Adjustments in Fish Stocks and in Life History Characteristics of the Nile perch, *Lates niloticus* L. in Lakes Victoria, Kyoga and Nabugabo.

by

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ADJUSTMENTS IN FISH STOCKS AND IN LIFE HISTORY CHARACTERISTICS OF THE NILE PERCH, LATES NILOTICUS IN LAKES VICTORIA, KYOGA AND NABUGABO

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Abstract

Adjustments in fish species diversity, prey selection and life history characteristics of Nile perch, Lates niloticus L. in lakes Victoria, Kyoga and Nabugabo before and after its establishment were examined and compared with the situation in Lake Albert and other habitats where the predator is native. Fish species diversity in the new habitats initially decreased from a level that was similar to that in Lake Albert to one that was significantly lower and then persisted when species that are apparently resilient to Nile perch predation remained. Afterwards, stocks of some species began to recover. The types of prey eaten in the new habitats changed from predominance of haplochromines to types, sizes and numbers similar to those eaten in Lake Albert and other native habitats. The condition factor of the Nile perch which was initially higher in the new habitats decreased and remained at values which although lower than in Lake Albert, are not below the lowest values recorded in a native habitat. Growth rates of juvenile Nile perch were within the ranges reported in native habitats. The size at first maturity shifted from smaller to larger sizes, which are similar to those in lake Albert; this increases overall reproductive potential because fecundity is proportional to the cube of the length. Only the proportion of females in invaded lakes decreased to significantly lower values than in Lake Albert but the reason for this is obscure. Since all but one of the

variables examined have converged on values indicative of the situation where Nile perch has remained in balance with its prey community for a long time, the fisheries of the lakes recently invaded by Nile perch can stabilize and sustain production.

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Chapter 1

The major disturbances causing adjustments in fish stocks in lakes Victoria, Kyoga and Nabugabo and the role of the Nile perch

Abstract

Lakes Victoria, Kyoga and Nabugabo had similar native fish faunas of high species diversity. Stocks of most of these species declined rapidly and others disappeared when an introduced predator, Nile perch, Lates niloticus L. became well established in these lakes. Predation by the Nile perch is thought to be the main disturbance that has depleted the fish stocks. However, over-exploitation of the stocks, competition between introduced and native tilapiines and environmental degradation have contributed. This paper discusses how these disturbances contribute to depletion in fish stocks in the three lakes. Predation by the Nile perch contributes a major part and can cause the fish stocks to collapse. Evidence on re-stabilization of the stocks in the presence of the Nile perch can be obtained from examination of adjustments in the number and diversity of fish taxa, prey selection and life history characteristics of the Nile perch in the three lakes.

Introduction

Lakes Victoria, Kyoga and Nabugabo had diverse fish faunas with many species in common (Graham 1929, Trewavas 1933, Greenwood 1965, Worthington 1929, Cambridge expedition 1962). Two tilapiine cichlids, Oreochromis esculentus (Graham 1929) and O. variabilis (Boulenger 1906) were native only to these lakes and a few small neighbouring lakes. They were originally the most important commercial species in lakes Victoria and Kyoga. There were also many other taxa such as Protopterus aethiopicus Heckel, 1851, Bagrus docmac (Forsk.) 1775, Clarias gariepinus (Burchell), Barbus species, mormyrids, Synodontis spp, Schilbe intermedius (Linn.) 1762 and Rastrineobola argentea Pellegrin, 1904 which were abundant in these lakes (Graham 1929, Worthington 1929, 1932, Kudhongania & Cordone 1974). Haplochromine cichlids were represented by more than 300 species in Lake Victoria alone, more than 99% of them endemic (Greenwood 1974, Witte & Oijen 1991, Witte et al 1992a, b). Haplochromines were also abundant in lakes Kyoga and Nabugabo (Worthington 1929, Trewavas 1933, Greenwood, 1965, 1966, Beadle 1962, 1981).

Stocks of most of the native fish species in lakes Victoria, Kyoga and Nabugabo have declined and others have completely disappeared since the Nile perch, Lates niloticus L., an introduced predator, became well established in these lakes (Ogutu-Ohwayo 1990a, b, Witte et al 1992a, b, Ogari and Dadzie 1988, Ogutu-Ohwayo 1993). Predation by the Nile perch is thought to be the main cause of depletion of the fish stocks and its feared that this will make the Nile perch fishery, which is currently very lucrative, unsustainable. However, overfishing (Jackson 1971), competition between introduced tilapiines and native cichlids (Ogutu-Ohwayo 1990a, b, Witte et al 1992a, b) and environmental degradation (Hecky & Bugenyi 1992, Hecky 1993, Mugidde 1993) have contributed to the changes and are likely to play a big role in stability of the current fisheries. This paper discusses the ways in which various disturbances that have contributed to the recent depletion in fish stocks and emphasises the extent to which predation by the Nile perch has contributed to the depletion.

Over-exploitation of the fisheries

Historically, over-exploitation was the main factor that depleted the native fish stocks of lakes Victoria, Kyoga and Nabugabo. For instance, stocks of the native tilapiines O. esculentus and O. variabilis, which formed the most important commercial fishery in Lake Victoria were reduced by selective fishing and their stocks were reduced by the 1960s (Jackson 1971, Fryer 1973). Labeo victorianus which was the most important riverine species of the Lake Victoria Basin was depleted through intensive gill netting and basket trapping of gravid individuals on breeding migrations.

The present fisheries of lakes Victoria, Kyoga and

Nabugabo are subjected to very high fishing pressure. The increases in total yield in lakes Victoria, Kyoga and Nabugabo following establishment of introduced species especially the Nile perch, was accompanied by intensified fishing effort. The number of fishing boats in the Ugandan region of Lake Victoria alone increased from 3264 in 1971 to 8674 in 1990 (Weatherall 1972, Tumwebaze and Coenen 1991). Use of destructive fishing gears such as seine and cast nets has also increased. The increase in fishing pressure has not only been fuelled by the growing human population but more so by an expansion of an export market for frozen Nile perch fillets. Fish processing factories, which were non-existent prior to establishment of Nile perch, now number about fifty. If this continues unchecked, it will enhance depletion of the stocks.

Environmental degradation

Eutrophication

The rapid increases in Nile perch stocks and depletion of native species were concurrent with changes in physical and chemical conditions and biological characteristics of lakes Victoria and Kyoga (Ochumba & Kibara 1989, Hecky & Bugenyi 1992, Hecky 1993, Mugidde 1992, 1993). There has been an increase in nutrient inputs into the lakes especially from the atmosphere and from changes in land use in the catchment area (Bootsma and Hecky 1993). Increased input of nutrients especially phosphorus and nitrogen has been recorded in Lake Victoria (Hecky 1993). This has stimulated algal production and led to changes in the taxa of dominant algae. Silicon concentration, which is vital for diatom growth has decreased by a factor of 10 probably due to increased inputs of phosphorus and increased sedimentation of silicon. Consequently, diatom composition has changed from dominance of Melosira to Nitzischia. The decrease in Melosira, which was important food of O. esculentus (Graham 1929) may have affected this species and contributed to its disappearance.

Algal biomass is now four to five times higher than the mean values of the 1960s and phytoplankton production has doubled (Mugidde 1992, 1993). Water transparency has decreased to a quarter of what it was during the 1960s. The algae are dominated by cyanobacteria which are not readily consumed by fishes and can also produce phytotoxins which can be dangerous to aquatic life and degrade domestic use of the water. Decay of the excess organic matter depletes the water column of oxygen. This has led to development of an anoxic water in deepest parts of the lake (> 40 m). Oxygen concentration in the hypolimnion during the period of stratification has decreased and anoxia now occurs for longer periods and extends to shallower depths (Hecky 1993, Hecky at al 1994). This has, and will as it expands, reduce habitable space for many fish species and is thought to have accelerated depletion of the deep water haplochromines by confining them to shallower waters where they fell easy prey to Nile perch (Hecky 1993). The reduction of haplochromine stocks may have reduced competition for invertebrate prey between juvenile Nile perch and haplochromines which would increase survival rates among juvenile Nile perch and produce larger adult Nile perch populations.

Anoxia has not been recorded in lakes Kyoga and Nabugabo however and yet similar changes in species diversity have occurred in these lakes. The three lakes also have different morphometries and species richness especially in respect to haplochromine cichlids before Nile perch introduction and none of these factors seem to have altered the eventual outcomes although they may have affected the time lags in each lake. This indicates that other factors especially Nile perch and introduced tilapiines are a major cause of the reduction in fish species diversity.

The composition of aquatic invertebrates in Lake Victoria and probably the other invaded habitats has also changed. Zooplankton composition in Lake Victoria has changed from dominance of calanoid to cyclopoid copepods (Mwebaza-Ndawula 1993). The benthic invertebrates are dominated by types like chironomid and chaoborids midges and the prawn <u>Caridina</u> <u>nilotica</u> Roux. These changes in food-web structure can favour some types of fishes over others.

Invasion by the water hyacinth

Lakes Victoria and Kyoga have been invaded by the water hyacinth, Eichhornia crassipes (Martius) Solms. Lake Kyoga was invaded in 1988 and Lake Victoria in 1990 (Twongo 1991). This plant can be inimical to some forms of aquatic life (Harley 1990). It thrives in shallow, sheltered bays which are suitable breeding and nursery grounds for many fish species. It can, therefore, affect breeding success and feeding by juvenile fishes. The zone below extensive areas of hyacinth mats is low in oxygen, which reduces habitable space for most fish and other aquatic organisms upon which fish may feed.

However, the presence of the water hyacinth can have some positive effects, especially in promoting fish species diversity and that of organisms upon which fish feed (Willoughby et al 1993). The hyacinth mats also provide refuges from Nile perch predation. The presence of the water hyacinth along the shores may reduce the effectiveness of beach seining and this could reduce a destructive fishing practice and help preserve fish populations.

Eutrophication may also have promoted the expansion of water hyacinth in Lake Victoria and probably Kyoga. Recent observations suggest that water hyacinth forms dense populations only where nutrients are in excess to demand of other plants. For instance on Lake Victoria, in Uganda, the biggest hyacinth expanses are in the areas where the city of Kampala releases sewage into the lake.

Impact of the introduced tilapiines

Besides the Nile perch, three herbivorous tilapiine cichlids O. niloticus, O. leucostictus and T. zillii, were introduced into lakes Victoria, Kyoga and Nabugabo. These species have similar ecological requirements to the native tilapiines and are likely to compete with them. The native tilapiines; O. esculentus and O. variabilis were spatially segregated with the smaller O. variabilis, occurring closer inshore than O. esculentus. When O. leucostictus and T. zillii became established, they occupied the same habitat as O. variabilis. Some evidence of competition between O. variabilis and T. zillii was observed by Fryer (1961). O. niloticus possibly competed for the more open waters with O. esculentus. In many areas, O. niloticus became dominant, apparently excluding O. esculentus (Welcomme 1966). Apart from T. zillii which feeds on macrophytes and are substrate spawners, the other species are all mouth-brooders and feed on suspended and planktonic matter. They may have competed for food and nursery grounds not only with the native tilapiines but also with other cichlids. In addition, O. niloticus grows to a larger size, has a faster growth rate, is more fecund, has a longer life span, a wider food spectrum and is less habitat restricted than any of the other tilapiine species (Fryer & Iles 1972). These characteristics could be advantageous to this invading species. Furthermore, O. esculentus and O. variabilis do not naturally occur anywhere with O. niloticus. Generally, *O. niloticus* seems to have competitive advantage over the other tilapiines and has displaced resident tilapiine species from waters where it has been introduced. For instance, *O. spirulus* disappeared from Naivasha (Kenya) and *O. macrochir* from Lake Itasy (Madagascar) following introduction of *O. niloticus* into these lakes (Siddiqui 1977, Welcomme 1984). Moreau *et al* (1988) have listed other examples where introduction of *O. niloticus* displaced resident tilapiine species.

Impact of the Nile perch

Nile perch, *Lates niloticus* Linnaeus, 1758, was introduced into lakes Kyoga, Nabugabo and Victoria from Lake Albert during the 1950's and early 1960's. Eight specimens from Lake Turkana were also introduced into Lake Victoria at Kisumu in 1963 (Gee, 1964). Nile perch is a predatory fish of high commercial and recreational value which can grow to a length of 2 m and a weight of 200 kg. The purpose of the introduction was for the Nile perch to feed on the small-sized haplochromine cichlids which were at that time abundant but not much exploited and convert them into a larger fish of greater commercial and recreational value (Graham, 1929; Worthington, 1929; Anderson, 1961). There were however, fears that the Nile perch might deplete stocks of the native commercial fish and affect the native predators such as *B. docmac* which depended on haplochromines for food. Also, the introduction was discounted as trophically wasteful because higher yields might be accomplished by direct harvest of haplochromines rather than indirect harvest through a predator (Fryer, 1960). Nile perch were initially introduced into Lake Kyoga in 1955 and 1956, and into Lake Nabugabo in 1960 ostensibly to find out what effect their introduction would have on fish faunas similar to that of Lake Victoria (Gee, 1964). In 1960, before these trials were evaluated, Nile perch were discovered in Lake Victoria. Additional introductions into Lake Victoria were made in 1962 and 1963 (Gee, 1964).

Stocks of the Nile perch started to increase rapidly in 1965, in Lake Kyoga, and in 1977, 1981 and 1983 respectively in the Kenyan, Ugandan and Tanzanian regions of Lake Victoria. This was followed by rapid increases in fish yield (Hughes 1983, Okaronon et al 1985, Goudswaard and Witte 1985). Increased abundance of the Nile perch was accompanied by a reduction and, in some cases, total disappearance, of many of the native species (Ogutu-Ohwayo 1990a, b, Ogari & Dadzie 1988, Ligtvoet & Mkumbo 1990). The haplochromines, which were the most abundant species in Lake Victoria and were expected to form the bulk of the food of the Nile perch were depleted and other species became scarce. About 60% of haplochromine species are believed to have become extinct (Witte et al 1992a, b). The food of the Nile perch changed to the extent that it started feeding on its own kind. Consequently, the condition factor and other life history parameters of the Nile perch started to be affected (Ogutu-Ohwayo 1990b). This has created fears that, although the Nile perch fishery had become very lucrative, it might not be sustainable.

