trophic diversity of fishes in Lake Victoria. Feeding by the different trophic groups played an important role in the flow of energy in the lake. During the mid 1980's major ecosystem changes started manifesting themselves in the lake. Algal blooms and mass fish kills became frequent (Ochumba, 1990). The depletion of the complex haplochromine community and changes in zooplankton reduced grazing pressure leaving much of the organic matter unconsumed. Decomposition of this organic matter depleted the water column of oxygen and led to anoxia. During the 1960s anoxia was infrequent in Lake Victoria and present only near the vicinity of the bottom sediments (Talling, 1966), but by 1990s anoxia was being recorded in shallower waters to 45 m (Hecky, 1993).

2.5 Relationship between Nile perch and haplochromines in Lake Victoria

Historically, Lake Victoria and its satellite lakes were predominantly rich fish fauna comprising of several hundred species of cichlids (Kaufman *et al*., 1997). However, in the 1950s the predatory Nile perch was introduced into Lake Victoria and, thereafter, the endemic haplochromine species disappeared (Ogutu-Ohwayo, 1990). Prior to the current ecological changes, intense fishing and introduction of exotic species, the Lake Victoria ecosystem was able to counteract perturbation (Ogutu-Ohwayo, 1990).

Phytoplanktivorous and detrivorous haplochromines constituted the highest number of species and biomass in Lake Victoria and were able to crop and digest algae thus maintaining a healthy lake ecosystem (Goldschmidt *et al.*, 1993). Predation by Nile perch led to the decline of haplochromines and by late 1980s haplochromines could no longer be caught in trawls at 8 – 50 m depth where formerly they were numerous (Witte *et al.*, 1992). During the Nile perch boom, which lasted up to early 1980s haplochromines were the main preys in Nile perch diet whereas between late 1980s and early 1990s haplochromines became rare in Nile perch diet (Mkumbo and Ligtvoet, 1992). In the period between 1997 and 2010 haplochromines again became more prominent in Nile perch diet (Njiru *et al.*, 2005; Njiru *et al.*, 2012).

Studies in Lake Victoria and its satellite lakes suggest that wetlands and rocky habitats play a crucial role in predator-prey interactions between the predatory Nile perch and the haplochromine species (Chapman *et el.*, 1996). From experimental work on Lake Victoria cichlids, the prey fish, haplochromine species, showed high levels of hypoxia tolerance and were thus able to seek refuge in wetlands which are less accessible to the less tolerant predator species Nile perch (Chapman *et al.*, 1995). The hypoxic conditions in wetlands created by thick mats of *Cyperus papyrus* also act as barriers to the dispersal of Nile perch (Chapman *et al.*, 1996, 2002; Schofield and Chapman, 2000). The satellite lakes of Lake Victoria, which are recognized as important biodiversity hotspots have also served as important refugia to haplochromines (Ojwang *et al.*, 2010). A study by Abila *et al.*, (2008) on the haplochromines of Lake Kanyaboli using mitochondrial DNA molecular markers, revealed high genetic distinctiveness, setting the satellite lake apart as a genetic reservoir of biodiversity.

The invasion of the lake by water hyacinth, *Eichhornia crassipes* has also increased hypoxic conditions providing further refuge to haplochromines (Njiru *et al.*, 2002: Aloo *et al*., 2013). The well oxygenated rocky shores and offshore rocky habitats may also serve as important refugia because of their structural complexity (Seehausen *et al*., 1997).

2.6 Methods of sex and maturity stage determination in fish

Different methods have been employed for sex and maturity stage determinations, among them the method of macroscopic staging and that of Gonadosomatic Index (GSI). Macroscopic staging involves determination of gonad maturity of fish on the basis of morphological appearance of gonads following the standards laid down by International Council for Exploration of the Sea (I.C.E.S) (Lovern and Wood, 1937), whereas GSI (Bagenal, 1971) uses gonad weight to somatic weight ratio to determine maturity stages of fish. Since the publication of the international standards, modifications have been made by researchers to suit the fishes they study (Bagenal, 1957; Holt, 1959; Raja, 1964; Hopson, 1972). However, as Morrison (1990) and Rideout *et al*., (2000) rightly observe, misclassifications may occur due to the subjectivity of the procedures, but with a detailed descriptive guide accurate macroscopic staging of gonads can be achieved. Gonadosomatic Index (GSI) on its own is difficult to use in predicting fish maturity but is often used to confirm the gonad maturity stages when developing a standard coding schedule and in growth and survival studies for estimations of natural mortality (Gunderson, 1997). Gonadosomatic Index (GSI) has often been used in reproductive biology studies of fishes to determine the spawning period, where peak values of GSI are indicative of the spawning period (Hoda and Qureshi, 1989). For GSI values to have meaning, comparisons have to be made with pre-determined standard values in use for the fish species population and each maturity stage, since it is inappropriate to compare GSI values across populations (de Vlamming *et al*., 1982). Relationship between gonad weight and body size may also change with development (de Vlamming *et al*., 1982, Hunter and Macewicz, 1985; West, 1990). Larger fish may have higher GSI values than smaller fish at the same maturity stage creating biasness when comparing GSI values for fish of different sizes (Hunter and Macewicz 1985; West, 1990).

CHAPTER THREE

MATERIALS AND METHODS

3.1 Study area

Lake Sare is located within the Yala swamp complex at 0° 02' 25"S; 034° 03' 42"E and an altitude of 1140 m above sea level (Fig. 1). It is about 5 km^2 in area and 5 m deep at its centre. The lake is surrounded by papyrus swamps which merge with the main Yala swamp. The lake used to be a gulf of Lake Victoria before it was separated by a culvert. Lake Sare, and lakes, Kanyaboli and Namboyo, are the three main satellite lakes of the Lake Victoria Nyanza basin, and are considered refugia to remnants of fish species that had disappeared from Lake Victoria (Aloo, 2003; Abila *et al.*, 2008: Aloo *et al.*, 2013).

3.2 Sampling

Samples of haplochromine species (Appendix I) and Nile perch (Appendix II) were collected at three different sites in Lake Sare once every month for a period of twelve months beginning September 2010 to August 2011. The sampling sites (Fig. 2) were located at the Goye causeway, the connection of Lake Sare with Lake Victoria (Station 1), at the open portion of the lake (Station 2), and one site at the shoreline where swamp water from river Yala enters into Lake Sare (Station 3). The choice of sampling sites was made such as to detect any variations in the samples collected along a gradient from close to Lake Victoria to the open portion of Lake Sare, as well as the influence of River Yala and the Yala swamp. To collect the fish samples, a passive monofilament net with eight mesh sizes; 1.25, 1.75, 2.00, 2.50, 3.25, 4.00, 5.00 and 5.75 inches, was set parallel to the shoreline overnight for twelve hours. The use of different mesh sizes was to enable assessment of mesh size catches as well as inshore and offshore movement of the fish species. Additional fish samples were purchased from randomly selected fishermen at the lake.

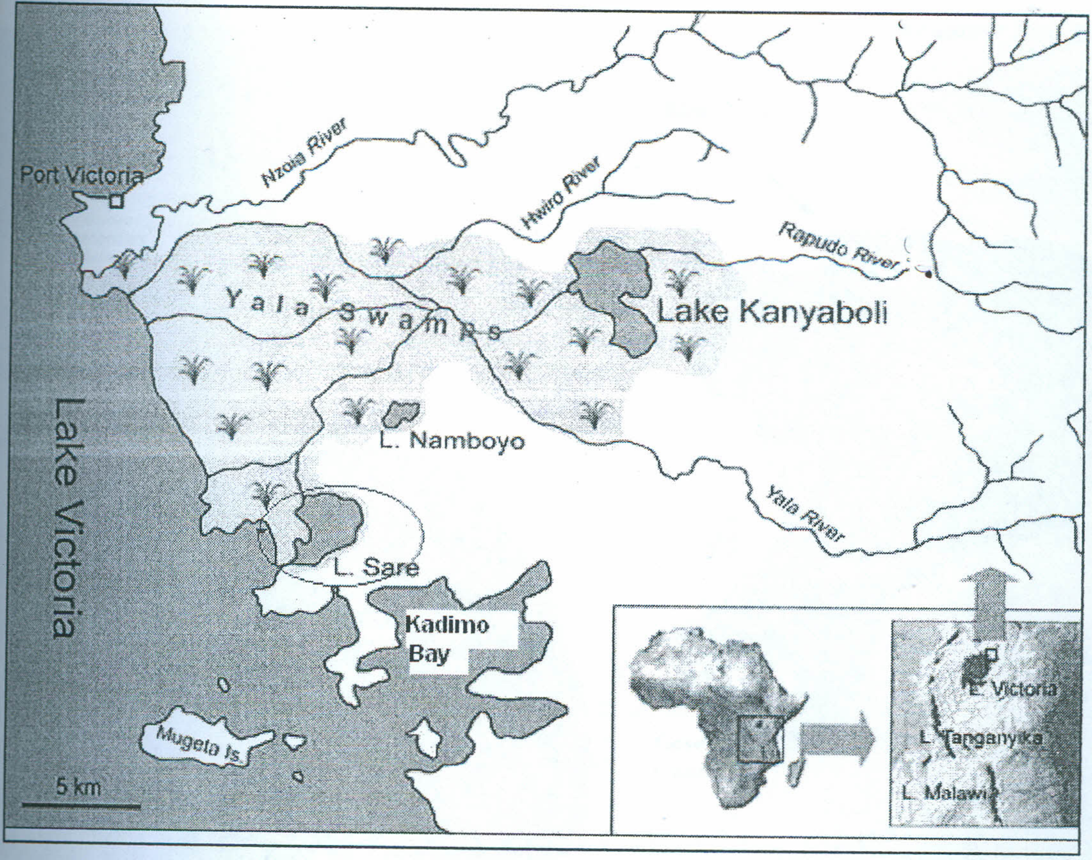

Figure 1: Map of Yala Swamp showing the location of Lake Sare where the present study was conducted. (Source: modified from Abila *et al*., 2008).

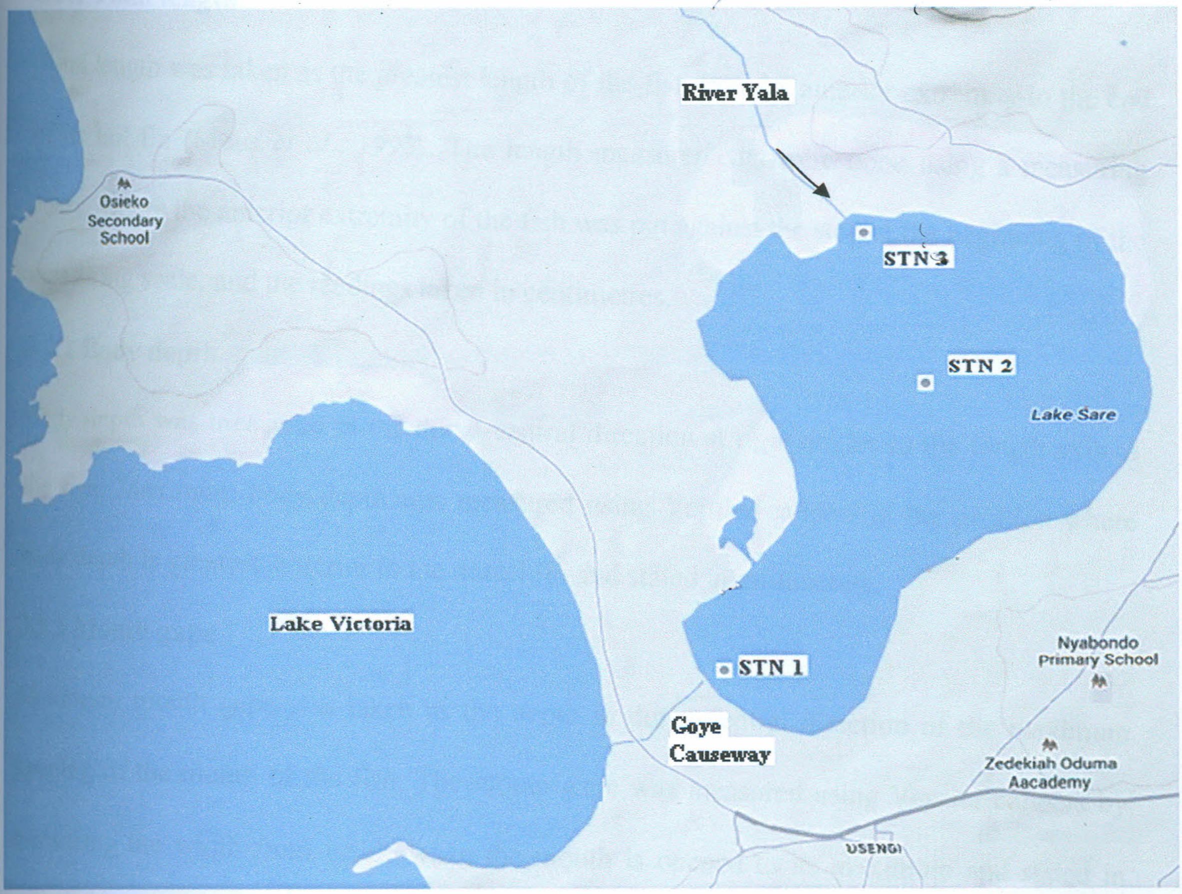

Figure 2: Map of Lake Sare showing the locations of the Sampling sites (Source: Google Maps, 2013). (➝) Arrow indicates direction of flow of River Yala

3.3 Morphometric measurements

The ratio of predator length to prey length is a good predictor of predation success (Evans, 1976). Establishing the relationship between length and body depth together with the establishment of the relationship between length and mouth gape of fish allows for the potential size ranges of their prey to be determined (Nilsson and Bronmark, 2000; Scharf *et al.,* 2002). Each fish specimen was given an identification number and the following measurements taken; Total Length (TL), Maximum Body Depth (BD), mouth gape (MG) and weight.

3.3.1 Total length

Total length was taken as the greatest length of the fish from its anterior extremity to the end of its tail fin (Mous *et al*., 1995). The length measurements were done using a measuring board, where the anterior extremity of the fish was put against the stop at the beginning of the measuring scale, and the readings taken in centimetres.

3.3.2 Body depth

Body depth was measured in the dorso-ventral direction at right angles to the length axis of the fish. Maximum body depth was measured using Vernier calipers at the position where body depth is greatest, anterior to the dorsal fin and stated in millimeters.

3.3.3 Mouth gape

Maximum mouth gape was taken as the depth in dorso-ventral direction of the maximum opening of the mouth of the fish. The mouth gape was measured using Vernier calipers by measuring the width from inside when the mouth is opened to its maximum and stated in millimeters.

3.3.4 Weight measurements

Fresh weights of individual fishes were measured using a sensitive weighing balance EJB series, Endel Global Weighing company, capable of weighing up to 6 kg with a sensitivity of 0.1 g.

3.3.5 Sex determination

The Nile perch and haplochromine specimens were cut open along their ventral axis for internal examination for sex and stage of maturity. Examination of the gonads was done following the macroscopic maturity stage coding by Hopson (1972) (Tables 1 and 2) to determine the sex and maturity stages of the specimens. For this study the method of macroscopic staging was preferred as the haplochromines belong to different species and the data used for the staging were pooled data.

Table 1: Coding of maturity stages of male and female Nile perch (After Hopson, 1972)

Males	**Females**
M1. Immature: Testes appear as a pair of thin transparent strands running longitudinally along the dorsal wall of the body cavity; sexes indistinguishable macroscopically	F1. Immature: Appearance of ovaries like testes; sexes indistinguishable macroscopically
M2. Early developing: Testes transparent grayish-white occasionally pinkish; narrow and flattened.	F2. Resting: Ovary grayish-white, white or pinkish; transparent, smooth and cylindrical; circular in transverse section; eggs not visible macroscopically; only slightly vascularized
M3. Late developing: Testes semi-transparent, grayish-white or pinkish; often well vascularized; more or less flattened in transverse section: no milt	F3. Early maturing: Ovary pinkish or reddish, semi-transparent; pear-shaped in section; eggs not visible macroscopically; tissue well vascularized
M4. Mature/resting: Testes opaque, whitish or pinkish; often well vascularized; firm, triangular in section; slight milt exudes from lumen when cut	F4. Late maturing: Ovary pinkish or reddish with small opaque yolky ova clearly visible; pear-shaped in section.
M5. Mature/ripe: Testes opaque, ivory white or pinkish; soft; triangular in section; lying in the longitudinal groove on ventral surface; copious milt when cut	F5. Ripe: Ovary yellowish-buff, opaque due to presence of large yolky ova clearly visible through superficial membrane; pear-shaped in section; large blood vessel on surface
M6. Ripe/running: Similar in appearance to stage M5 but milt running freely from vent when slight external pressure applied to fish	F6. Running: Ova yellowish-brown in colour; oil globule present; slight external pressure causes ripe ova to be extruded from vent
	F7. Spent: Ovaries loose and flabby containing torn follicular tissue rich in blood with a few residual stage F5 ova

Table 2: Coding of maturity stages of male and female haplochromines (after Witte and van Densen, 1995)

Males	**Females**
M1. Immature: A pair of thin transparent strands running longitudinally along the median of the dorsal wall of the body cavity; sexes indistinguishable macroscopically	F1. Immature: Appearance like testes; sexes indistinguishable macroscopically
M2. Early developing; Strands start to thicken; testes are whitish- yellow	F2. Early developing: Ovaries recognized by small whitish dots(eggs);caudal part of ovaries more thickened than the rostral part
M3. Developing: Testes are pinkish-reddish and sideways flattened	F3. Developing or recovering: Eggs developing inside the ovaries, unequal in size
M4. Early ripening: Testes thick and straight, increasing in volume. When cut and squeezed milt comes out	F4. Early ripening: Eggs equal in size but not fully grown; all colored yellow
M5. Ripe: Testes thick and straight; When cut and waterish-white milt comes out	F5. Ripe: Eggs large and ovaries visible from the ventral side of the cavity
M6. Late ripe: Testes thick and often curled or lobed, white in colour. When cut milt comes out	F6. Spent: Eggs or juveniles in buccal cavity; ovaries recovering, thin and reddish; eggs unequal in size, often including a few residual stage F5 eggs

3.4 Diet determination

3.4.1 Stomach fullness

The stomachs of the fish specimens were removed and visually assessed, and the degree of fullness determined using a subjective scale of scores (Table 3), ranging from empty (0) to full stomach (10), following the method of Hynes (1950) (cited in Hyslop, 1980). Each stomach was then labeled with the identification number of the specimen it was dissected from and preserved in vials with 5% neutral buffered formalin for further analysis.