Interaction between the disturbances

The disturbances discussed above can act either independently or in combination to cause a fishery collapse. The picture displayed above is quite similar to the history that the North American Great Lakes went through. Intense fishing pressure, changes in physical and chemical environment, the appearance of a foreign predator (the sea lamprey) and foreign competitors such as the alewife either singly or in combination caused a collapse of some fisheries in the Great Lakes (Smith 1968). Once one of the disturbances has reduced the resilience of the population, a slight addition of another disturbance can cause a population collapse. For instance, in the Great Lakes, stocks of certain species such as the lake herring in Lake Erie had been reduced by human exploitation but their stocks could not recover even after the fishing pressure had been relaxed because of the changes in physical and chemical environment, and the invasion by a foreign predator and foreign competitors. Similarly, the collapse of the lake trout in Lake Michigan is thought to have been caused by a combination of fishing and predation by the sea lamprey (Smith 1968). Smith has argued that addition of even small mortality on a commercially exploited species which is already at its maximum sustainable yield may be enough to cause a collapse. As Holling (1973) has put it, once a population has been forced to the boundary of the domain, it can crash or be displaced by even a small disturbance.

In the three lakes invaded by the Nile perch especially Victoria and Kyoga, fishing pressure, changes in the physical chemical and biological environment, predation by the Nile perch and competition from the introduced tilapiines all seem to contribute to destabilization and will determine sustainability of the fish stocks. All these factors should be incorporated into any management model for these lakes if the fisheries have to sustain production. In this study I will confine myself to seeking evidence for adjustments and attainment of stable states of the fish stocks in presence of intense predation pressure by the Nile perch so as to provide some data that can be input in such a model in respect to Nile perch predation.

The question that I will attempt to answer is whether fish stocks in lakes Victoria, Kyoga and Nabugabo can stabilize and support a sustainable fishery in the presence of the predation pressure by Nile perch and how the new stable state, if there will be one, will relate to the prior steady state and provide information on some factors that may, in respect to predation by Nile perch, affect stability. Two possible routes have been suggested concerning the future of the fish stocks in the three lakes (FAO 1985). The first is that Nile perch will overshoot its food resources. This will deplete and cause a collapse of the stocks of the prey species and subsequently those of the Nile perch itself due to inadequate food supply. The second is that the numbers and types of prey and those of the predator will reach an equilibrium level where they will stabilize and sustain production but at a level which cannot be predicted.

For the fishery to remain viable, the second pathway would have to be followed. For this to happen, I assumed that the number and diversity of fish taxa without Nile perch predation were stable, and that other factors like human exploitation and environmental changes had their primary effects prior to the rapid increases in Nile perch stocks. Subsequently, intense predation pressure by the Nile perch caused significant declines in the number and diversity of fish taxa. After those prey species that could not persist in the presence of the Nile perch were eliminated the number and diversity of fish taxa re-stabilized to a new steady state comprising those species that were resilient and could persist in the presence of the Nile perch. Afterwards, some species that may have survived under refugia may develop behavioral responses to reduce predation losses and they may recolonize the lakes and multiply. The number and diversity of fish taxa could then increase to a new equilibrium position. Prey selection by the Nile perch would then stabilize on those types which can persist under its predation pressure. The biological characteristics of Nile perch such as growth rate, condition factor, size at first maturity and fecundity would also stabilize at values that could be maintained by the available prey. The systems would therefore reach a state when there would be no further significant changes and would stabilize and sustain production. The following adjustments in the invaded fish community and in Nile perch biology were predicted:

1. The number and diversity of fish taxa would decline due to predation by Nile perch and re-stabilize.
2. Prey selection by Nile perch would change due to the decline in the number and diversity of fish taxa and then stabilize.
3. Life history characteristics of the Nile perch such as the condition factor, size at first maturity, sex ratios, fecundity should adjust to levels which can be maintained by the available food and stabilize.

Chapter 2

Study areas and general methods of data analysis

Method used to examine the adjustments

The qualitative model of Holling (1973) and the quantitative method suggested by Connell and Sousa (1983) were used to design a conceptual model (Fig. 2.1). This model was used to examine adjustments that occurred in fish species diversity, prey selection and in life history characteristics of the Nile perch due to intense predation pressure by the Nile perch. Its was also used to judge whether the fishery had or would become resilient to predation and sustain production or when it would be overcome by Nile perch predation and collapse.

According to (Holling 1973), when a force such as that due to predation by the Nile perch disturbs a character which is in a stable state as in box A, the character will oscillate with a magnitude of varying amplitude as depicted by the oscillations within box B. After some time, stability occurs and the character attains a new steady state (as in box C) (May 1973, Goodman 1975). The smaller the amplitude of oscillations, the more stable the character. The changes in the character should, in a steady state remain within certain limits and should not move outside its normal range of variance. The more these limits tend to zero, the more stable the character.

The quantitative view of stability according to Connell and Sousa (1983) is that for a system to be considered stable, there must exist one or more equilibrium states (such as boxes A and C) or limit cycles in which the system

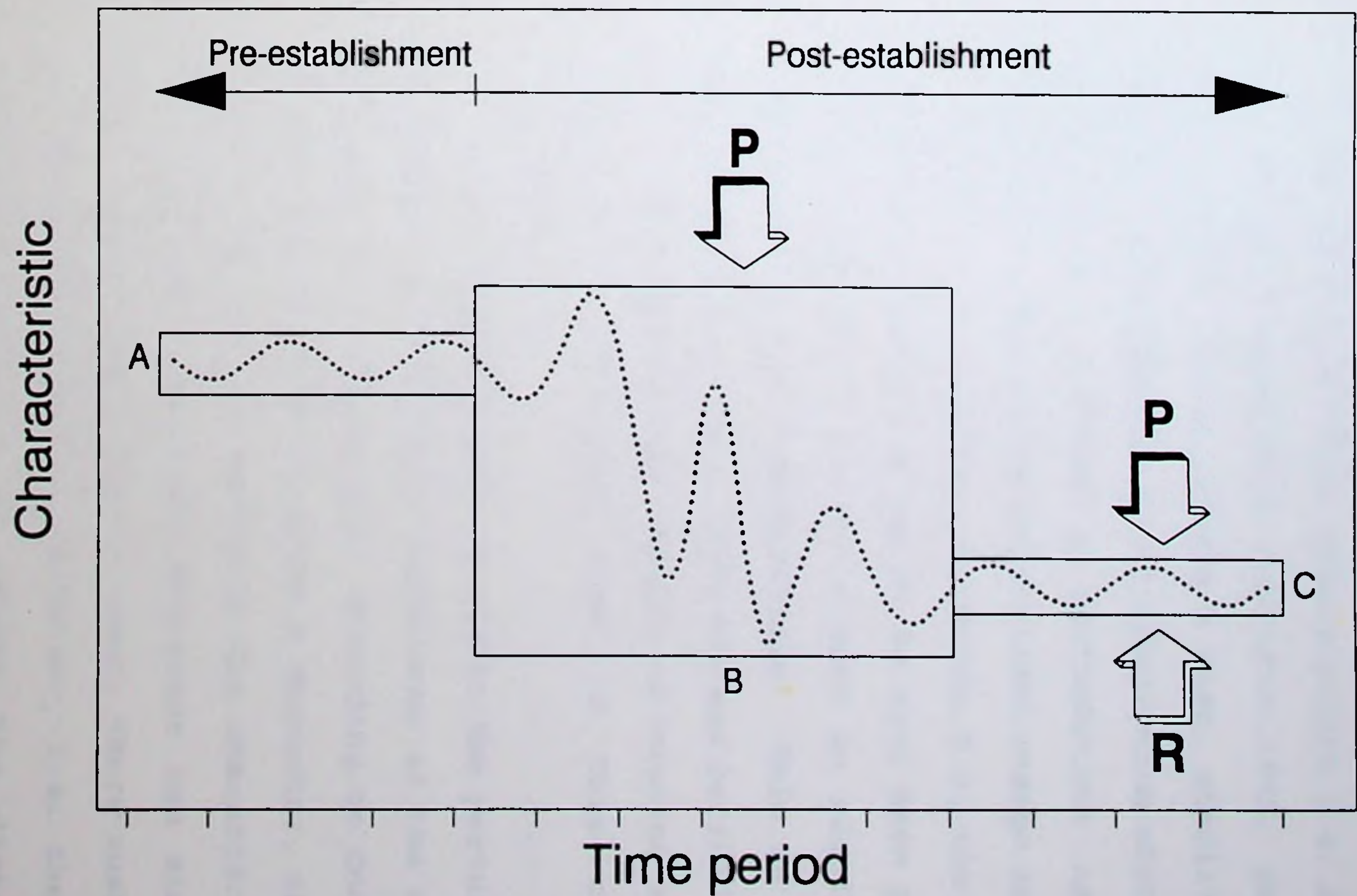


Figure 2.1. A diagrammatic presentation of changes in a characteristic (dotted line) following a disturbance P, due to Nile perch predation. Box A represents the original steady state, B an unstable condition due to the disturbance and C the steady state in the presence of the disturbance. R is the resilience to P. Based on Holling (1973) and Connell Sousa (1983).

remains when faced with a disturbing force or to which it returns when perturbed by the force. However, a perturbed system can have multiple stable points i.e. it can return to one or more equilibria (Lewontin 1969, Sutherland 1974, 1981, 1990). As in Holling's case, stability occurs when the character persists in an equilibrium state. Connell and Sousa (1983) defined a perturbation as a force or disturbance that causes significant change in a character of interest. For instance, in Figure 2.1, the character must be moved out of box A for it to have been perturbed. The change from box A to box C must be significant for the disturbance to be a perturbation. This is in contrast to Sutherland (1974, 1981, 1990) who has defined a perturbation as a force potentially capable of causing a change in the character of interest even if this change is not significant.

The disturbing force P due to the perturbation and the resisting force R due to resilience of the system to P are illustrated in Figure 2.1. According to Connell and Sousa (1983), when a force disturbs a character, the force has to cause a significant change in the character, the force is then resisted and before character can stabilize. This means that for stability to occur, there must be resistance or resilience to the perturbation, i.e. the system should have the capability to absorb the disturbance. For stability to occur and the changes in the character to remain steady and persistent, R should in a mechanical sense be equal and opposite to P. However, in this study, in order for the fishery to be prevented from collapsing or becoming unviable, I assumed that R should be equal to or greater than P, resilience should be seen to be overcoming the perturbation.

This model was used to examine changes in the number and diversity of fish taxa, prey selection and life history characteristics of Nile perch in several lakes: 1) Victoria, where Nile perch were introduced around 1961 and were well established by 1977, 2) Kyoga, where Nile perch were introduced in 1955 and were well established by 1965, 3) Nabugabo where Nile perch were introduced in 1960 and re now well established and 4) Albert, the site from which the Nile perch stocks were introduced into the three lakes. Also, any information that was available in the literature for native habitats of the Nile perch was used to assess characteristics of the Nile perch in their native habitats.

Data collected during this study and historical data collected by the Fisheries Research Institute of Uganda were analyzed. Detailed methodology of data collection are given in Chapters dealing with specific aspects. Only the study areas and an overview of the methods and data analysis are given in this Chapter.

It was assumed that Lake Albert represented the predictable stable state of low amplitude oscillations. The number and diversity of fish taxa and certain biological characteristics of the Nile perch in the new habitats would change due to predation by Nile perch on a fish community not previously exposed to such a large predator. After a time, the system would become resistant to predation and the character would stabilize at either a level similar to what is recorded in Lake Albert or one that is unique to the new habitats. Alternatively, the disturbing force would so destabilize the system that it would continue to changes until the fishery collapses i.e. becomes unviable.

The adjustments in the number and diversity of the fish taxa involved in the fishery were examined by analyzing changes in commercial catch records and experimental catch composition data collected from lakes Victoria, Kyoga and Nabugabo during the period just before and after the rapid increases in Nile perch stocks and compared to that in Lake Albert. Similar analysis was made for the changes in prey selection and in life history characteristics of the Nile perch. The data analyzed were collected from Lake Albert between 1989 and 1992, Lake Victoria between 1964 and 1992, Lake Nabugabo between 1991 and 1993, and Lake Kyoga between 1967 and 1993.

The data were divided into specific blocks representing the evolution of Nile perch driven changes. The data collected from Lake Albert from 1989 to 1992 was treated as one block. Data from Lake Victoria were classified in four blocks. The first two represented the period before the rapid increases, the third represented the transitional period between the pre- and post-establishment periods and the fourth represented the period after rapid increases in Nile perch stocks. The first block consisted of data collected between 1964 and 1967 soon after introduction of the Nile perch and before the predator had spread over much of the lake and its effects on the fish community were not yet apparent. These data came from commercial fish catches and did not contain any information on the types of prey eaten during that period. However, Gee (1964, 1969) examined the food of the Nile perch soon after it introduction and his observations correspond to this period. The second block comprised data collected between 1968 and 1977 from commercial catches and experimental trawl surveys conducted on Lake Victoria between 1968 and 1977 (Kudhongania & Cordone 1974). By this time the impact of the Nile perch on the fish community was still not yet apparent. However, these data were separated from the previous set because they contained more information, including types of prey ingested, missing from the 1964-67 set. The third block consisted of data collected from Lake Victoria in 1982 when Nile perch stocks started increasing rapidly in the Ugandan region of the lake (Okaronon et al 1985); effects on the fish community were expected to become more apparent after this period. There were, however no data on the type of prey eaten at that time. The fourth block consisted of data collected during 1988-92 and represents the period after Nile perch had become well established and its effects on the fish community had been manifested.

Data from Lake Nabugabo comprised one set collected between 1991 and 1993. These were treated as one block. By this time, Nile perch had already become well established in the lake (Ogutu-Ohwayo 1993) and its effects on the fishery had become apparent.

The data for Lake Kyoga covered a period of 26 years (1967-93). Nile perch were well established throughout this period and its effects on the stocks had been manifested. It was however divided into four blocks. The first block consisted of data collected in 1967 and 1968. By this time, the diet of the Nile perch had already shifted from what it had fed on immediately after its introduction (Gee 1964, Hamblyn 1966, Okedi 1971). After 1968, there were no data from the lake until 1978 when data were collected more regularly up to 1993. No major changes in fish community were apparent from 1978 to 1990. However, in 1991 haplochromines started to appear again, suggesting that some changes were occurring in the fish community. The data from 1991 to 1993 were therefore treated as a separate block. The data for 1978 to 1990 covered a period of 22 years and consisted of two sets of data collected between 1978-80 and 1988-90; these were treated as two different blocks.

In analysis of the data, I assumed that life history characteristics in Lake Albert represented the equilibrium state. Since lakes Victoria, Kyoga and Nabugabo had similar native fish faunas (Graham 1929, Worthington 1929, Fryer &

Iles 1972, Beadle 1981), I assumed that the changes in prey selection and life history characteristics of the Nile perch in the three lakes would follow a similar pattern. The different data sets were arranged in blocks along an ecological time scale as follows:

Block 0. The original and native habitat of Nile perch stocks which were introduced into lakes Victoria, Kyoga and Nabugabo. Current data for Lake Albert were collected during 1989-93

Block 1. Lake Victoria, 1964-67; soon after introduction of Nile perch and when haplochromines were still abundant and formed the main prey of Nile perch (Hamblyn 1966, Gee 1964, 1969).