Table 3: Criteria for determining the stomach fullness index (adopted from Hynes, 1950) (as used in Hyslop, 1980)

Criteria	Fullness index
Level 1: stomach completely empty	0
Level 2: very little food present; stomach fills to less than ¼ (between 1-25% full) when pressed from anterior to distal end	2.5
Level 3: half full; stomach fills to about one half (between 26-50%) when pressed from anterior to distal end	5
Level 4: stomach nearly full but wall not bulging; food fills to about ¾ (between 51-75%) when pressed from anterior to distal end	7.5
Level 5: stomach fully distended with food from anterior to posterior end (between 76-100%)-	10

3.4.2 Food composition

Each of the preserved fish stomachs was cut open and the contents emptied into a Petri dish, mixed with water to form a homogenous mixture and examined under a stereo microscope, mgx50. Food items from individual stomach specimens were then sorted into diet categories. Each food category in the stomach was quantified using a modified version of the Points method (Hynes, 1950) (cited in Hyslop, 1980) with points ranging from 1 to 10. The area occupied by each food item was determined from the field of view and estimated to the nearest 10% according to how much it contributes to the amount of food found in the stomach. 10 points was allocated to a food item occupying the whole stomach contents while 1 point was allocated to a food item occupying 10% of the stomach contents.

3.5 Physicochemical parameters of Lake Sare

3.5.1 Dissolved Oxygen

Dissolved oxygen which refers to the amount of oxygen dissolved in a unit volume of water was measured *in-situ* using a submersible multiparameter data logger, XR-420/620 RBR Europe LTD, UK and stated in milligrams per litre (mg/L).

3.5.2 Temperature

Temperature measurement was done *in-situ* using a submersible multiparameter data logger, XR-420/620 RBR Europe LTD, UK and stated in degrees Celsius (^{o} C).

3.5.3 Secchi disc transparency

Secchi disc transparency was measured using a Secchi disc of diameter 30 cm. The Secchi disc visibility depth in metres was recorded as the greatest depth at which the white parts were visible.

3.5.4 Conductivity

Conductivity, a measurement of the ability of water to conduct an electrical current due to the presence of ions or mineralization or Total Dissolved Solids, was measured in-situ using the submersible multiparameter data logger, XR-420/620 RBR Europe LTD, UK, and stated in milli-Siemens per centimetre (mS/cm). Conductivity is a good indicator of the amount of nutrients that enter into the lake.

3.5.5 pH

pH, a quantitative measure of hydrogen ions concentrations in water that describes the acidity or alkalinity of the water, was measured *in-situ* using the same submersible multiparameter data logger, XR-420/620 RBR Europe LTD, UK.

3.5.6 Turbidity

Turbidity, a measure of relative clarity, measures the optical property of water by measuring the amount of light scattered by suspended solids in the water. The submersible multiparameter data logger, XR-420/620 RBR Europe LTD, UK, was used to measure turbidity as an indication of Total Suspended Solids based on Nephelometric Turbidity Units (NTU) (EPA method 180.1, 1993).

3.5.7 Alkalinity

Alkalinity, a measure of the buffering capacity of water, which is its ability to resist change in pH is important in determining the ability of the lake to neutralize acidic pollution from rainfall or wastewater. Alkalinity was measured by titration with an acid using methyl red indicator and stated in mg/l (APHA, 1989).

3.5.8 Total Suspended Solids

Total suspended solids (TSS), refers to the quantitative measure of solids of organic and inorganic origin held in suspension in water. A gravimetric analysis involving weights and using glass-fibre filters with units of measurement in mg/l was employed (APHA, 1989).

3.5.9 Total Dissolved Solids

Total dissolved solids (TDS) refer to a measure of all inorganic solids dissolved in the water. This means that it measures ions that contribute to water hardness, like calcium, but also those that do not, like sodium. The TDS measurement is a better reflection of the total mineral content of the water rather than a water hardness measurement. TDS was measured using gravimetric analysis (APHA, 1989) involving weights and expressed in mg/l.

3.5.10 Hardness

Water hardness is the measurement of the amount of divalent cations dissolved in the water and is related to total dissolved solids. The more divalent cations dissolved in the water the "harder" the water. Generally the most common divalent cations are calcium and magnesium;

however other divalent cations may contribute including iron, strontium, aluminium, and manganese. Typically the other divalent cations contribute little or no appreciable additions to the water hardness measurement. Hardness was determined using EDTA Titrimetric method: Calcium and magnesium ions in the sample are sequestered upon the addition of disodium ethylenediamine tetraacetate (Na_2 EDTA). The end point of the reaction is detected by means of Eriochrome Black T indicator, which has a red color in the presence of calcium and magnesium and a blue color when the cations are sequestered and expressed in mg/l (APHA, 1989).

3.5.11 Salinity

Salinity is the amount of dissolved salt in water, usually sodium chloride or salts of alkali metals. Salinity was measured *in-situ* using the submersible multiparameter data logger, XR-420/620 RBR Europe LTD, UK, and recorded as weight in grams / kg of water (ppt.)

3.6 Data analysis

3.6.1 Community dynamics

Species composition and relative abundance were estimated from percentage contribution by the number of each species captured in the sampling stations. Species diversity was determined based on the number of species present in the sampling stations following the Shannon-Wiener Index (Maguran, 1988).

Shannon-Wiener Index: $H = -\sum pi \ln pi$, where,

H is the diversity index, ln is the natural logarithm, i is an index number for each species present in a sample, and pi is the number of individuals within a species (ni) divided by the total number of individuals (N) present in the entire sample.

Species richness and evenness was assessed following the index methods developed by Maguran (1988)

Species richness, $d = (S-1) / \ln N$, where, S is the number of species and N is the number of individuals in the sample.

Evenness index, $J = H / \ln S$, where,

H is the Shannon-Wierner index for the sample and S is the number of species recorded in the sample.

3.6.2 Diet analysis

3.6.2.1 Frequency of occurrence

Frequency of occurrence of a food item was determined by the number of stomachs of each species in which the food item occurred and expressed as a percentage of the sum total of non- empty stomachs, using the formula by Hynes (1950) (cited in Hyslop 1980) below:

Frequency of occurrence, $F_i = 100\, n_i / n$, where,

F_i = frequency of occurrence of the i^{th} food item in the sample, n_i = number of stomachs in which the i^{th} food item is found and n = the total number of stomachs with food in the sample.

3.6.2.2 Relative abundance

Relative abundance was calculated by the sum of the points awarded to a food item expressed as a percentage of the total points for all foods ingested by a particular species. Each food category in the stomach was quantified using a modified version of the Points method (Hynes, 1950) (cited in Hyslop, 1980) with points ranging from 0 to 10. The area occupied by each food item was determined from the field of view and estimated to the nearest 10% according to how much it contributes to the amount of food found in the stomach. 10 points was allocated to a food item occupying the whole stomach contents while 1 point was allocated to a food item occupying 10% of the stomach contents.

3.6.2.3 Prominence value

Prominence values were estimated using relative abundance and percentage occurrence to show the relative importance of each food item consumed (Prominence Value = Relative Abundance x Frequency of Occurrence; Hyslop, 1980; Abila *et al.*, 2008; Abila, 2011).

The Prominence Values were then used to determine the coefficient of similarity of the food items ingested by the two fishes, Nile perch and the haplochromines as follows:

$C = 2 \times PV(\text{low}) / PVN1 + PVN2$ where;

C is the coefficient of similarity index, PV (low) is the value of the lower prominence values calculated for each of the food items taken in common by the two species to be compared and PVN1 and PVN2 are the prominence values of each food item for the species 1and 2 respectively; C ranges between 0 and 1, where 0 shows no sharing of the food item between the two species being compared and 1 shows total food overlap.

3.6.3 Morphometric Relationships

3.6.3.1 Length - Frequency distributions

Length - frequency distributions were used to show the structure of the fish stock. The lengths were grouped into size classes and presented as histograms.

3.6.3.2 Fish Condition Factor

Condition Factor is an indication of the physiological state or well-being of a fish, the heavier a fish is for a given length, the higher its condition factor (K) (Ricker, 1975). Fulton's coefficient of condition (K) (Lagler, 1956) was computed for the species and gonad maturity stages as follows:

$K = W/L^3$, where K = Condition Factor; W = weight; L = Total length.