Block 2. Lake Victoria 1968 to 1977; before Nile perch became well established and haplochromines were still abundant.

Block 3. Lake Victoria 1982; the year when Nile perch populations increased rapidly in the northern region of Lake Victoria but when haplochromines were still abundant (Okaronon et al 1985).

Block 4. Lake Victoria, 1988 to 1992; after haplochromines had been depleted and were no longer important as prey.

Block 5. Lake Nabugabo 1991 to 1993; after Nile perch were well established and haplochromines had been depleted (Cambridge expedition 1962, Ogutu-Ohwayo

1993).

Block 6. Lake Kyoga, 1967 to 1968; after Nile perch were well established and haplochromines had been depleted and were no longer important as prey (Okedi 1971).

Block 7. Lake Kyoga 1978 to 1980; ten years after block 6.

Block 8. Lake Kyoga 1988 to 1990; ten years after block 7.

Block 9. Lake Kyoga 1991 to 1993; when haplochromines were starting to recover and were again becoming prominent as prey.

The above descriptions show that no major changes were apparent between blocks 4, 5 and 6 and these could have been treated as a single block representing the post-Nile perch establishment period. They were treated as separate blocks because the data came from different lakes. Also, although no major changes occurred in Lake Kyoga between 1967 and 1990, the period was considered to be too long to be treated as single block. These data were therefore divided into three blocks approximately 10 years apart.

Some life history characteristics vary with size of the Nile perch. The type, size (length), and number of prey ingested by the Nile perch in most habitats varies with its length (Worthington 1929, Hamblyn 1966, Gee 1969, Okedi 1971, Ogutu-Ohwayo 1985, Hopson 1972). Nile perch of less than 20 cm total length feed predominantly on invertebrates, those of 20 cm to 60 cm on invertebrates and fish, those of 60 cm to 100 cm on small fish prey such as <u>Rastrineobola</u>

argentea Pellegrin and small tilapiines and those of more than 100 cm on large fish prey such as Oreochromis niloticus L. Males mature at about 50 cm total length while females mature around 95 cm (Holden 1963, Hopson 1972, 1982). These variations could affect comparisons of changes in life history characteristics depending on the size range of the Nile perch which had been examined in each block. On this basis, data of each block were grouped in length classes as follows:

Class A: <20 cm - immature and feeding mainly on invertebrates.

Class B: >=20 cm and <60 cm - immature females and mature or maturing males feeding on invertebrates and fish.

Class C: >=60 cm and <100 cm - Mature males and maturing or immature females feeding on many small fish prey, e.g. haplochromines, small tilapiines, young Nile perch and R. argentea in lakes Victoria, Kyoga and Nabugabo and Alestes spp. in Lake Albert.

Class D: >=100 cm - All mature and feeding mainly on one or two large fish prey especially O. niloticus in lakes Victoria, Kyoga and Nabugabo and Hydrocynus spp. in Lake Albert.

The life history characteristics were first examined for each length class within each block and the differences between the classes compared. Comparison were then made for each length class or for a combination of specific length classes between the blocks.

Connell and Sousa (1983) suggested that a time scale of the perturbation is important in judging whether the characteristic under consideration stabilized or not. In this study, I assumed that the character was stable when it persisted within certain limits for a recognized period of time before moving to another equilibrium state.

About the lakes

The lakes examined in this study are shown in Figure 2.2.

Lake Albert is located within the Western Rift valley between latitude 1° 0' N and 2° 20' N and longitude 30° 20' E and 31° 20' E. It covers an area of 5500 km^2 and has an average depth of 40 m and a maximum of 58 m. It is about 35 km wide and 150 km long.

The Lake Albert ecosystem seems to be ecologically very efficient. The lake is well mixed to the bottom most of the year and undergoes very limited or no stratification (Talling 1963) which facilitates good circulation of nutrients and oxygen in the water column. Most of the ecological niches are occupied (Beadle 1981) and this provides an efficient flow of energy through the lake. Phytoplankton primary production seems not to have changed since the 1960s (Talling 1963, Mugidde 1992).

Lake Albert has a soudanian fish fauna which is

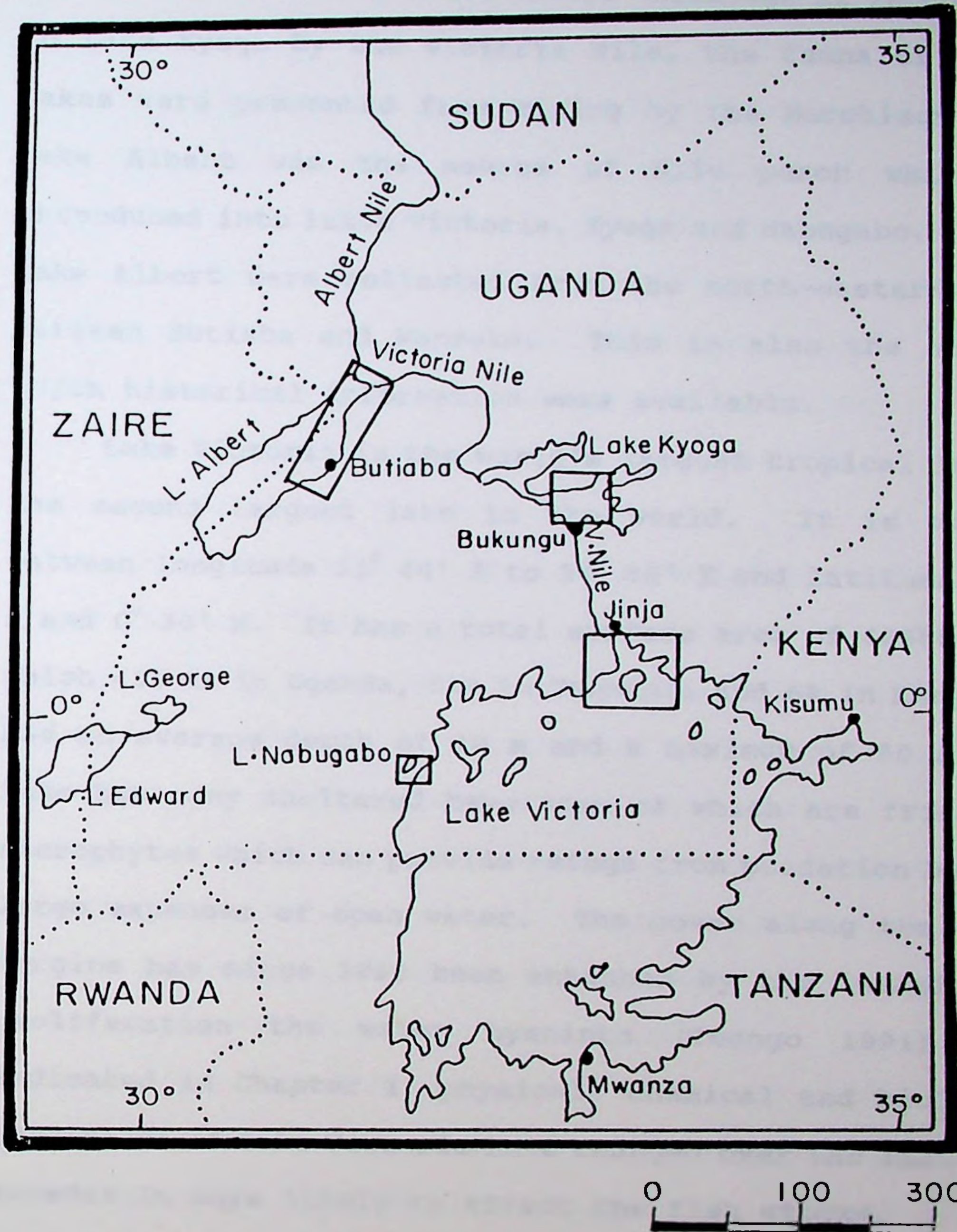


Figure 2.2. The map of Uganda showing the location of lakes Victoria, Nabugabo, Kyoga and Albert. The main sampling zone on each lake is indicated by a rectangle.

different from that of lakes Victoria, Kyoga and Nabugabo in their native state (Beadle 1981). Although it is connected to Lake Kyoga by the Victoria Nile, the fauna of the two lakes were prevented from mixing by the Murchison Falls. Lake Albert was the source of Nile perch which were introduced into lakes Victoria, Kyoga and Nabugabo. Data on Lake Albert were collected from the north-eastern region between Butiaba and Wanseko. This is also the area for which historical information were available.

Lake Victoria is the world's largest tropical lake and the second largest lake in the world. It is situated between longitude 31° 40' E to 34° 50' E and latitude 3° 0' S and 0° 30' N. It has a total surface area of 68680 km^2 of which 43% is in Uganda, 51% in Tanzania and 6% in Kenya. It has an average depth of 40 m and a maximum of 80 m. The lake has many sheltered bays some of which are fringed by macrophytes which can provide refuge from predation but with large expanses of open water. The cover along the lake's margins has since 1990 been enhanced by the invasion and proliferation the water hyacinth (Twongo 1991). As indicated in Chapter 1, physical, chemical and biological conditions of Lake Victoria have changed over the last three decades in ways likely to affect the fish stocks.

In Lake Victoria, most data were collected from the northern part of the lake near the station of the Fisheries Research Institute at Jinja; this includes Napoleon Gulf, Buvuma Channel, Hannington Bay and Thruston Bay. This area was chosen because of its accessibility and because most of the available historical data were collected from the same area.

Lake Nabugabo is located off the western shores of Lake Victoria. It is about 24 km^2 in surface area and maximum depth is. Lake Nabugabo is believed to have been formed when a sand bar separated a portion of water from Lake Victoria about 4000 years ago (Worthington 1932, Trewavas 1933, Beadle 1962, 1981). The lake is surrounded by a swamp which can provide refuge for fish from predation. Data were collected from most parts of the lake.

Lake Kyoga is situated between longitude 32° E and 34° E and latitude 1° N and 2° N. It has an area of 2700 km^2, and an average depth of 3.5 m. Its indented shoreline is fringed in many place by papyrus and <u>Phragmites</u> which provide some refuge from predation. Since 1988, the vegetation along the lake's margin has been enhanced by the spread of the water hyacinth. On Lake Kyoga samples were mainly collected from the area between Bukungu and Muntu, where most historical data were collected.

Besides the differences in the mophormetry of the lakes, and current limnological conditions, the native fish fauna of lakes Victoria, Kyoga and Nabugabo were similar. The only exception was that Lake Victoria had a larger number of species especially among the haplochromine cichlids. The available data also indicates that the changes in fish species composition in the three lakes have responded in a similar manner both to fishing and to fish species introductions (Ogutu-Ohwayo 1985, 1993). Therefore, the changes due to predation by the Nile perch were expected to follow a similar pattern in these lakes although the individual characteristics of the lakes would affect the timing of the changes.

Chapter 3

Changes in the number and diversity of fish taxa in lakes Victoria, Kyoga and Nabugabo in presence of the Nile perch, *Lates niloticus* L.

Abstract

The changes in the number and diversity of fish taxa just before and after rapid increases in stocks of Nile perch in lakes Victoria, Kyoga and Nabugabo were examined and compared with the situation in Lake Albert to see whether fish species diversity in the habitats invaded by Nile perch had stabilized or was decreasing further. Before the rapid increases in Nile perch populations, fish species diversity in Lake Victoria was not different from that of Lake Albert and commercial landings comprised about 12 taxa. After establishment of the Nile perch, fish species diversity in Lake Victoria decreased significantly to a level which was even lower than that of Lake Albert. Similar changes in fish species composition occurred in the three lakes invaded by Nile perch. All of them became dominated by two introduced species; <u>Lates niloticus</u> L. and <u>Oreochromis niloticus</u> L. and one native species, <u>Rastrineobola argentea</u> following establishment of the predator. Fish species composition in these lakes has not changed and diversity has not decreased further since the three species became dominant suggesting that these three are resilient and can persist in the presence of the predator. Also some species especially among haplochromines have started to recover suggesting that fish species diversity had reached the lowest level and may in future increase.

Introduction

There have been considerable changes in fish species composition in lakes Victoria, Kyoga and Nabugabo since the Nile perch was introduced. Populations of most of the native species have declined and many species may have become extinct (Witte et al 1992a, b). The original decline in the fish stocks was attributed to overfishing (Jackson 1971, Ogutu-Ohwayo 1990a) but the recent and more drastic decline has been due to predation by the Nile perch (Ogari & Dadzie 1988, Ligtvoet & Mkumbo 1990, Ogutu-Ohwayo 1990a, b, Witte et al 1992a, b).

Young Nile perch feed on invertebrates and change to fishes as they grow larger (Hamblyn 1966, Gee 1969, Okedi 1971, Ogutu-Ohwayo 1990a, b). Haplochromine cichlids, were the most abundant fishes in Lake Victoria (Kudhongania & Cordone 1974) and formed the most important prey of the Nile perch soon after its introduction (Hamblyn 1966, Gee 1964, 1969). As population of Nile perch increased, those of haplochromines and other native species declined rapidly due to predation by the Nile perch (Ogutu-Ohwayo 1985, 1990a, b, c, Ogari and Dadzie 1988, Ligtvoet & Mkumbo 1990, Hughes 1986). As these were depleted, Nile perch switched to other prey types including its own young. There are fears that the Nile perch will overshoot its food supply, resulting in a reduction of its own population, and subsequently, a collapse in the fishery (FAO 1985).

Introduction of predatory fishes can be dangerous and have in many cases disastrously reduced or even eliminated resident species (Welcommme 1984). Many examples exist around the world for instance, Cichla ocerallis which was introduced into the Chagres River, Panama, and found its way into Gatun lake eliminated many of the local species (Zaret & Paine 1973). Introduction of the largemouth bass in the Mexican Lake, Lago de Patzcuaro depleted many species including important native food fishes and that of the rainbow trout into Lake Titicaca damaged a species flock of at least 19 fish species (Welcomme 1984). The black bass, Macropterus salmoides which were introduced into Lake Naivasha, Kenya, depleted other species from the lake (Siddiqui 1977). Trout and large mouth bass which was introduced into Southern Africa to form a sport fishery eliminated at least three native species (Jackson 1960, FAO/CIFA 1985). However, the introduction of the Nile perch into lakes Victoria, Kyoga and Nabugabo provides one of the most spectacular examples of the effects of introducting a large predator into a lake (Barel et al 1975).

The changes in fishery yield and species diversity in lakes Victoria, Kyoga and Nabugabo were examined to see how the numbers and diversity of fish taxa had changed in the presence of the Nile perch and if there was any evidence that these would stabilize and the fishery remains viable. It was assumed that species diversity initially declined rapidly due to predation by the Nile perch on a fish community not previously exposed to such a large predator.