3.6.3.3 Correlation analysis

Correlation analyses between the following measurements were performed to determine the percent predation vulnerability of the haplochromines; total length and mouth gape, total length and body depth, total length and weight.

3.6.4 Statistical Tests

Mean values for each parameter studied was calculated for Nile perch and the haplochromines and the students' *t*-test was used to determine significant differences between the sexes and gonad maturity stages of the two fishes, whereas regression analysis was used to determine the relationship between fish length and their mouth gapes. Maximum mouth gape size of Nile perch was compared to maximal body depth of the haplochromines to determine the percent predation vulnerability of the haplochromine population in the Lake.

CHAPTER FOUR

RESULTS

4.1 Species composition

A total of 1317 fish specimens were examined during the study period of which 1218 were obtained from gillnet catches in Lake Sare and 99 specimens randomly purchased from fishermen working at the lake. Only specimens obtained from the set gillnets were used in calculation of fish species relative abundance (size, maturity and diet analysis included the purchased specimens) as the method used by the fishermen could have been selective. At 24.4% relative abundance of the total catch the haplochromines were the most abundant followed by Nile perch (24.1%) and *Brycinus species* (21.9%). Mormyridae, majorly *Gnathonemus longibarbis,* comprised 15.1%, tilapiines (4.7%), *Synodontis* spp. (3.7%), *Gambusia affinis* (2.7%) while 3.4% of the total catch was made up of other fish species (Table 4). Nile perch, haplochromines, *Brycinus* species, *G. longibarbis* and tilapiines were found in all the three study sites while *Synodontis* spp. was found in stations 1 and 3. *Gambusia affinis* was found only in station 2. All the Nile perch and haplochromine specimens from the three stations, as well as the purchased specimens were pooled for analysis of size, maturity and diet.

4.2 Size structure and maturity

The maturity stages of Nile perch and haplochromines in Lake Sare during the study are given in Table 5, whereas Table 6 shows the gonad maturity stages and Fulton's coefficient of condition for the two fishes during the same period. 85.7% of the Nile perch population in the lake comprised mainly of immature stages up to the male maturity stage 2 and female maturity stage 3 (Hopson, 1972; Table 1). Male maturity stages 3 to 6 and female maturity stages 5 to 7 were not encountered. In contrast, the haplochromines population comprised about 60% mature stages of fish (Tables 2, 5 & 6).

Table 4: Relative abundance (%) of fish species in Lake Sare during the period September 2010 to August 2011.

Species name	Station 1 N = 513	Station 2 N = 357	Station 3 N = 348	Pooled N = 1218
Nile perch	14.6	22.7	39.7	24.1
Haplochromines	16.4	45.4	14.7	24.4
Brycinus spp.	36.3	7.6	15.5	21.9
Gnathonemus longibarbis	25.7	3.4	2.6	12.6
Other mormyrids	1.8	2.5	3.5	2.5
Synodontis spp.	3.5	0.00	7.8	3.7
Gambusia affinis	0.00	9.2	0.00	2.7
Tilapiines	1.2	3.4	11.2	4.7
Other fish species	0.5	5.8	5.0	3.4
Total %	100	100	100	100

Relative Abundance = (n/N) x100 where n is frequency of a particular fish in a station and N is total catch per station.

Table 5: Maturity stages of Nile perch and haplochromines in Lake Sare during the period September 2010 to August 2011.

	Relative abundance (%) of fish maturity stage	
Maturity stage	Nile perch N = 315	Haplochromines N = 375
IMMATURE (M1andF1)	85.7	40.0
M2	3.8	1.6
M3	0.0	12.8
M4	0.9	14.4
M5	0.0	12.8
M6	0.0	5.6
F2	7.6	0.0
F3	1.0	3.2
F4	1.0	0.8
F5	0.0	8.0
F6	0.0	0.8

M1-male maturity stage 1 to M6-male maturity stage 6

F1-female maturity stage 1 to F6-female maturity stage 6

Table 6: Condition Factor and maturity stages of haplochromines and Nile perch in Lake Sare during the period September 2010 to August 2011

	Haplochromines	Nile perch
MATURITY STAGE	CONDITION FACTOR (K)	CONDITION FACTOR (K)
IMMATURE (M1 and F1)	0.0151876	0.0112718
M2	0.0148907	0.0116529
M3	0.0159519	*
M4	0.0166651	0.0083163
M5	0.0150433	*
M6	0.0165659	*
F3	0.0142012	0.0104159
F4	0.0156797	0.0106985
F5	0.0167383	0.0093218
F6	0.0176729	*
Average	0.0124186	0.0102795

M1 - male maturity stage 1 to M6-male maturity stage 6

F1 - female maturity stage 1 to F6-female maturity stage 6

* Maturity stage not encountered during the study

4.3 Community dynamics

Sampling station 3 had the highest values of the Shannon-Wiener Index (H' = 1.8222) and species richness index (d = 1.3670) (Table 7). However, these figures did not reflect any significant differences in fish species diversity and richness from the other two sites. The least values for these indices (H' = 1.5647; d = 1.1217) were recorded in Station 1. Meanwhile, Station 2 had the highest value of the Evenness Index (J = 0.7683) and Station 3 the least (J = 0.6293). Species diversity as indicated by Shannon-Wiener Index and the species richness and evenness Index were relatively low due to over representation by four fishes, Nile perch, haplochromines, *Brycinus* spp., and *Gnathonemus longibarbis,* while the other species had very low abundance.

Table 7: Fish species diversity, richness and evenness in Lake Sare

	Shannon-Wiener Index (H')	Species richness Index (d)	Evenness index (J)
Pooled	1.8429	1.2529	0.8004
Station 1	1.5647	1.1217	0.7525
Station 2	1.5977	1.1909	0.7683
Station 3	1.8222	1.3670	0.6293

4.4 Diet analysis

4.4.1 Composition of diet

The stomach fullness indices for Nile perch and haplochromines in Lake Sare during the study are given in Table 8, whereas Table 9 show the frequency of occurrence, relative abundance and prominence values of the food categories present in the stomachs of the two fishes during the same period. The food items taken by Nile perch and the haplochromines were categorised as the shrimp *Caridina nilotica*, fish remains, plant material and insects including Odonata, Coleoptera, Ephemeroptera, chironomids and other unidentified insects, and molluscs, detritus, algae and zooplankton. In the Nile perch the main food categories taken as shown by the frequency of occurrence were fish remains which were present in 57% of the stomachs examined and *C. nilotica* present in 55% of the stomachs. The other food categories present had very low frequency of occurrences with some categories like the Coleoptera, Ephemeroptera, algae, detritus, zooplankton and chironomids completely lacking. In the haplochromines the food categories with high frequencies of occurrence were algae, occurring in 45% of the stomachs examined, and detritus in 39% of the stomachs. This was followed by chironomids (23%), zooplankton (14%), Coleoptera (14%) and other unidentified insects (11%). Molluscs comprised 11% of haplochromine diet while Ephemeroptera and plant material had low occurrences. Fish remains, *C. nilotica* and Odonata did not occur in the haplochromines.

The importance of the food items taken, indicated by their relative abundance, revealed that in the Nile perch high amount of food taken comprised of fish remains (50%) and *C. nilotica* (41%). Odonata, molluscs, plant materials and other unidentified insects made up only a total of 9% of the food taken by Nile perch, with each of these food items consumed in very low quantities. The haplochromines had a broader resource base compared to Nile perch. The highest amount of food taken by the haplochromines were algae (21%) and detritus (21%)

while chironomids, coleopterans, molluscs, zooplankton, other unidentified insects and plant materials were consumed in lower quantities. Only three food categories, plant materials, molluscs and insects were shared between Nile perch and the haplochromines.

The Coefficient of similarity index is used to show feeding overlaps between species, where the value 0 means no feeding overlap and the value 1 shows total feeding overlap in the shared food item. Of the three shared food categories between Nile perch and the haplochromines, plant materials, with a coefficient of similarity index value of 0.6090 was the highest followed by insects with an index of 0.2102 (Table 10). Molluscs had the lowest index value of 0.1238. The analysis indicates minimal dietary overlap between the Nile perch and the haplochromines, with plant materials being the most shared food category, followed by insects and molluscs.

Table 8: Stomach fullness indices for Nile perch and haplochromines in Lake Sare

Fullness Index	(%) of examined stomachs	
	Nile perch	Haplochromines
0	32.4	45.6
2.5	18.1	25.6
5.0	17.2	12.8
7.5	15.2	4
10	17.1	12

Table 9: Dietary composition of Lake Sare Nile perch and haplochromines expressed as percentage Frequency of Occurrence (FO), Relative Abundance (RA) and Prominence Values (PV)

	Nile perch			Haplochromines		
Food category	FO (%)	RA (%)	PV	FO (%)	RA (%)	PV
Fish	56.6	49.8	2820.5	0	0	0
Caridina nilotica	55.3	41.2	2278.4	0	0	0
Odonata	4.0	3.5	13.7	0	0	0
Plant materials	9.2	0.8	7.0	4.6	3.5	16
Molluscs	4.0	1.8	7.1	10.8	10.1	108.3
Other unidentified insects	2.6	2.9	7.5	10.8	6	64.3
Ephemeroptera	0	0	0	6.1	6.3	38.7
Algae	0	0	0	44.6	21.4	954
Detritus	0	0	0	38.5	20.8	798.0
Zooplankton	0	0	0	13.8	7.1	98.1
Chironomids	0	0	0	23.1	14.3	330.3
Coleoptera	0	0	0	13.9	10.7	148.1

Table 10: Trophic relationships between Nile perch and the haplochromines in Lake Sare

Food category	Co-efficient of similarity Index (C)
Caridina nilotica	0.0000
Fish	0.0000
Plant materials	0.6090
Molluscs	0.1238
Other unidentified insects	0.2102
Odonata	0.0000
Coleoptera	0.0000
Ephemeroptera	0.0000
Algae	0.0000
Detritus	0.0000
Zooplankton	0.0000
Chironomids	0.0000

4.5 Length - Frequency distributions

Tables11-12 and figures 3-10 show the morphometric characteristics and length-frequency distributions of Nile perch, and the haplochromines found in Lake Sare during the study period. 96% of all Nile perch in the lake were less than 30 cm in length. Length measurements for the haplochromines ranged between 2 cm and 16 cm, with the majority (80%) being less than 10 cm in length. There was no significant difference in mean length and weight for Nile perch in stations 1 and 2 but station 3 had higher means while that of the haplochromines was the same for stations 1and 3 with lower means in station 2 (Table 11). Mouth gape and body depth measurements were the same in stations 1and 3 with lower means in station 2 for both Nile perch and haplochromines (Table 12). There were significant positive relationships between total length and mouth gape for Nile perch (R^2 = 0.788) and body depth for haplochromines (R^2 = 0.977) (fig. 9-10).

Table 11: Mean weight and mean Total length of Haplochromines and Nile perch in Lake Sare.

		Weight (g)	Total length (cm)
Pooled	Haplochromines	10.2 ± 0.65	7.1 ± 0.18
	Nile perch	99.9 ± 9.28	18.3 ± 0.38
Station 1	Haplochromines	13.5 ± 1.21^{a}	8.8± 0.29^{a}
	Nile perch	58.9 ± 4.04*	16.8 ± 0.36*
Station 2	Haplochromines	5.4 ± 0.65^{b}	5.2 ± 0.25^{b}
	Nile perch	69.9 ± 6.87*	16.9 ± 0.58*
Station 3	Haplochromines	17.5 ± 2.70^{a}	8.1 ± 0.65^{a}
	Nile perch	103.9 ± 13.40**	18.6 ± 0.60**
Purchased	Haplochromines	11.8 ± 1.38	8.5 ± 0.25
	Nile perch	335.2 ± 89.38	26.9 ± 2.63

Key:

* and ** depict significantly different measurements for same parameter in Nile perch

^{a} and ^{b} depict significantly different measurements for same parameter in haplochromines

Table 12: Mean Mouth gape and Body depth of Haplochromines and Nile perch in Lake Sare.

		Mouth gape (mm)	Body depth (mm)
Pooled	Haplochromines	10.1 ± 0.30	19.5 ± 0.51
	Nile perch	26.8 ± 0.46	43.1 ± 0.94
Station 1	Haplochromines	12.8 ± 0.52^a	24.1 ± 0.88^a
	Nile perch	26.2 ± 0.52*	41.7 ± 1.11*
Station 2	Haplochromines	6.9 ± 0.37^b	14.4 ± 0.69^b
	Nile perch	24.3 ± 0.72**	38.3 ± 1.36**
Station 3	Haplochromines	11.7 ± 1.03^a	22.8 ± 1.80^a
	Nile perch	27.6 ± 0.77*	43.2 ± 1.36*
Purchased	Haplochromines	12.6 ± 0.42	23.2 ± 0.72
	Nile perch	34.3 ± 2.55	66.1 ± 7.15

Key:

* and ** depict significantly different measurements for same parameter in Nile perch

^{a} and ^{b} depict significantly different measurements for same parameter in haplochromines

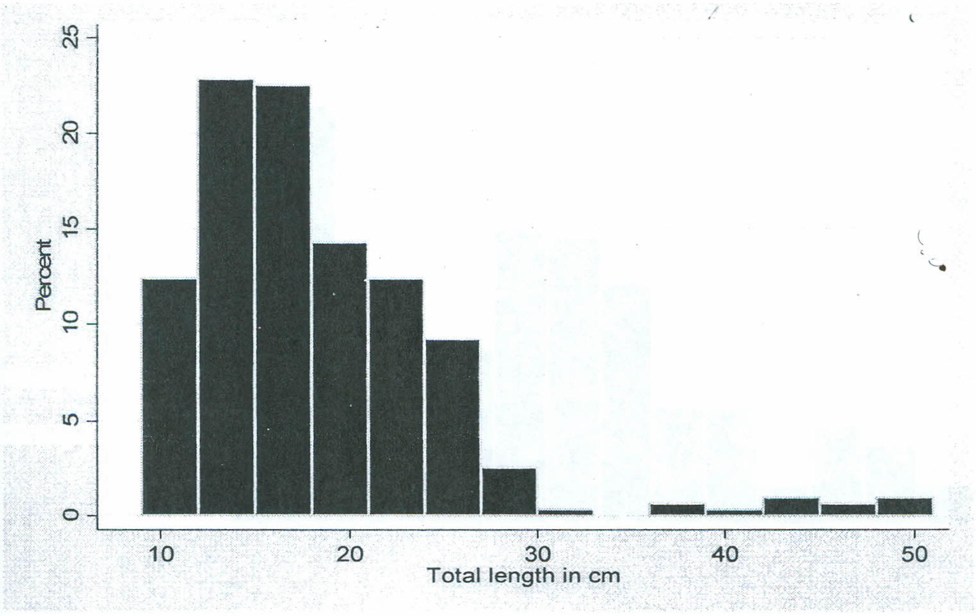

Figure 3: Length-frequency distribution of Nile perch in Lake Sare

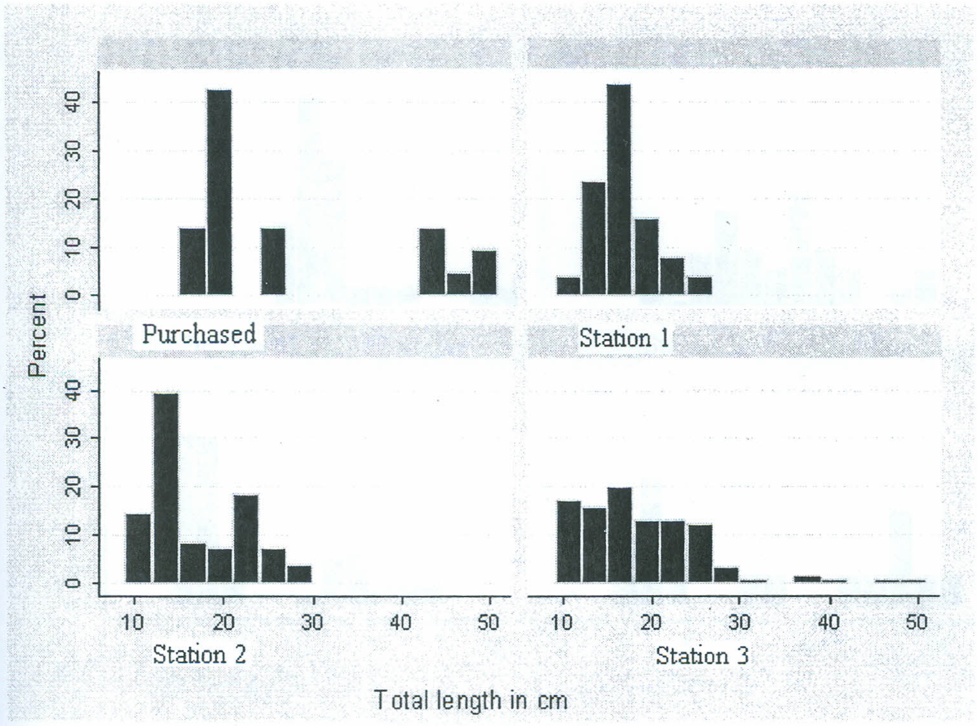

Figure 4: Length-frequency distribution of Nile perch at the different study sites in Lake Sare