After vulnerable species were eliminated, it would stop declining when resilient species persist. The number and diversity of fish taxa would stabilize at a level which would be determined by the resilient species. This would occur at a level which is either unique to the new habitats or one which would have similarities to that of Lake Albert and other native habitats of the Nile perch. Alternatively, the number and diversity of fish taxa would continue to decline to a level where the fishery would become unviable.

Materials and methods

The changes in the number and diversity of fish taxa were examined by analyzing commercial catch records and experimental fishing data collected from lakes Albert, Victoria, Nabugabo and Kyoga. Analyses were based on:

1). Commercial catch records collected by Fisheries Departments of Uganda, Kenya and Tanzania just before and after the rapid increases in Nile perch stocks. These included: commercial catch records of Lake Kyoga from 1963 to 1989, the Kenyan, Ugandan and Tanzanian regions of Lake Victoria and Lake Albert between 1970 and 1990. These were the only time series data that were available for this analysis. However, these data give a fair picture of what was happening in the lakes because fishermen on these lakes exploit virtually all species available from the smallest species such as R. argentea to the very large Nile perch and also use a mixture of gears from gill nets to seines of various mesh sizes. The methods of fisheries statistical data collection are also similar for the countries bordering Lake Victoria and follow a system designed by FAO. Furthermore, experimental fishing data was used to see whether what was recorded in commercial catches was a fair representation of what was in the lakes.

2). Experimental trawl catch composition data collected from Lake Victoria between 1970 and 1992.

3). Experimental catch composition data collected from lakes Victoria, Kyoga, Nabugabo and Albert between 1988 and 1993.

Experimental fishing was conducted using gill nets, seines and trawl nets. Two seines were used. A fine mesh seine of 10 mm stretched mesh and 20 m in length was used to sample small fish like R. argentea and juveniles of larger species. This was the least selective gear and was capable of catching even the smallest species such as R. argentea. The second seine of 100 m length with wings of 102 mm mesh and a bag of 51 mm stretched mesh was used to catch larger fish. Trawling was done only in Lake Victoria using a codend of 19 mm stretched mesh. The data from trawling were compared with earlier surveys of Kudhongania and Cordone (1974) and Okaronon et al (1985). The gill nets used were of 25.4 mm to 305 mm stretched mesh. In each lake, an effort was made to sample different habitat types in respect to location (inshore or offshore), water depth, substratum type, and presence or absence of aquatic macrophytes and other refugia.

Experimental fishing on Lake Albert was logistically difficult. Because of this, commercial fishermen's catches were sampled. These were considered representative because the size ranges of gill nets and the seines used by commercial fishermen were, with the exception of the fine 10 mm seine, similar in mesh size ranges to those used in experimental fishing on lakes Victoria, Kyoga and Nabugabo. Only the 10 mm mesh seine was operated on Lake Albert.

The total number and weight of species captured was recorded. For Lake Albert, the whole catch from a single boat was treated as one sample.

Fish species diversity was estimated using Shannon-Weaver Index of diversity H' (Pielou 1969). The Diversity Index H' was calculated using the formula:

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

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

Results

Changes in commercial catch composition in Lake Victoria

The changes in yield of different taxa in the Kenyan, Ugandan and Tanzanian regions of Lake Victoria between 1970 and 1990 are illustrated in Figures 3.1, 3.2 and 3.3. Before stocks of the Nile perch started to increase rapidly, twelve to fourteen taxa occurred regularly among commercial catches. Two tilapiines (O. esculentus and O. variabilis), the catfishes, Bagrus docmac Forsk. 1775 and Clarias gariepinus Burchell, 1822, the lungfish, Protopterus aethiopicus Haeckel, 1851, and haplochromine cichlids were the major commercial species. Less common species included the cyprinids, Labeo victorianus Boulenger, 1901, R. argentea and Barbus spp, the cat fish, Schilbe intermedius Ruppell, 1932 and Synodontis spp, mormyrids, and the characid Brycinus spp.

In the Kenyan region (Fig. 3.1), the total quantity of fish landed remained between 14,918 and 18,677 tonnes between 1970 and 1976. As the introduced species became established, total yield increased rapidly from 19,332 tonnes in 1977 to 165,802 tonnes in 1990. This was due to an increase in the yield of the two introduced species; L. niloticus from 94 tonnes in 1976 to 71,414 tonnes in 1990 and O. niloticus from 421 tonnes in 1976 to 38,305 tonnes in 1990. The only native species whose yield persistently increased during this period was R. argentea. The yield of

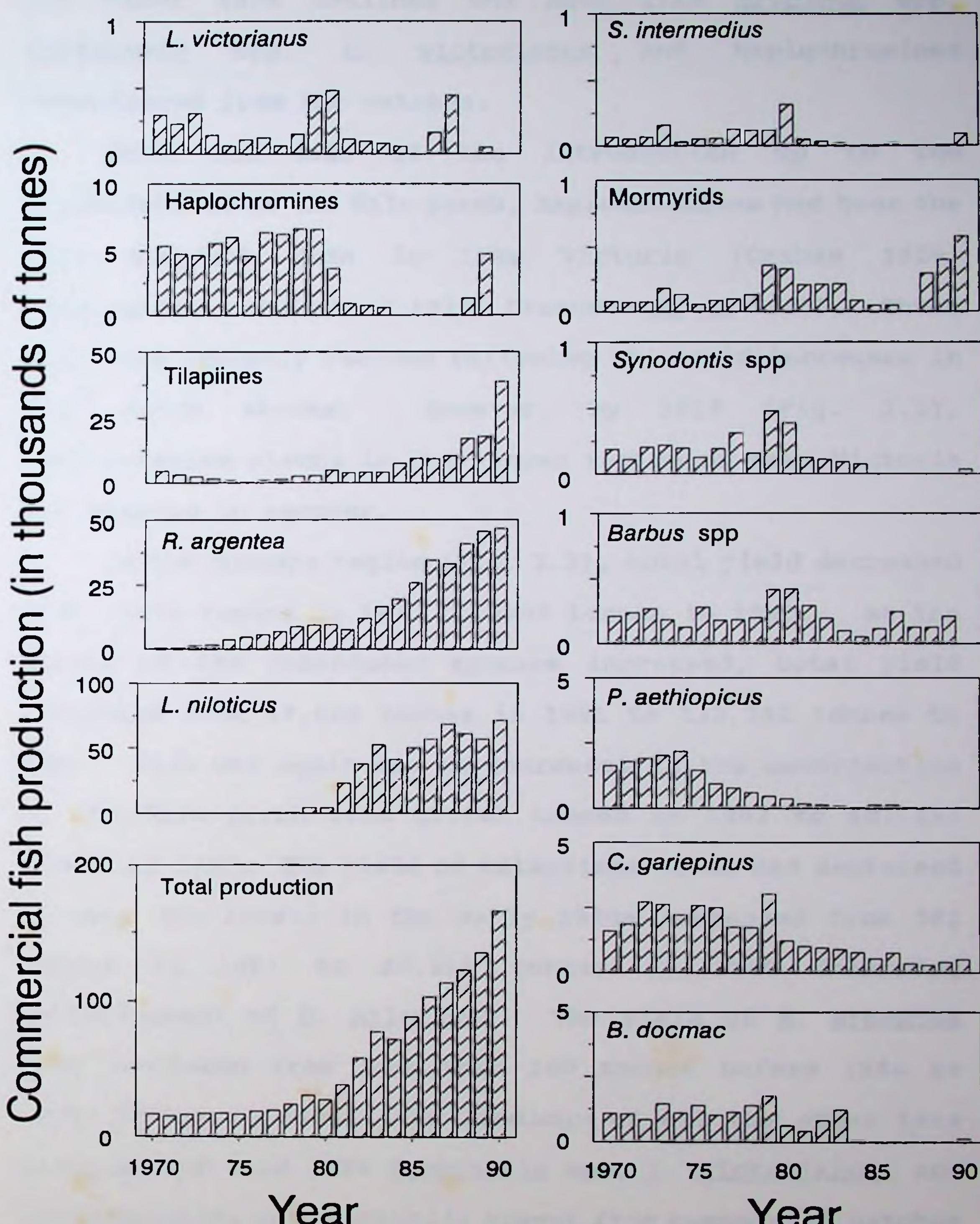


Figure 3.1. Changes in commercial fishery yield from the Kenyan region of Lake Victoria between 1970 and 1990.

all other taxa declined and some like _Brycinus_ spp, _Synodontis_ spp, _L. victorianus_ and haplochromines disappeared from the catches.

From the time of the introduction up to the establishment of the Nile perch, haplochromines had been the most abundant fish in Lake Victoria (Graham 1929, Kudhongania and Cordone 1974, Okaronon _et al_ 1985). These fish were severely reduced following the rapid increases in Nile perch stocks. However, by 1989 (Fig. 3.1), haplochromine stocks in the Kenyan region of Lake Victoria had started to recover.

In the Ugandan region (Fig. 3.2), total yield decreased from 41670 tonnes in 1970 to 9999 tonnes in 1980. As the stocks of the introduced species increased, total yield increased from 17,000 tonnes in 1981 to 132,382 tonnes by 1989. This was again due to increases in the contribution of the Nile perch from 13,980 tonnes in 1983 to 101,257 tonnes in 1989. The yield of tilapiines which had decreased to very low levels in the early 1980s increased from 382 tonnes in 1983 to 20,218 tonnes in 1989 following establishment of _O. niloticus_. The yield of _R. argentea_ also increased from less than 100 tonnes before 1984 to 7,052 tonnes by 1989. The landings of all the other taxa declined and some like _Synodontis_ spp, _L. victorianus_, and haplochromines were virtually absent from commercial catches by 1983.

Detailed commercial catch records for the Tanzanian

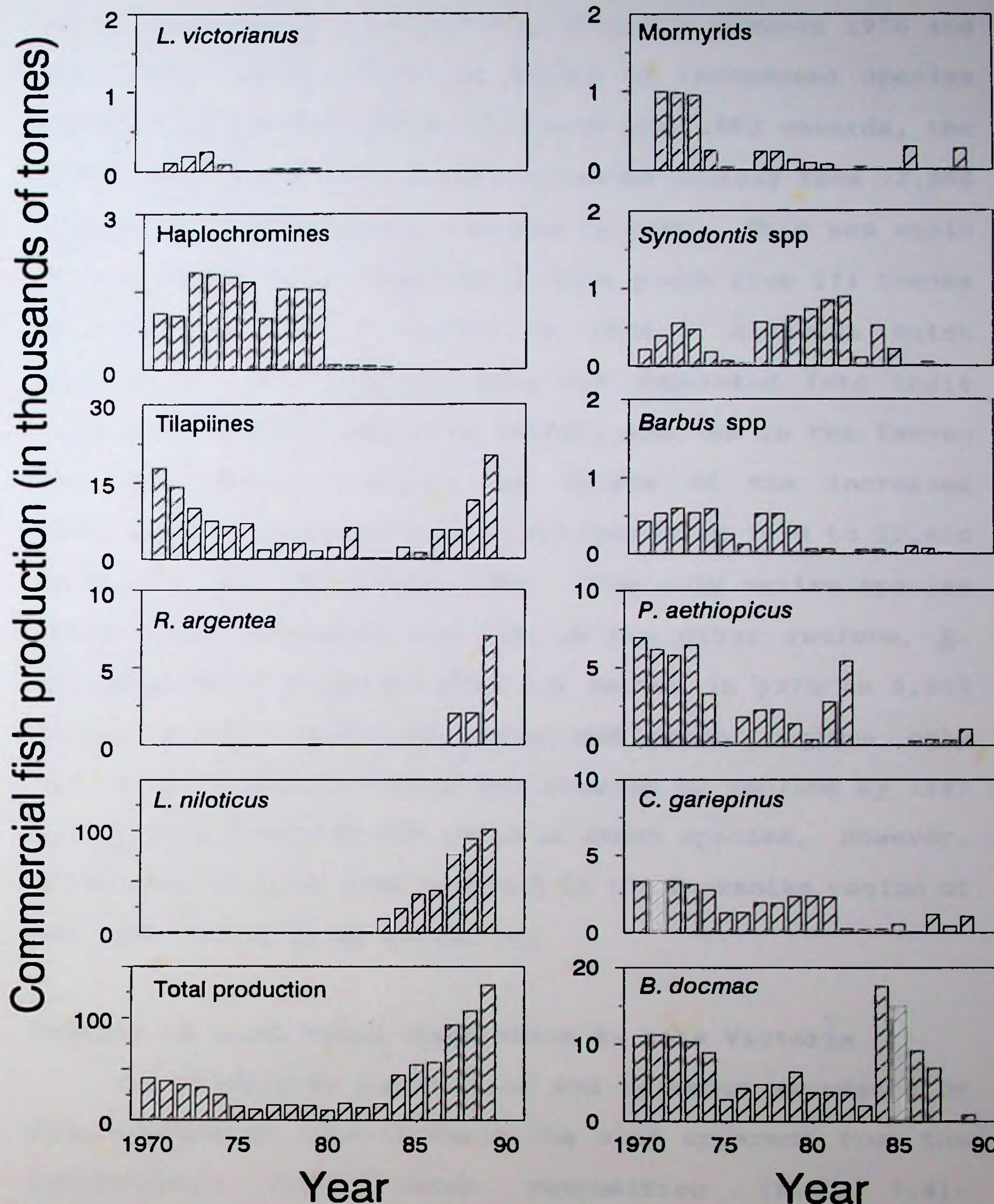


Figure 3.2. Changes in commercial fishery yield from the Ugandan waters of Lake Victoria between 1970 and 1990

region of Lake Victoria are available only up to 1987. Total fish yield increased only slightly between 1970 and 1982 (Fig. 3.3). When the stocks of introduced species especially the Nile perch increased from 1983 onwards, the total quantity of fish landed increased rapidly from 72,586 tonnes in 1983 to 216,403 tonnes in 1986. This was again due to increases in landings of Nile perch from 274 tonnes in 1981 to 123,879 tonnes in 1986. Although catch statistics for tilapiines were not separated into their composite species, the Nile tilapia was, as in the Kenyan and the Ugandan regions, the source of the increased landings of tilapiines from 6,359 tonnes in 1970 to 17,630 tonnes in 1986 (Bwathondi 1987). The only native species whose yield increased was, as in the other regions, _R. argentea_ which increased from 252 tonnes in 1976 to 9,825 tonnes in 1986. Unlike the Kenyan and Ugandan regions, only the yield of haplochromines had started to decline by 1987 with little change in the yield of other species. However, these species later also declined in the Tanzanian region of the lake (Witte _et al_ 1992a, b).