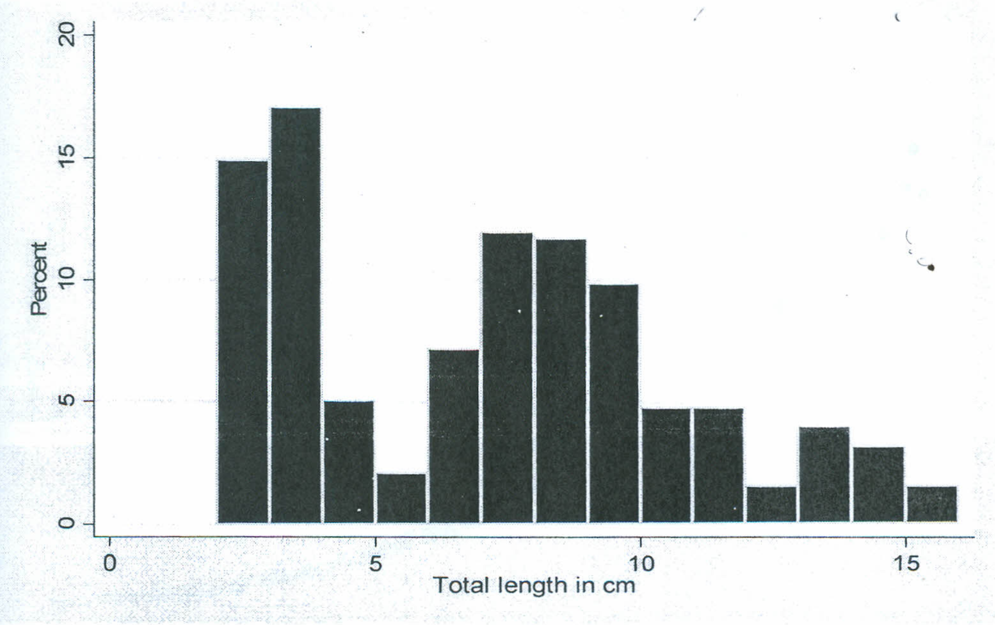

Figure 5: Length-frequency distribution of haplochromines in Lake Sare

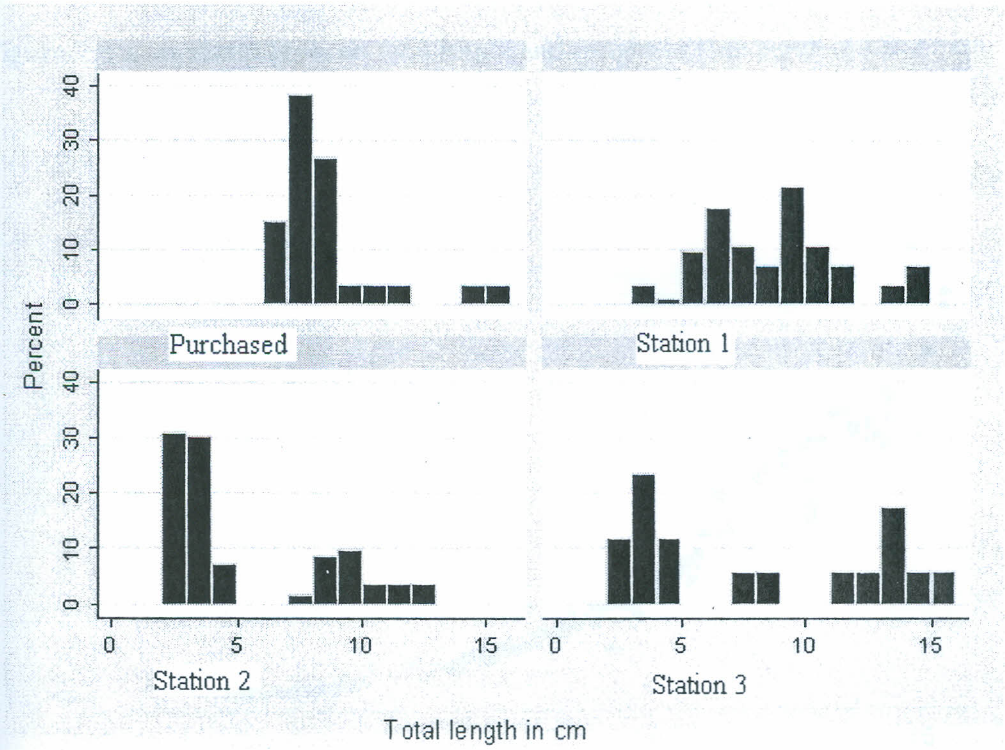

Figure 6: Length-frequency distribution of haplochromines at the different study sites in Lake Sare

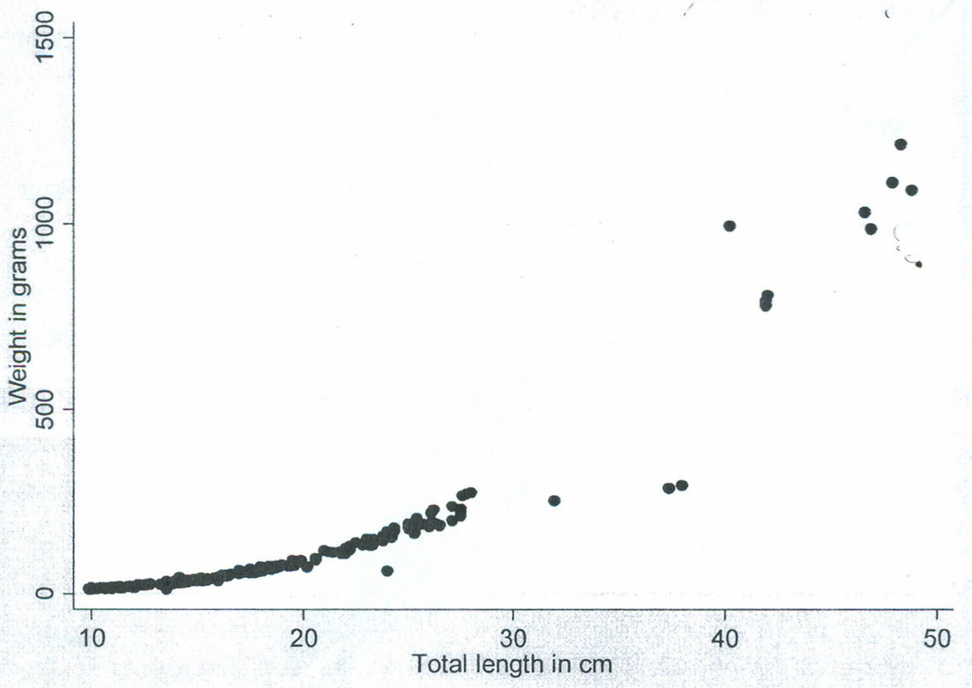

Figure 7: Relationship between total length and weight of Nile perch in Lake Sare

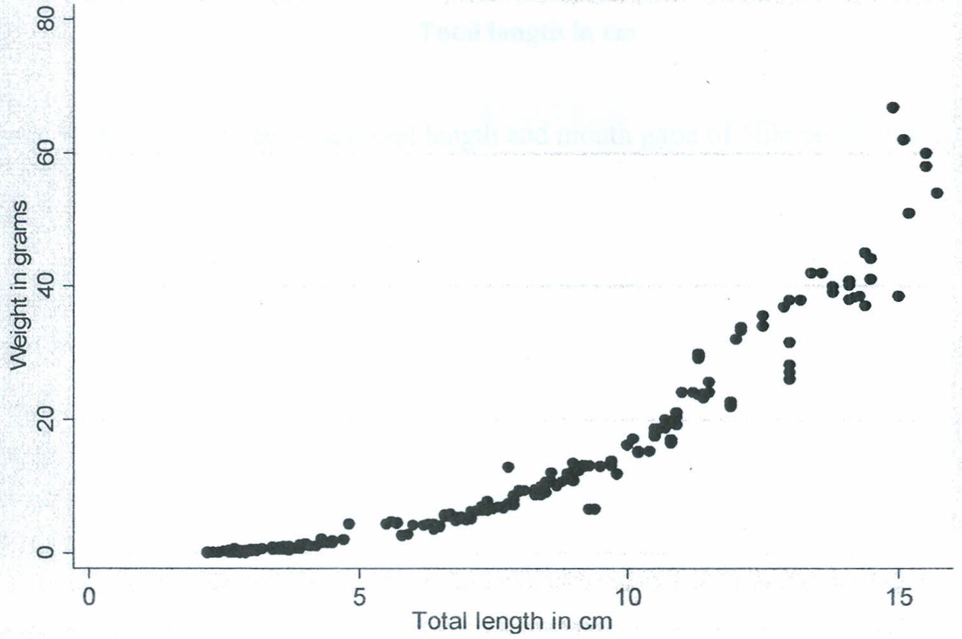

Figure 8: Relationship between total length and weight of haplochromines in Lake Sare