Changes in trawl catch composition in Lake Victoria

The changes in composition and relative abundance of fish species in Lake Victoria was also apparent from the experimental trawl catch composition (Fig. 3.4). Haplochromines comprised up to 80% of the demersal fish stocks in Lake Victoria in 1970 (Kudhongania & Cordone,

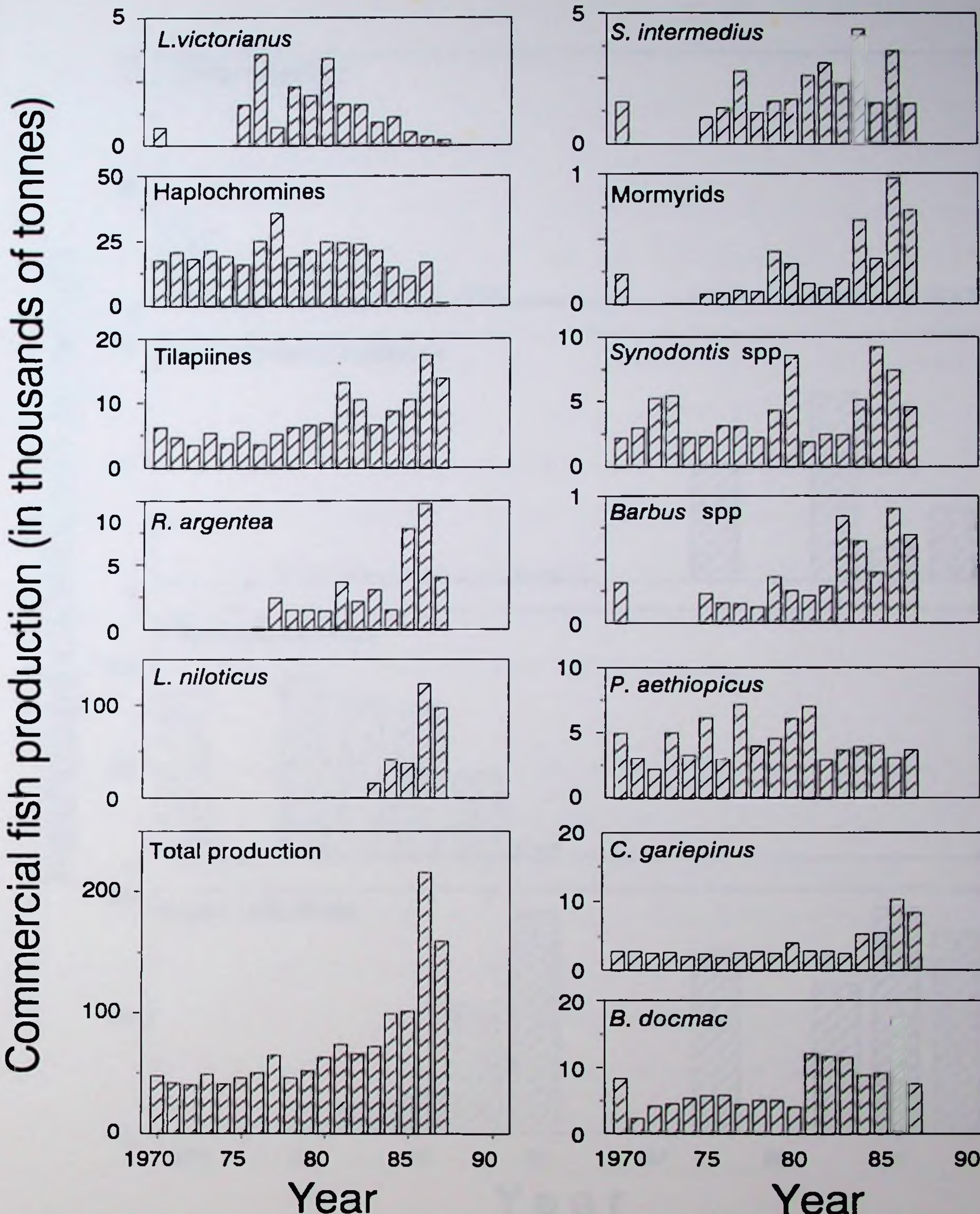


Figure 3.3. Changes in commercial fishery yield from the Tanzanian region of Lake Victoria between 1970 and 1990. Data for 1988 to 1990 were not available.

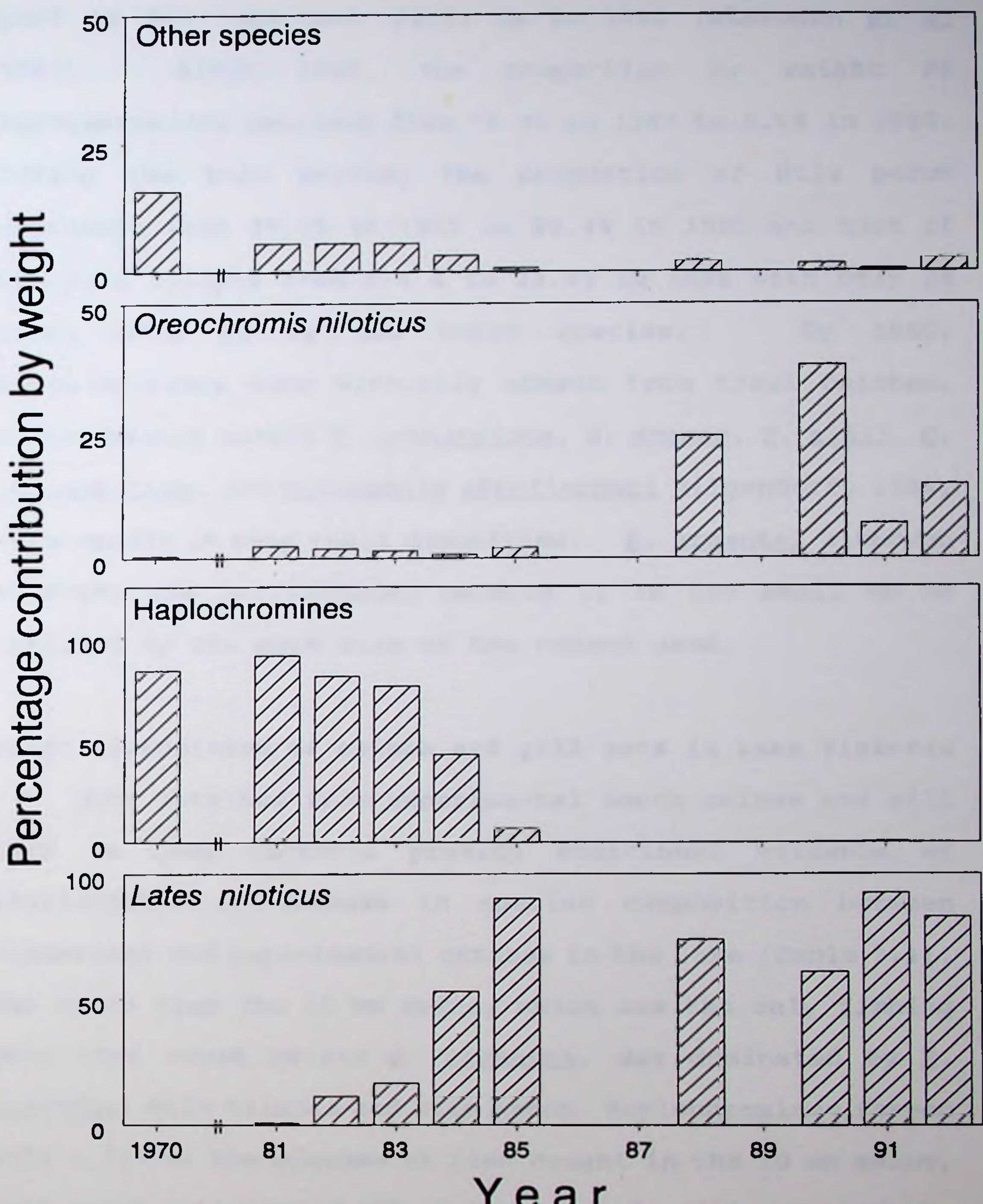


Figure 3.4. Changes in trawl catch composition in the northern region of Lake Victoria between 1970 and 1992.

1974) and remained the most abundant taxa in the northern part of the lake near Jinja up to 1982 (Okaronon et al 1985). After 1982, the proportion by weight of haplochromines declined from 76.2% in 1983 to 6.9% in 1985. During the same period, the proportion of Nile perch increased from 16.8% in 1983 to 90.4% in 1985 and that of the Nile tilapia from 0.4 % to 23.9% in 1988 with only 2% being made up by the other species. By 1985, haplochromines were virtually absent from trawl catches. Other species namely P. aethiopicus, B. docmac, T. zilli, O. leucostictus, and Synodontis afrofischeri Hilgendorf, 1888, were caught in very small quantities. R. argentea although abundant was not recorded because it is too small to be retained by the mesh size of the codend used.

Catch composition of seines and gill nets in Lake Victoria

Data obtained from experimental beach seines and gill nets in Lake Victoria provide additional evidence of similarities in changes in species composition between commercial and experimental catches in the lake (Table 3.1). The catch from the 10 mm seine, which was the only fishing gear that could retain R. argentea, was dominated by R. argentea, Nile tilapia and Nile perch. Haplochromines formed only 5.77% of the biomass of fish caught in the 10 mm seine. Nile perch contributed 97% of the catch in gill nets and the 51 mm mesh seine followed by the Nile tilapia. Haplochromines, mormyrids, O. leucostictus and T. zillii

Table 3.1. Percentage contribution by weight, of different fish taxa caught in experimental sampling in Lake Victoria from 1988 to 1992.

Type of fishing gear:	10 mm seine	51 mm seine	Gill nets	19 mm Trawl
Fish taxa:				
<u>Lates</u> <u>niloticus</u>	18.13	97.89	97.17	80.01
<u>Oreochromis</u> <u>niloticus</u>	22.76	1.93	1.01	14.43
<u>Rastrineobola</u> <u>argentea</u>	39.10			
Haplochromines	5.77	0.06	0.03	0.09
Mormyrids			1.77	
<u>Bagrus</u> <u>docmac</u>				0.74
<u>Clarias</u> <u>gariepinus</u>				0.05
<u>Oreochromis</u> <u>leucostictus</u>			0.01	0.00
<u>Protopterus</u> <u>aethiopicus</u>				0.92
<u>Synodontis</u> <u>afrofischeri</u>				0.09
<u>Tilapia</u> <u>zillii</u>		0.13	0.02	0.12
Unidentified tilapiines	14.25			3.47
Weight sampled (kg)	213	4847	1836	5580

were caught in very small quantities.

Changes in commercial catch composition of Lake Kyoga

Fish species composition of Lake Kyoga prior to the establishment of introduced species was similar to that of Lake Victoria (Worthington 1929). O. esculentus, O. variabilis, P. aethiopicus, B. docmac, C. gariepinus, S. intermedius, Barbus spp and mormyrids were the major commercial species. Haplochromines were also abundant. These remained the dominant species up to the time of the introduction of the Nile perch (Ogutu-Ohwayo 1985).

Nile perch and the non-native tilapiine species were introduced earlier and spread faster in Lake Kyoga than in Lake Victoria (Gee 1964). However, unlike in Lake Victoria, the catch statistics of Lake Kyoga were not split into their constituent species. Stocks of the introduced species in Lake Kyoga increased rapidly from 1963 onwards (Fig. 3.5). This resulted in increases in yield from 18,261 tonnes in 1964 to a peak of 167,200 tonnes in 1978. These were due to a rise in the contribution of Nile perch from 657 tonnes in 1964 to 71,000 tonnes in 1978 and that of the introduced tilapiines especially the Nile tilapia from 589 tonnes in 1964 to 80,960 tonnes in 1985. The yield of the native tilapiines which had dominated the fishery since its development and that of all the other native species declined. However, total yield declined from 167,200 tonnes recorded at peak production in 1978 to 54,706 tonnes by

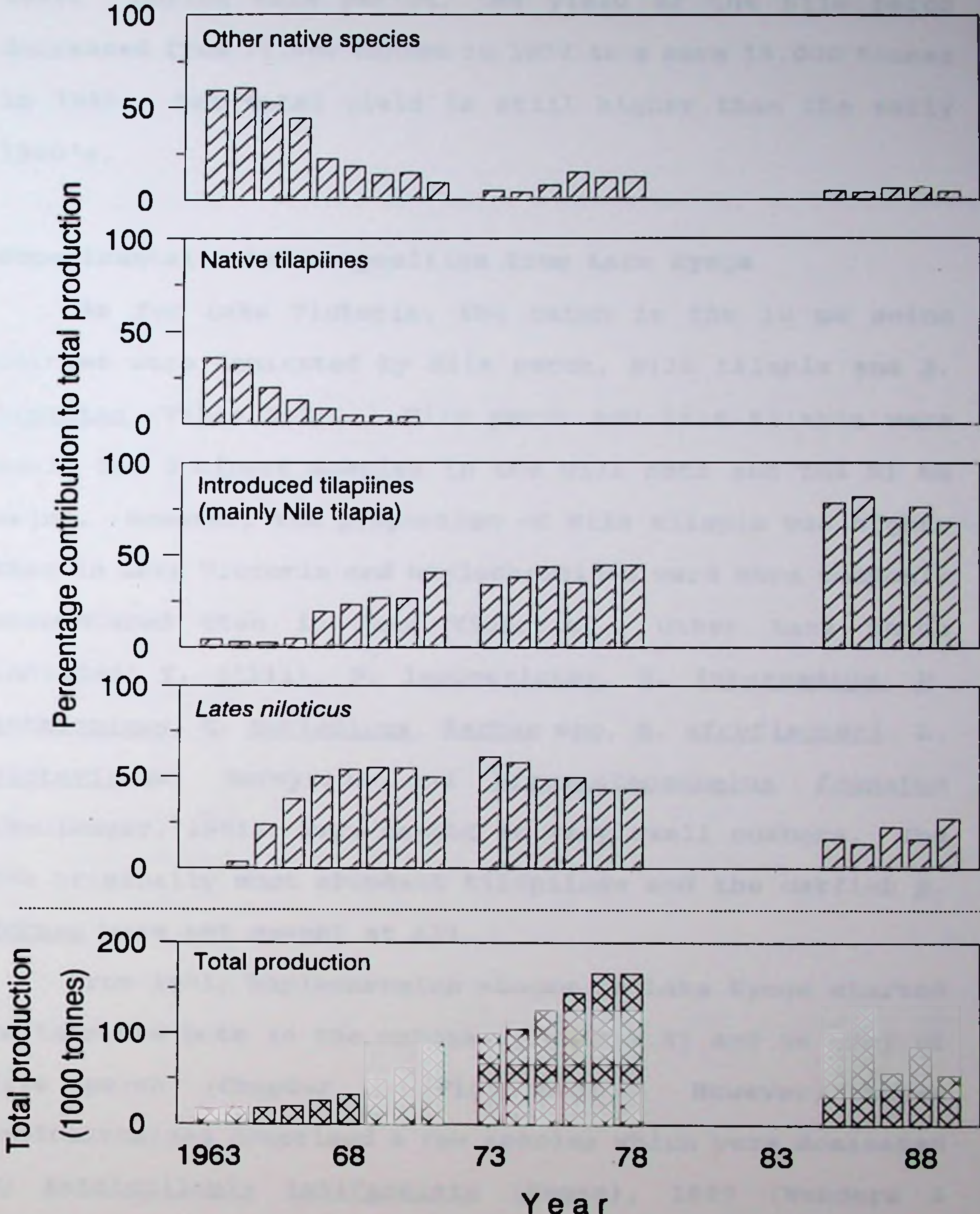


Figure 3.5. Changes in the contribution of different fish taxa to total yield since establishment of introduced species in Lake Kyoga. Data for 1979 to 1984 were not available.