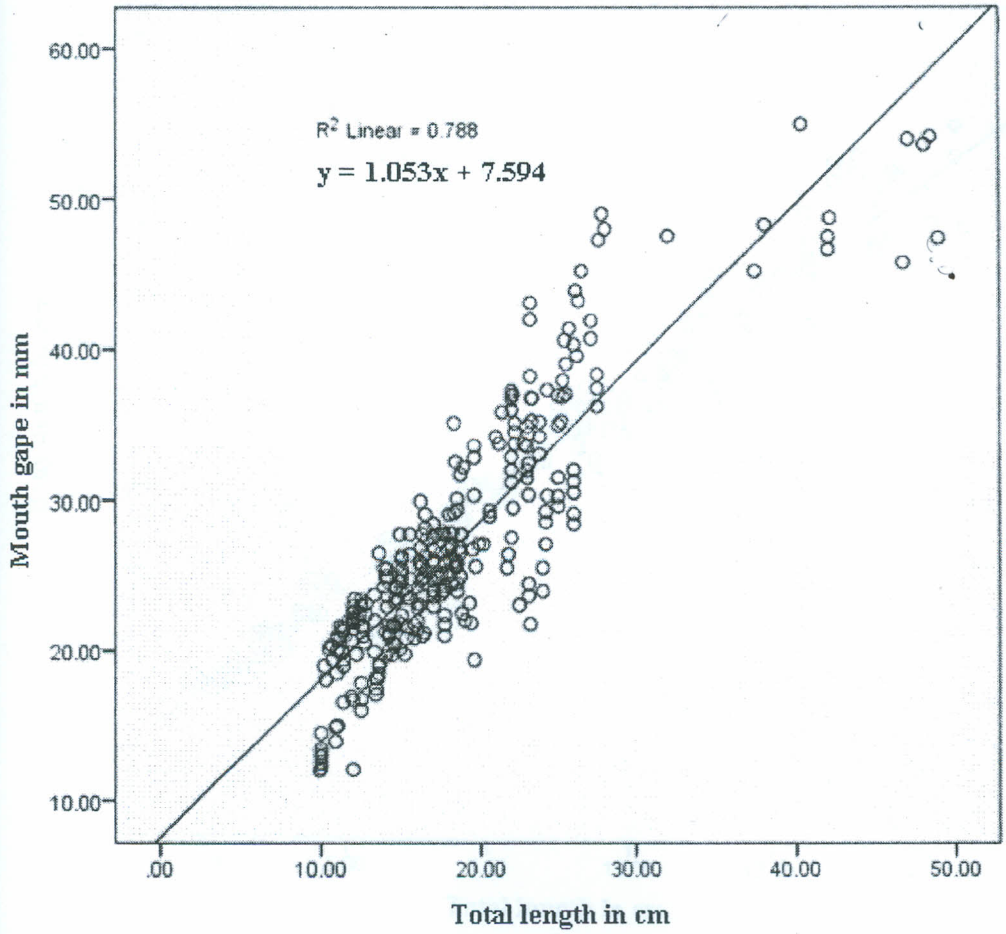

Figure 9: Relationship between total length and mouth gape of Nile perch in Lake Sare

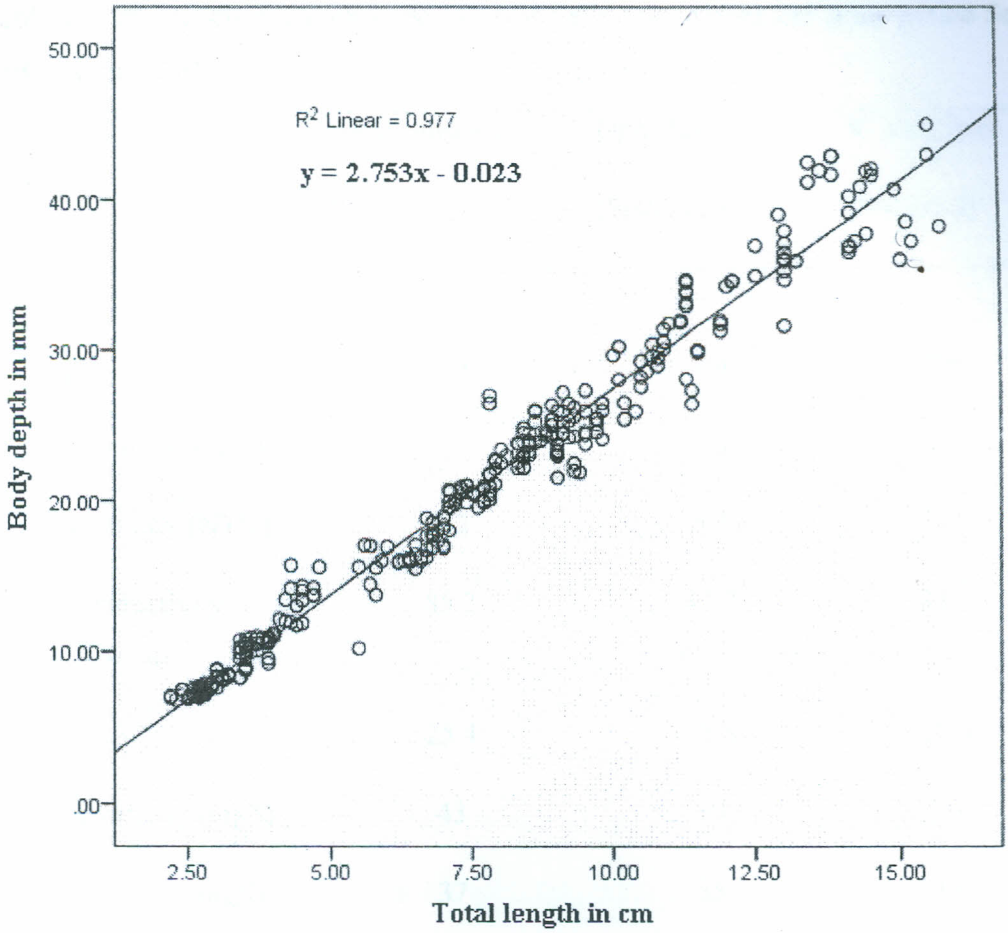

Figure 10: Relationship between total length and body depth of haplochromines in Lake Sare

4.6 Physicochemical characteristics of Lake Sare

The physicochemical characteristics prevailing in Lake Sare during the period September 2010 to August 2011 are summarized in Table 13. Generally, the physicochemical parameters were uniform throughout the lake. However, secchi disc transparency was highest in the open water portion of the Lake, whereas turbidity was highest in Station 3 where River Yala enters the lake.

Table 13: Physicochemical characteristics of Lake Sare during the study period September 2010 - August 2011

	Goye causeway (Station 1)	Open lake (Station 2)	R. Yala inlet (Station 3)
pH	7.9	7.9	7.9
Secchi-depth (m)	1.5	1.8	1.3
Turbidity (NTU)	5.3	5.4	7.3
Conductivity (mS/cm)	85.2	85.7	83.5
Temp °C	25.4	25.8	25.6
Alkalinity (mg/l)	43	39	39
Hardness (mg/l)	37	35	35
TSS (mg/l)	6	8	6
DO (mg/l)	5.4	6.1	5.0
TDS (mg/l)	44	42	47

CHAPTER FIVE

DISCUSSION AND CONCLUSIONS

5.1 Discussion

5.1.1 Species composition and diversity

This study has confirmed that Lake Sare is home to a number of fish species, including the haplochromines, Nile perch, Mormyrids, Tilapiines and *Brycinus* species. The haplochromines, Nile perch and *Brycinus* spp. are the most abundant species in the lake. A study done in Lake Nabugabo, Uganda, also a satellite of Lake Victoria, by Schofield and Chapman (1999) had also revealed the presence of *Brycinus* species, Nile perch and haplochromines. In Lake Sare, *Gnathonemus longibarbis* was the most abundant of the Mormyridae while *Synodontis victoriae* and *S. afrofischeri* were the only members of Mochokidae family encountered in the lake. Of the tilapiines the most abundant was *Tilapia rendallii* while *Oreochromis leucostictus* and *O. niloticus* were present in low numbers. Relative abundance has been used to provide insight into how a community functions and is a pointer to aspects such as competition and predation within the community (Verberk, 2012). When two populations within a community have equal relative abundance then neither of the two has adverse effects on the other and therefore competition and predation, key factors that determine coexistence between species, may be deemed as having no significant effects on the population dynamics of the two species. A comparison of the relative abundance (Table 4) of the haplochromine and Nile perch populations in Lake Sare indicates that the two fishes are present in equal proportions within the lake, a possible exhibition of the phenomenon of coexistence between the two predator-prey species.