1989. During this period, the yield of the Nile perch decreased from 71,000 tonnes in 1977 to a mere 15,000 tonnes in 1989. But total yield is still higher than the early 1960's.

Experimental catch composition from Lake Kyoga

As for Lake Victoria, the catch in the 10 mm seine catches were dominated by Nile perch, Nile tilapia and R. argentea (Table 3.2). Nile perch and Nile tilapia were again the dominant species in the gill nets and the 51 mm seine. However, the proportion of Nile tilapia was higher than in Lake Victoria and haplochromines were more commonly encountered than in Lake Victoria. Other taxa which included; T. zillii, O. leucostictus, S. intermedius, P. aethiopicus, C. gariepinus, Barbus spp, S. afrofischeri, L. victorianus, mormyrids and Afromastecembelus frenatus (Boulenger, 1901), were caught in very small numbers. The two originally most abundant tilapiines and the catfish B. docmac were not caught at all.

From 1991, haplochromine stocks in Lake Kyoga started to increase both in the catches (Table 3.3) and as prey of Nile perch (Chapter 4: Fig. 4.2). However, these haplochromines comprised a few species which were dominated by Astatotilapia latifasciata (Regan), 1929 (Wandera & Namulemo personal communications). This increase may, therefore, not represent a recovery in the haplochromines species flock but merely an improvement in stocks of a few

Table 3.2. Percentage contribution of different fish taxa, by weight, in experimental sampling on Lake Kyoga between 1988 and 1993.

Fishing gear:	10 mm seine		51 mm seine net		Gillnets	
	1988 1990	1991 1993	1988 1990	1991 1993	1988 1990	1991 1993
Fish taxa:						
L. niloticus	59.23	61.60	25.75	74.48	65.55	79.50
O. niloticus	34.63	13.03	68.25	23.31	32.54	18.85
R. argentea	5.17	13.17				
Haplochromines	0.98	0.78	0.00	0.04	0.04	0.26
T. zillii		5.55	5.29	1.57		0.20
O. leucostictus		0.19	0.38	0.37		0.01
Barbus spp		0.04	0.01	0.01	0.39	0.92
S. intermedius			0.02		1.31	0.02
C. gariepinus					0.18	0.41
Mormyrids						0.02
P. aethiopicus			0.29	0.13		
S. afrofischeri			0.00	0.04		0.00
A. frenatus			0.02	0.06		0.00
L. victorianus		0.12				0.00
Other tilapiines		5.52				
Weight (kg)	38.8	51.5	2737	903	1855	5027

Table 3.3. The catch rates of haplochromine cichlids per fishing night in 25.4 mm and 38.1 mm stretched mesh gillnets of 90 m length in Lake Kyoga. The fishing fleet had one net of each mesh.

Period:	1988/90	1991	1992	1993
Number of fishing nights:	40	91	93	73
Maximum number in a night:	30	48	348	213
Mean number per night:	1.58	2.14	13.52	21.27
1 SE of the mean:	0.83	0.85	4.19	4.97

species that may have survived among some refugia and may have some capacity to persist in the presence of the Nile perch.

Experimental catches from Lake Nabugabo

There were no commercial catch statistics for Lake Nabugabo. When the Cambridge expedition surveyed the lake in 1962, the most important fishes among commercial catches were similar to those of lakes Victoria and Kyoga and comprised; P. aethiopicus, B. docmac, S. intermedius, C. gariepinus, O. esculentus, O. variabilis and haplochromines. The expedition also recorded thirteen non-cichlids and eight haplochromine species from experimental samples (Cambridge expedition 1962, Ogutu-Ohwayo 1993).

The relative importance of the fish taxa recorded from Lake Nabugabo between 1991 and 1992 is shown in Table 3.4. The 10 mm seine was dominated by juveniles of Nile perch, Nile tilapia, R. argentea and T. rendalli. Nile perch and Nile tilapia were again the most abundant species in the gill nets and the 51 mm seine. However, S. intermedius was caught in large numbers in gill nets in the lake and contributed 6.96% to the gill net catches. Also T. rendalli, B. jacksonii and T. zillii made significant contributions to gill net catches. Other taxa which included, C. gariepinus, mormyrids, O. leucostictus and S. afrofischeri were, as in lakes Victoria and Kyoga, caught only in very small quantities.

Table 3.4. Percentage contribution of the different fish taxa by weight, in experimental sampling in Lake Nabugabo between 1991 and 1992.

Type of fishing gear:	10 mm seine	51 mm seine	Gill nets
Fish taxa:			
Lates niloticus	78.72	86.92	67.73
Oreochromis niloticus	8.92	8.28	15.17
Rastrineobola argentea	5.10		
Haplochromines	0.28	0.59	1.66
Schilbe intermedius		0.77	6.96
Mormyrids		0.01	0.05
Clarias gariepinus			0.25
Oreochromis leucostictus			0.19
Synodontis afrofischeri	0.00	0.01	0.08
Brycinus jacksonii	0.07	0.14	2.77
Tilapia zillii	0.00	1.31	2.23
Tilapia rendalli	6.91	1.97	2.92
Barbus spp	0.00		
Weight sampled (kg)	196	280	317

Changes in commercial catch composition of Lake Albert

The original state of the fishery of Lake Albert is given by Worthington (1929). The most important commercial taxa, in order of importance were Citharinus citharus Boulenger, 1905, Lates spp (comprising L. niloticus and L. macrophthalmus, Nile tilapia, Bagrus spp, Alestes baremose, Boulenger 1901, Hydrocynus forskalii, Cuvier 1819, Synodontis shall, Bloch & Schneider, 1801, and Mormyrus caschive, Linne, 1758.

The contribution of different taxa to total yield in Lake Albert for the period 1971 to 1989 is illustrated in Fig. 3.6. The fish species composition of the lake has not changed much from what was recorded by Worthington about 60 years ago. Fourteen taxa still occur regularly among commercial catches. Lates spp, tilapiines (mainly O. niloticus), and two pelagic Characid taxa, Hydrocynus spp and Alestes spp were still among the most important commercial species. The only originally important species which was no longer abundant among commercial catches was C. citharus. This species was depleted due to overfishing during the first part of this century (Cadwalladr & Stoneman 1966).

Experimental sampling carried out on Lake Albert in 1990 to 1992 (Table 3.5) showed that the commercial catch records gave a good picture of what was present in the lake. Lates spp, Hydrocynus spp, Alestes spp and tilapiines were the most abundant taxa in the sample examined. Even C.

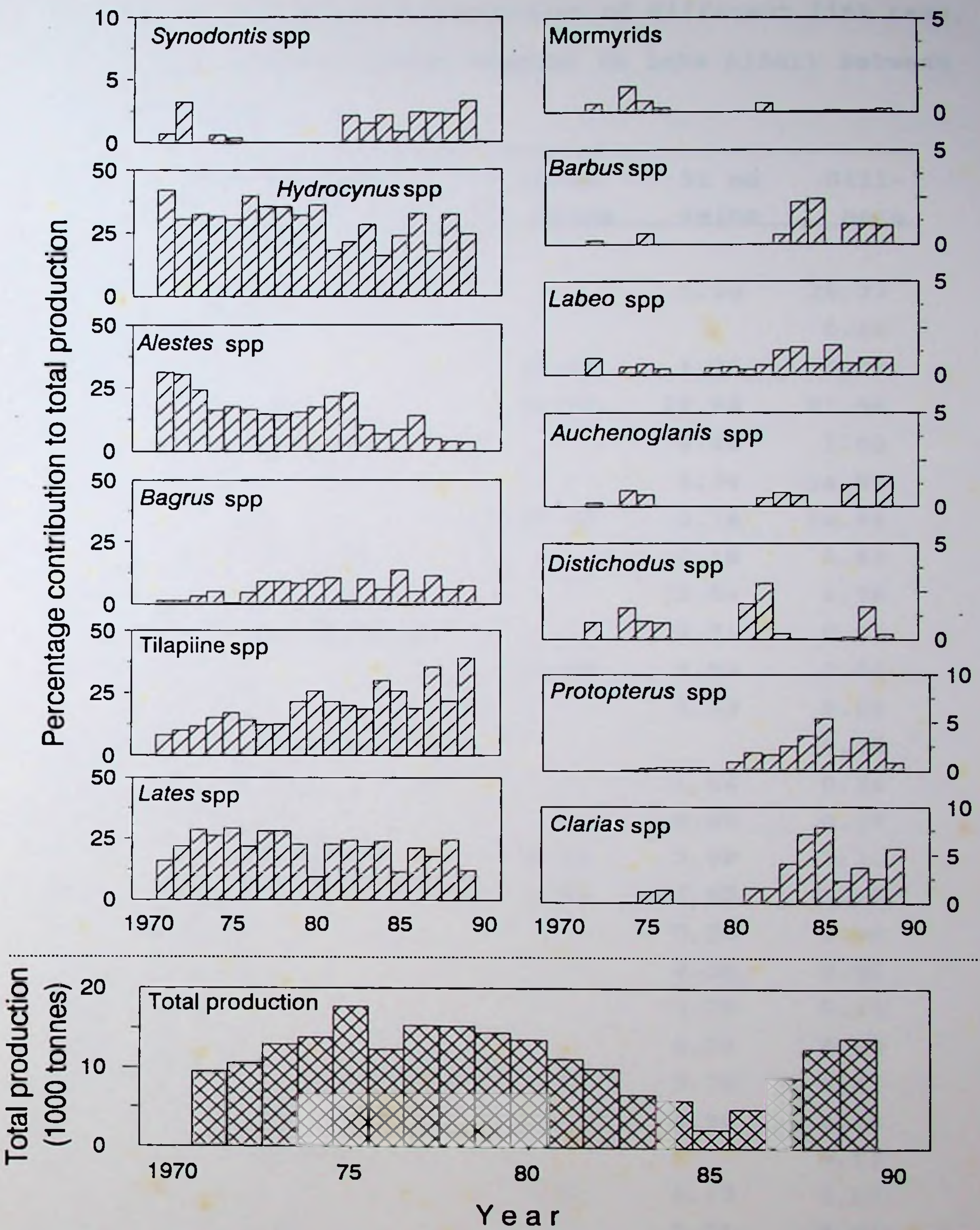


Figure 3.6. The contribution of different fish taxa to total yield in Lake Albert from 1971 to 1989.

Table 3.5. Percentage contribution of different fish taxa, by weight, to experimental samples in Lake Albert between 1989 and 1992.

Type of fishing gear:	10 mm seine	51 mm seine	Gill-nets
Fish taxa:			
Alestes baremose		1.96	25.27
Alestes dentex			0.65
Alestes nurse	21.03	1.76	0.01
Lates niloticus	24.66	22.65	21.96
Lates macrophthalmus		8.42	1.03
Barbus bynni		2.34	14.95
Hydrocynus spp	15.08	0.78	14.66
Distichodus niloticus		0.18	8.63
Oreochromis niloticus		32.54	4.76
Oreochromis leucostictus		0.31	0.03
Tilapia zillii	14.90	0.56	0.08
Mormyrops spp		1.35	2.05
Mormyrus niloticus			0.36
Mormyrus kannume		1.66	0.34
Gnathonemus spp		0.09	0.19
Clarias gariepinus	0.13	2.68	1.31
Bagrus bayad	3.05	14.55	1.30
Bagrus docmac		0.36	0.39
Synodontis spp		0.26	0.61
Labeo horie		0.75	0.45
Labeo coubie		0.03	0.20
Auchenoglanis occidentalis	1.91	5.75	0.44
Malapterurus electricus		0.90	0.14
Citharinus citharus			0.11
Haplochromines	4.63	0.13	0.03
Schilbe intermedius		0.01	0.02
Neobola bredoi	0.12		
Barilus niloticus	14.50		
Weight sampled (kg)	69	1145	4830

citharus which had been feared to be extinct in the lake was encountered although in very small numbers. Unlike in lakes Victoria, Kyoga and Nabugabo, where many species have disappeared, none has vanished from Lake Albert since the first fishery survey of the lake.

Changes in fish species diversity

The changes in fish species diversity following establishment of the Nile perch in the new habitats were examined by comparing changes in Shannon-Weaver indices of diversity H' in the Kenyan, Ugandan and Tanzanian regions of Lake Victoria between 1970 and 1990 before and after the rapid increases in Nile perch stocks and that of Lake Albert. Nile perch stocks started increasing rapidly in 1977 in the Kenyan region (Hughes 1986), in 1982 in the Ugandan region (Okaronon et al 1985) and in 1983 in the Tanzanian region of Lake Victoria (Goudswaard & Witte 1985). It was assumed that predation by the Nile perch had reduced H' from the level recorded before its stocks started increasing rapidly to a significantly lower level. Before the rapid increases in Nile perch stocks, H' was assumed to have remained in limits within which it did not change significantly. After prey species which were not resilient and could not persist in the presence of the Nile perch were eliminated by predation, H' declined to a significantly lower level and again remained in limits within which it did not change significantly and at which it was maintained by prey species that were resilient and could persist in the presence of the predator.

The critical limits for the period before the rapid increases in Nile perch stocks were determined using values of H' from 1970 up to the year when Nile perch stocks in that region of the lake started increasing rapidly. That for the period after rapid increases in Nile perch stocks was derived from the value outside and below those of the period before the rapid increases. The centre value for each of the periods was determined by taking the average of H' values for each period. The critical limits were determined by calculating the average moving ranges between consecutive values and using a Control Chart Table (Griffiths 1989). The level of confidence attached to these limits is 99%.

The changes in H' for the period before the rapid increases in Nile perch stocks and that after the rapid increases for the different regions of Lake Victoria and those of Lake Albert are illustrated in Figure 3.7. In the Kenyan and Ugandan regions, there were two distinct levels of fish species diversity corresponding to the period before and after the rapid increases in Nile perch stocks. After the rapid decline in H' in these regions, H' did not decline further and remained within the critical limits except for one value in the Kenyan region for 1989 which was above the critical limits. However, any increase of H' above the critical limits would indicate that resilience was exceeding

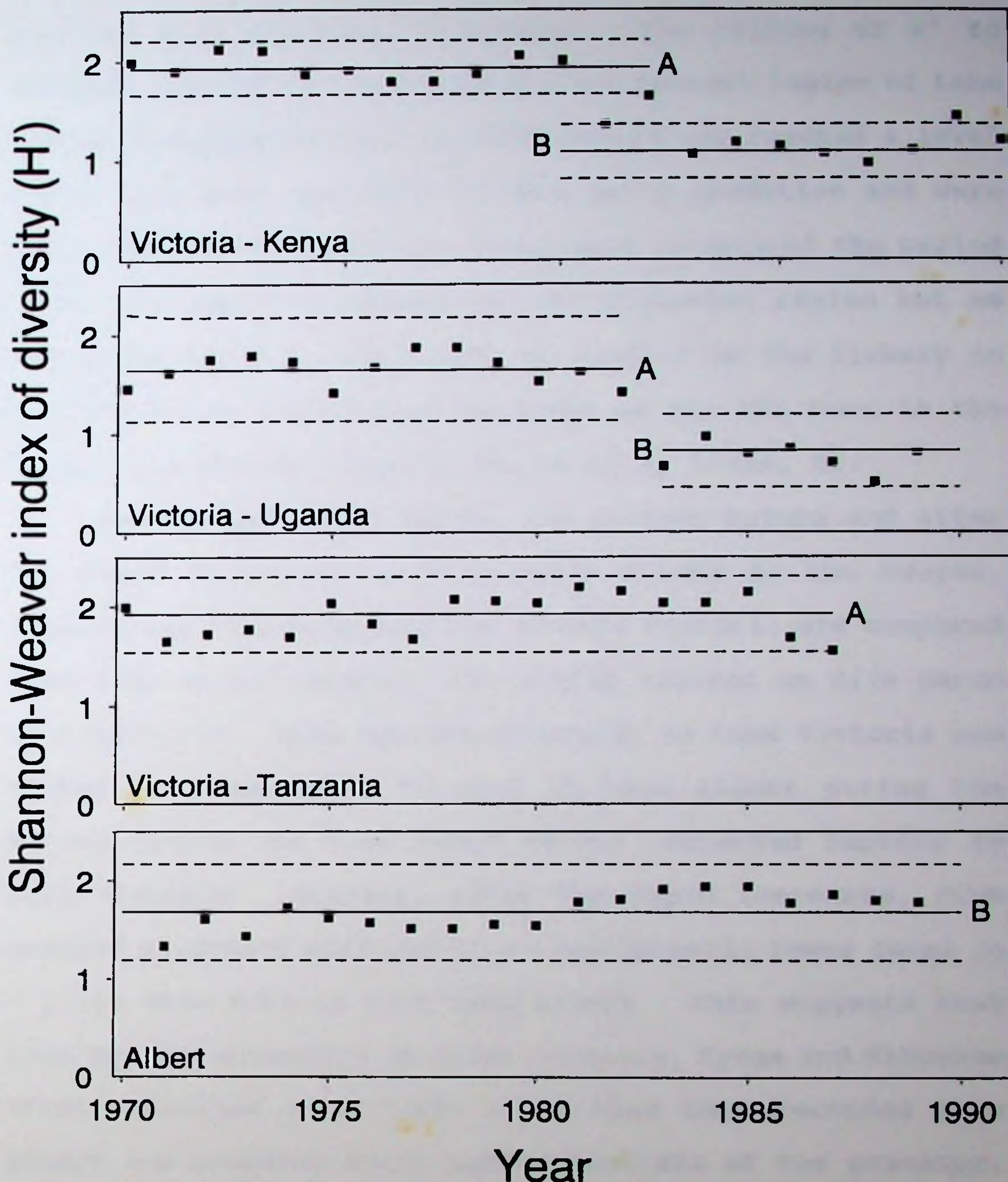


Figure 3.7. Changes in fish species diversity in lakes Victoria and Albert between 1970 and 1990. In each case the solid line represents the centre line and the long dash lines the critical limits within which H' occured before and after rapid increases in Nile perch stocks in Lake Victoria and those for Lake Albert. A is the pre and B the post perch level of diversity.

the perturbation due to Nile perch predation and some species were starting to recover. The failure of H' to decline further in the Kenyan and the Ugandan region of Lake Victoria suggested that the fish stocks had reached a level where they were resilient to Nile perch predation and were stable during that period. There were no data of the period after the rapid increases for the Tanzanian region but as mentioned earlier, the number of species in the fishery in the Tanzanian region also declined as was the case in the Kenyan and Ugandan regions (Witte et al 1992a, b).

The changes in H' during the periods before and after the rapid increases in Nile perch stocks in the Kenyan, Ugandan and Tanzanian regions of Lake Victoria are compared with that of Lake Albert, the native habitat on Nile perch in Figure 3.8. Fish species diversity in Lake Victoria was higher and comparable to that in Lake Albert during the period before the Nile perch stocks increased rapidly in Lake Victoria. However, after the rapid increases, fish species diversity declined to a significantly lower level ($p < 0.01$) than that of even Lake Albert. This suggests that fish species diversity in lakes Victoria, Kyoga and Nabugabo might stabilize at a lower value than that recorded Lake Albert and probably other native habitats of the predator.

Discussion

Haplochromines which were the most abundant fish species in lakes Victoria, Kyoga and Nabugabo prior to the

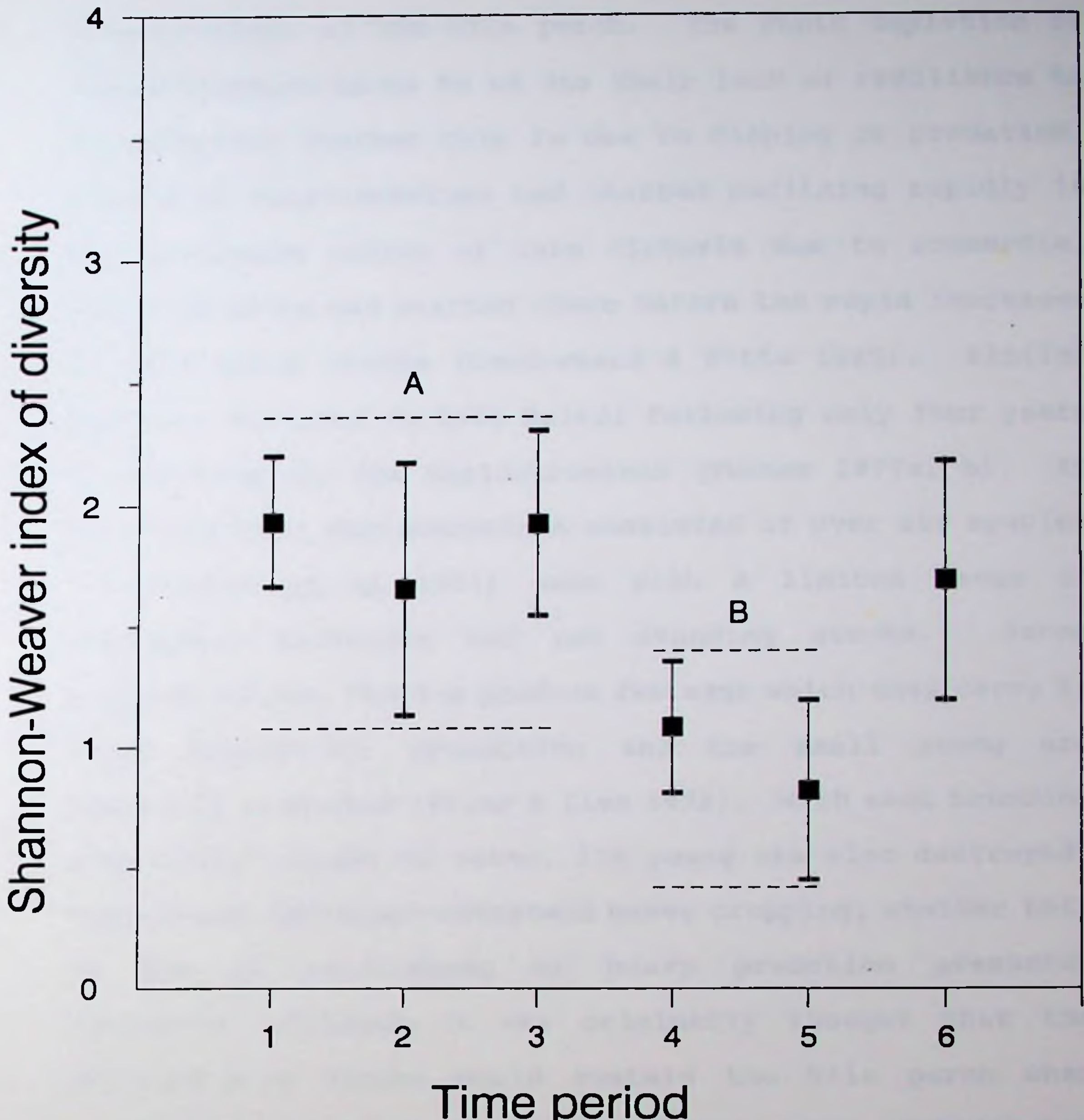


Figure 3.8. A comparison of Shannon-Weaver indices of diversity during the pre (A) and (B) post-establishment periods of the Nile perch in the Kenyan (1 & 4), Ugandan (2 & 5) and Tanzanian (3) regions of Lake Victoria and Lake Albert (6). Vertical bars represent upper and lower critical limits ($p < 0.01$).

establishment of Nile perch were depleted rapidly following establishment of the Nile perch. The rapid depletion of haplochromines seems to be due their lack of resilience to exploitation whether this is due to fishing or predation. Stocks of haplochromines had started declining rapidly in the Tanzanian region of lake Victoria due to commercial trawling which had started there before the rapid increases in Nile perch stocks (Goudswaard & Witte 1985). Similar declines occurred in Lake Malawi following only four years of trawling for the haplochromines (Turner 1977a, b). In Lake Victoria, haplochromines consisted of over 300 species (van Oijen et al 1981) each with a limited range of ecological tolerance and low standing stocks. Among haplochromines, females produce few eggs which they carry in their mouths for protection and the small young are similarly protected (Fryer & Iles 1972). With each brooding fish either caught or eaten, its young are also destroyed. They cannot therefore withstand heavy cropping, whether this is due to overfishing or heavy predation pressure. Therefore, although it was originally thought that the haplochromine stocks would sustain the Nile perch when introduced into Lake Victoria (Graham 1929, Worthington 1929, Anderson 1961), current knowledge suggests that they do not have the capability to do so.

Following the establishment of Nile perch, the diversity of exploited fish taxa in lakes Victoria, Kyoga and Nabugabo has declined from about 12 taxa before establishment of Nile perch to only three, L. niloticus, O. niloticus and R. argentea. Since this change, the number of fish taxa has not decreased further and fish species composition has not changed for at least 10 years in Lake Victoria and for probably longer periods in lakes Kyoga and Nabugabo where Nile perch were introduced and became well established earlier. This suggest that O. niloticus, R. argentea, and apparently Nile perch itself are resilient and can persist in the presence on the predator.

The parallel success of O. niloticus alongside the predatory Nile perch may be related to their origin. Both are native to Lake Albert, the Nile below Murchison Falls, Lake Turkana, the Chad basin and rivers of West Africa (Lowe McConnell 1988, Skelton 1988). O. niloticus is likely to be less vulnerable to predation from the Nile perch than the indigenous tilapiines of lakes Victoria, Kyoga and Nabugabo as it has evolved with the predator. O. niloticus may have evolved behavioral responses to reduce predation losses from the Nile perch. Similar behaviour by the native tilapiines in lakes Victoria, Kyoga and Nabugabo would not have been necessary.

The only native species which has persisted in the presence of Nile perch is R. argentea. The success of R. argentea could be due to the shoaling behaviour and the pelagic position it occupies in the water column. Hamblyn (1966) has shown that Nile perch is least successful in capturing pelagic prey or those swimming near the surface.

R. argentea could reduce predation losses by taking up a pelagic position. Lakes occupied by L. niloticus or Lates spp in general eg. Lake Tanganyika are dominated by pelagic species (Coulter 1965).

There are some similarities between the current fisheries of the lakes invaded by Nile perch and those of Lake Albert and other native habitats of the Nile perch. Nile perch and Nile tilapia, which are the dominant species in the three lakes are also among the dominant species in Lake Albert (Worthington 1929 & this study) and in Lake Turkana (Beadle 1981, Hopson 1982). At least one of the two remaining major components of the catch in Lake Albert Alestes spp (the other being the piscivorous Hydrocynus spp) is pelagic and can be regarded as ecologically analogous to R. argentea, at least in respect to their lower susceptibility to predation by the Nile perch. Alestes spp are also abundant in Lake Chad (Hospon 1972). However, species diversity of the lakes invaded by Nile perch is lower than that of Lake Albert suggesting that fish species diversity in the new habitats might stabilize at a different level although further improvement is possible as stocks of some taxa in the invaded habitats eg. the haplochromines and B. jacksoni have started increasing. B. jacksoni (formerly Alestes jacksoni) is similar in size and appearance to Alestes nurse which is a major prey of L. niloticus in Lake Albert (Greenwood 1966).

Total yield of lakes Victoria, Kyoga and apparently

Nabugabo (where no commercial catch records are available) increased following establishment of the Nile perch. It appears, however, that these fisheries will not sustain the peak yields recorded in these lakes. Total yield from Lake Kyoga where Nile perch became established earlier than Lake Victoria has declined (Fig. 3.5). Although this was attributed to intensive use of small mesh seines (Twongo personal communication), the declines were more prominent among Nile perch populations and could have been partly due to the reduction in food supply. The large quantities of Nile perch landed in lakes Victoria and Kyoga soon after establishment of the predator were originally supported by the large quantities of vulnerable haplochromines which at that time formed the main prey of Nile perch (Hamblyn 1966, Gee 1964, 1969, Okedi 1971). Since these haplochromines have been depleted its is unlikely that production can be maintained at that level.