5.1.2 Size structure and maturity

Nile perch attains reproductive maturity at between 50 – 55 cm and 85 – 100 cm length for males and females, respectively (Ogutu-Ohwayo, 1994). A frame survey carried out in Lake Victoria in the year 2000 established that male Nile perch at first maturity measured 54 cm in total length, a size reached at the age of 1½ years while the females at first maturity measured 76 cm in total length after 2½ years (Lowe-McConnell, 2009). Earlier work by Hughes (1992) had established that Nile perch in their first year of life attained a size of 10 cm in length, and reached approximately 50 cm in length after 3 years growth. According to the data presented here, the population of Nile perch in Lake Sare during the twelve month study period comprised mainly of immature individuals, none of which had reached the breeding stage (Table 5). Most of the Nile perch caught were of small sizes, with more than 96% measuring less than 30 cm (Fig. 3), way below the average size at first maturity recorded for this species. Considering the size structure of Nile perch in Lake Sare, and the fact that breeding size Nile perch were not found in the lake, it is probable that spawning of Nile perch does not occur in Lake Sare but in the main Lake Victoria, of which it forms a satellite. Since the Nile perch practices broadcast spawning with no parental care, it can be deduced that their larvae drift in from the main Lake Victoria into Lake Sare which is then used as nursery grounds by this species. Hopson (1972) also reported movements of indigenous Nile perch larvae in Lake Chad into shallow waters at the end of their pelagic larval period. On the other hand, Goudswaard *et al*, (2002) reported a preference by Nile perch greater than 25 cm for water depths greater than 12 m. Since Lake Sare has a maximum depth of only 5 m, it may be argued that the larger sizes of Nile perch swim back into Lake Victoria as the depth of Lake Sare cannot support their sizes, thus reducing overlap between the prey haplochromine and predator Nile perch species. Research by Goudswaard *et al.* (2002) also revealed significantly lower densities of Nile perch in shallow water less than 4 m in depth. In assessing the interaction between Nile perch and its prey, an important factor to consider is the degree to which both species composition and habitat use vary with the ontogenetic development of the predator since ontogenetic shift in diet is often accompanied by shift in habitat use and activity thereby occasioning a differing in the ecology of predator juveniles and adults. For example, in a study in Lake Nabugabo, Uganda, Schofield and Chapman (1999) reported a diet shift by Nile perch from feeding on invertebrates to piscivory that occurred at a size of approximately 30 cm. It has also been shown that predator size can cause substantial difference in relative survival of prey that affect both density and structure of the prey population (Rice *et al.*, 1993; Claessen *et al.*, 2002). The Nile perch population in Lake Sare comprises of individuals that have morphological size limitation for successful predation on haplochromines. This is probably one of the reasons as to the coexistence of the Nile perch and haplochromines in Lake Sare.

5.1.3 Predator-Prey body size ratio and foraging success

In aquatic communities body size of both predator and prey has been related directly to foraging success, whereby the range of prey size eaten expands with increasing body size of the predator (Wootton, 1990; Campbell *et al.*, 2005). Studies carried out in Lake Victoria between 1988 and 1992 (Ogutu-Ohwayo, 1994) on dietary composition of Nile perch revealed that the diet of fish less than 20 cm in length was dominated by invertebrates especially *Caridina nilotica* while fish measuring 20 - 60 cm had equal proportions of invertebrates and fish, with *Rastrineobola argentea* and juvenile Nile perch as the most common fish prey. Fish measuring 60 - 100 cm had diets comprising 80% fish with juvenile Nile perch as the main component, and fish measuring greater than 100 cm were exclusively piscivorous on small Nile perch, juvenile tilapia and haplochromines. According to optimal foraging theory an efficient forager will consider appropriate prey in terms of size and nutritional value, minimizing energy spent on capturing prey, and thus having more food energy for metabolism and growth and maximizing net energy gain. The relationship between cost of capture and prey size has been found to be U-shaped along the gradient of prey size such that for any predator, there is an intermediate prey size which minimizes cost but maximizes net energy gain (Wootton, 1990). The profitability of prey to predator as a function of prey size has also been found to be dome-shaped further supporting the theory that there is a predator size that translates to maximum energy gain (Scharf *et al.*, 2002). A study in Lake Nabugabo by Schofield and Chapman (1999) showed that fish in the diet of juvenile Nile perch less than 30 cm in length consisted primarily of *R. argentea.* The maximum prey size recorded for Nile perch is approximately 50% of predator length (Ogari and Dadzie, 1988) but a preference for prey of 20-35% total length has been reported (Hamblyn, 1966; Okedi, 1970). The magnitude of predator-prey interaction is associated with their size ratios which includes body size as a central variable for individual predation risk or size-dependent susceptibility to predation (Rojas and Ojeda, 2010). More than 96% of Nile perch in Lake Sare measure less than 30 cm total length (Fig. 3) thus not achieving the required predator-prey body size ratio for successful predation on haplochromines given the high cost of capture.

5.1.4 Predator mouth gape and prey body depth

Evidence abounds that prey body depth in relation to piscivore mouth size is important in determining the sizes of prey consumed by gape-limited piscivores. Hambright (1991) in a feeding experiment using largemouth bass *Micropterus salmoides* as the predator on fathead minnows, *Pimephales promelas,* and pumpkinseeds, *Lepomis gibbosus,* observed that largemouth bass never ingested prey of body depth greater than their own external mouth width. Reports also indicate that a predator consumes fish with body depth smaller or equal to its maximum mouth gape although piscivores tend to feed on prey that are smaller than the maximum size possible (Hambright, 1991; Bronmark and Miner, 1992). If the body depth of the prey is larger than the gape size of the largest individual in the predator population then the prey fish is considered to enjoy an absolute size refuge from predation. Although the haplochromines of Lake Sare do not have an absolute size refuge from Nile perch, most of the haplochromines' body depth measurements (66%) fall within the same range as most (95%) mouth gape measurements of Nile perch (range 12 mm to 45 mm) (Fig. 9 & 10) thus according partial size refuge to the former, leading to their coexistence. This category of haplochromines and Nile perch behave like the same population with no exhibition of predator-prey relationship. As such, the proportion of haplochromines vulnerable to predation by Nile perch is low and so is the proportion of Nile perch able to prey upon the haplochromines, resulting in their coexistence.

5.1.5 Resource partitioning

The food resource base of haplochromines and Nile perch of Lake Sare comprises a variety of food items including *C. nilotica*, fish, plant material, zooplankton and insects (Table 9). The computed coefficients of similarity index for the various food categories, however, indicate that there is little dietary overlap in most of the food categories (Table 10). The plant materials food category with a coefficient of similarity index of 0.6090 had the highest and most significant food overlap while two other categories (molluscs and insects) had lower non-significant values. Values of overlap greater than 0.6 are considered significant (Mookerji *et al.*, 2004) therefore the two fishes Nile perch and haplochromines displayed insignificant niche overlap in terms of food resource as only one food category had a significant overlap value but with very low intake in terms of occurrence and quantity as measured by relative abundance in both species (Table 9). Plant materials intake, especially in Nile perch was of insignificant quantity and could have probably resulted from incidental intake rather than from deliberate feeding. The haplochromines showed a wider diet breadth while Nile perch exhibited a more restricted diet of mainly *C. nilotica* and fish. The low dietary overlap signified resource partitioning and minimal competition for food between Nile perch and haplochromines and could be one of the reasons for the coexistence of the two fishes in Lake Sare.

5.1.6 Limnology of Lake Sare

The physicochemical characteristics prevailing in Lake Sare during the study period were within the expected ranges (EPA, 2000) for freshwater lakes. The water quality especially clarity in Lake Sare favours vision which, according to Fryer and Illes (1972) is important in haplochromine reproduction for courtship behavior, picking up of eggs by the mouth brooding females and for fertilization. In addition according to Ogutu-Ohwayo (1990) predation tendencies of Nile perch in Lake Victoria was seemingly favoured by the deteriorating water quality and whether this had any impact on the coexistence of the two fishes, Nile perch and haplochromines in Lake Sare is still unclear and may require investigation. However, due to the abundance of haplochromines encountered in Lake Sare during this study, there exists the possibility that water quality in the lake maybe one of the factors that influences the coexistence of the two fishes.

5.2. Conclusions

Interspecific interactions are defined as the degree of affinity between species, and one measure of affinity is the extent to which species overlap in their utilization of common resources. From this study the following conclusions may be drawn:

1. That the Nile perch in Lake Sare are at non-piscivorous stage as depicted by their size structure. In Lake Sare therefore Nile perch do not pose a real predation threat to the

haplochromines since their mouth gapes are not large enough to engulf the predominantly larger haplochromines' body depths. The two fishes in terms of sizes behave as one population and exhibit no predator-prey relationship.

2. That the haplochromines and Nile perch of Lake Sare show no competitive interaction but rather coexistence based on food resource partitioning and size structure as major factors. The low dietary overlap points to there being almost no competition for food resource between Nile perch and haplochromines in the Lake. That resource access for both fishes and predation risks for haplochromines are not limiting factors to the community structure of Lake Sare.
3. That species diversity as indicated by Shannon-Wiener Index and the species richness and evenness Index were relatively low due to over representation by four fishes, Nile perch, haplochromines, *Brycinus* spp., and *Gnathonemus longibarbis,* while the other species had very low abundance.

5.3 Recommendations

5.3.1 Recommendations based on the present study

1. Lake Sare should be given recognition as an in-situ laboratory for studies on size-structured interspecific population interactions using the coexistence of Nile perch and haplochromines as a model.

2. The feeding habits of Nile perch and haplochromines in Lake Sare need to be appraised from time to time to note any changes.

3. Lake Sare should be protected in order to conserve its biodiversity.

5.3.2 Recommendations for future studies

1. Further investigation is needed on the possible influences of environmental attributes such as water quality on the interactions between Nile perch and halochromines.
2. Further research is needed on interactions between fish populations in Lake Sare using stable isotopes to supplement data on gut content analysis and trace the source of carbon and nitrogen.
3. The use of Lake Sare as a potential source of seeds of resurgence for haplochromines to restock Lake Victoria as there is an open direct dispersal corridor between the two lakes.

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