Factors that have facilitated improvement of haplochromine stocks in Lake Kyoga would be useful in enhancement of some of the fish species that were depleted from the lakes to which Nile perch were introduced. The increase in haplochromine stocks in Lake Kyoga coincided with the invasion and spread of water hyacinth <u>Eichhornia crassipes</u> (Martius) Solm which invaded the lake in 1988 and became well established between 1991 and 1992 (Twongo 1991). Floating beds of water hyacinths provide cover and as they move disperse haplochromines which survived under cover among macrophytes along the margins of the lakes and among other refugia and allows them to recolonize the lake and multiply. Goeltenboth and Kristyanto (1987) have noted that the water hyacinth can provide a valuable habitat as long as it is kept under control. Areas covered by the hyacinth can support a large and diverse community of aquatic organisms (Willoughby et al, 1993). The planned control of the water hyacinth in lakes Victoria and Kyoga, is likely to re-expose the haplochromines to predation and might result in their decline. Also, even if the hyacinth has invaded Lake Victoria, its distribution may not become as extensive as in Lake Kyoga, because Victoria is deeper and more open. The water hyacinth thrives in shallow sheltered areas. The haplochromine cichlids may, therefore, never recover to the same extent in Lake Victoria as in Kyoga. The recovery in haplochromines may also have been enhanced by possible reduction in Nile perch stocks due to the very high fishing pressure and the indiscriminate use of seine nets. However, as mentioned earlier, haplochromines are not generally resilient to exploitation. The recovery of haplochromines in the habitats invaded by the Nile perch can only be of long term benefit if the fish have developed behavioral characteristics to reduce predation losses. Structural refugia such as that provided by the water hyacinth cannot be relied on to sustain Nile perch stocks although it provides temporary relief and once the cover is removed, the haplochromines will again be depleted. The sustainability of the Nile perch fishery in lakes Victoria and Kyoga cannot depend on this recovery if the recovery itself is not sustainable.

Even if haplochromines stocks in lakes Victoria, Kyoga and Nabugabo improve, these are likely to consist of a few species that can persist in the presence of the Nile perch. Only a few species have so far recovered in open waters of Lake Kyoga (Wandera & Namulemo personal communication). Generally the lakes in which Nile perch is native have very few haplochromine species; Lake Albert has four and Lake Turkana only three (Greenwood, 1974). The only exception is Lake Tanganyika, which has haplochromine species-flocks, but these occur in the presence of different species of Lates. Also the Lake Tanganyika haplochromines are confined to rocky inshore areas where there is permanent refugia in which they can take shelter from Lates spp (Fryer & Iles, 1972). As in Lake Tanganyika, it is the rock-dwelling haplochromines which have been least depleted in Lake Victoria (Ogutu-Ohwayo 1990c, Witte et al, 1992a, b) but such rocky habitats are generally lacking in the lakes invaded by the Nile perch. Nevertheless, protection of refugia such as rocky outcrops and marginal vegetation will be beneficial to the preservation and recovery of the haplochromines and other species in lakes to which the Nile perch was introduced.

Apart from the introduced species especially Nile perch, other factors, especially over-exploitation and environmental degradation, have affected and are likely to continue to affect stability and viability of fisheries in lakes Victoria, Kyoga and Nabugabo. Over-exploitation and use of destructive fishing practices contributed greatly to depletion of fish stocks in these lakes prior to establishment of Nile perch (Jackson 1971, Ogutu-Ohwayo 1990a). Whereas _Alestes nurse_ Myers, 1929 and the prawn, _Caridina nilotica_ Roux, which are major prey of Nile perch in Lake Albert are not commercially exploited in that lake, _R. argentea_ is heavily exploited in lakes Victoria and Kyoga _C. nilotica_ is being exploited in some parts of Lake Victoria (Ogari & Asila 1992). Juvenile Nile perch which are major prey of sub-adult and adult Nile perch are also heavily exploited especially by the seine fishery. There is already a decline in the mean size of _R. argentea_ cropped by the commercial fishery in Lake Victoria due to the combined effects of predation and human exploitation (Wandera 1992). Control of exploitation of _R. argentea_, juvenile Nile perch and _C. nilotica_ will contribute greatly to the stability of fish stocks in lakes Victoria, Kyoga and Nabugabo.

Conclusion

Following establishment of Nile perch, the number and diversity of fish taxa in commercial landings in lakes Victoria, Kyoga and Nabugabo declined from about 12 to three taxa; _L. niloticus_, _O. niloticus_ and _R. argentea_. After this, there was no further decline in the number of species and in diversity indicating that these three species are resilient to predation and can sustain the fishery. Also stocks some native species especially haplochromines and _A. jacksoni_ have started recovering in some of these lakes indicating that more species may be able to persist in presence of the predator. This should prevent the stocks from collapsing.

Chapter 4

Changes in the types, sizes and numbers of prey eaten by Nile perch, *Lates niloticus* L. in lakes Victoria, Kyoga and Nabugabo

Abstract

Before Nile perch became well established in lakes Victoria, Kyoga and Nabugabo, haplochromine cichlids were the main prey of all but the smallest sizes of the predator. At that time, the average sizes and numbers of prey eaten increased linearly with predator size. After haplochromines were depleted, Caridina nilotica Roux and anisopteran nymphs became the dominant prey of juveniles with the exception of Lake Nabugabo where C. nilotica is absent while larger Nile perch ate Rastrineobola argentea Pellegrin, juvenile Nile perch and Oreochromis niloticus (L.). There were no further changes in the types of prey eaten for 23 years in Lake Kyoga where Nile perch got established earliest, suggesting that these types of prey were resilient. Thereafter, haplochromines again became important as prey in the lake in addition to the above types. Similar trends were observed in lakes Victoria and Nabugabo. The types of prey eaten in lakes Victoria, Kyoga and Nabugabo are now similar to those eaten in native habitats where Nile perch has remained in balance with its prey for a long time. Therefore, the current types of prey can persist and sustain the Nile perch fishery in lakes Victoria, Kyoga and Nabugabo.

Introduction

In lakes Victoria, Kyoga and Nabugabo, the diversity of fish taxa has declined and the abundance of haplochromines which were initially the most important prey of the Nile perch, Lates niloticus L. has dropped. These declines were attributed to predation by the Nile perch (Witte et al. 1992a, b) and have created fears that prey would fall to a level where there would not be enough food to sustain Nile perch stocks (FAO 1985). This would make the Nile perch fishery unviable. An alternative scenario is that some resilient prey are not be depleted and others adopt to the presence of the predator. The populations of the prey and those of the predator then come into equilibrium leading to a sustainable fishery.

Diet selection i.e. the way an organism selects it food, affects its fitness (Pyke 1984). According to optimal foraging theory, individuals while feeding should maximize their net rate of energy gain and foraging behaviour should be dominated by those characteristics that enhance individual fitness. Diet selection theory predicts that: 1) prey types are either always taken upon encounter, or never taken upon encounter, 2) prey items are added to the diet in order of their ratio of energy per attack to handling time per attack and 3) inclusion of a prey type in the diet does not depend on its own encounter rate but depends only on its profitability and on the characteristics of types of a higher rank (Pyke 1984). When a more profitable prey is abundant, the theory predictd that a predator should select this prey and avoid the inferior types (Shoener 1969, 1971).

Field observations and laboratory experiments (Hrbacek et al. 1961, Gerking 1962, Brooks & Dobson 1965, Reif & Tappa 1966, Werner & Hall 1974, Lazzaro 1978, Gerking & Plantz 1980) using zooplankton prey, have shown that when a predator is introduced into a habitat, as in the case of the Nile perch, it chooses the most profitable prey on the basis of size, abundance and catchability. In virtually all the cases, the larger members of the prey population are depleted or eliminated leaving smaller types to dominate the prey population. When a predator is faced with this type of situation, it switches to the smaller prey and may meet its energy requirements by adjusting the numbers of prey eaten.

Changes in the types, sizes and numbers of prey eaten by the Nile perch in the habitats to which it was introduced were examined and compared with the situation in native habitats. It was predicted that Nile perch initially fed on the most suitably sized and vulnerable types of prey. They then switched sizes and numbers of prey eaten as those prey types which were not resilient and could not persist in the presence of the predator were eliminated. Thereafter, the predator switched to other available prey until only those prey that were resilient remained abundant. Later, stocks of some species, especially those that would have survived e.g. among macrophytes or rocky outcrops then increased. These changes would be accompanied by shifts in types, sizes and numbers of prey as a new steady state is approached. This state should either be unique to the new habitats or be similar to those in native habitats of the Nile perch. In steady state, the types, sizes and numbers of prey eaten by the Nile perch in the new habitats should not change outside a range of normal variance.

Materials and methods

The changes in the types, sizes and numbers of prey eaten by Nile perch were examined by comparing data from Lake Victoria between 1968 and 1992, Lake Nabugabo from 1991 to 1993, Lake Kyoga between 1967 and 1993 and Lake Albert between 1989 to 1992. Previous information for lakes Victoria and Kyoga was obtained from the reports of Gee (1964, 1969) and Hamblyn (1966). That for other native habitats of Nile perch were obtained from the reports of Hopson (1972, 1982) for lakes Chad and Turkana and Kenchington (1939) for the Nile at Sennar.

Nile perch were obtained from commercial landings and experimental fishing. Biometric data taken on individual Nile perch included total length, standard length, weight, sex, maturity state and stomach fullness. Lengths were measured to the nearest mm. Sex and maturity states were determined as outlined in Chapter 7. Stomach contents were preserved in 5% formalin solution and analyzed in the laboratory. Stomach contents of Nile perch which contained large fish were measured in the field. In the laboratory, the stomach contents were blotted to remove surface moisture and their total weight recorded. Prey were separated in taxonomic groups, and the weight and number of each type and the total length of individual specimens recorded.

Changes in the types, sizes and numbers of prey eaten by the Nile perch over different periods in each lake were analyzed and compared as detailed in Chapter 2.

Results

The type of prey

Most Nile perch stomachs contained only one or two types prey. Therefore, frequency of occurrence of prey in the stomach was considered as a satisfactory way of presenting the importance of prey items in individual fish. The percentage frequency of occurrence of prey items in the stomachs of different size groups of Nile perch in lakes Victoria, Kyoga, Nabugabo and Albert during different periods is illustrated in Figure 4.1.

There were no information on the types of prey ingested by Nile perch of < 20 cm total length in the data collected from Lake Victoria during 1968-77. During this period, ten different types of prey were eaten. Haplochromine cichlids were the dominant prey in most sizes of Nile perch (Fig. 4.1). Other types of prey which were occasionally encountered in the stomachs included; <u>Clarias</u> spp, tilapiines, <u>Protopterus</u> <u>aethiopicus</u> Heckel, mormyrids,

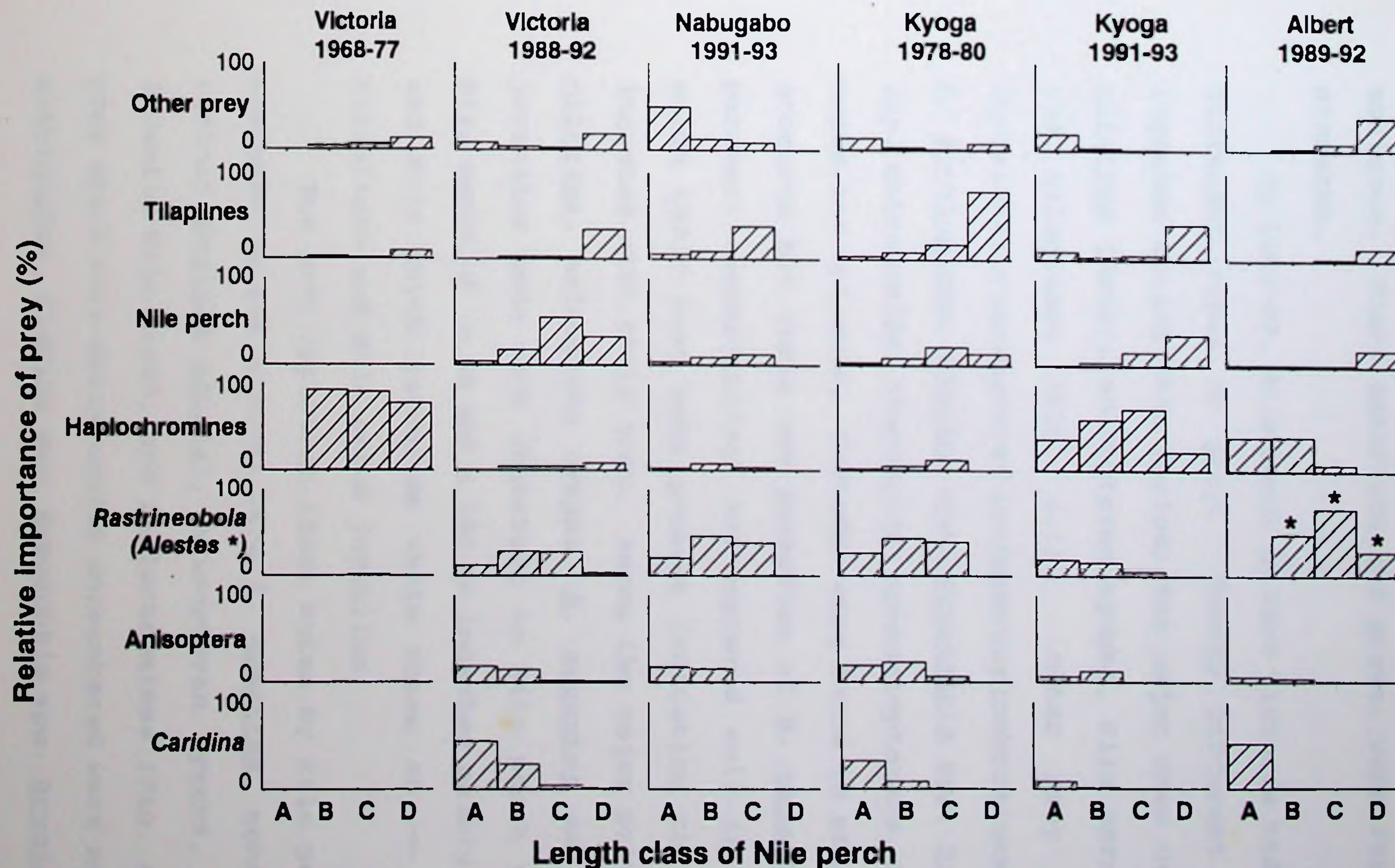


Figure 4.1. The relative importance of prey eaten by Nile perch of different length classes in lakes Victoria, Nabugabo, Kyoga and Albert over different periods. Length classes are:- A: < 20 cm; B: >= 20 cm & < 60 cm; C: >= 60 cm & < 100 cm and D: >= 100 cm.

Synodontis spp, Rastrineobola argentea Pellegrin and molluscs. Plant materials and gravel were found in a few stomachs.

By 1988-92, Nile perch in Lake Victoria had switched to different types of prey. Twenty different items were ingested during this period; the major ones were Caridina nilotica (Roux), anisopteran nymphs, Nile perch juveniles and tilapiines (Fig. 4.1). Other prey which were occasionally encountered included haplochromines, mormyrids, P. eathiopicus, Clarias spp, Synodontis spp, Mastacembelus spp, chironomids, chaoborids, ephemeropterans, Notonectids, crabs and molluscs. Cestodes were found in some Nile perch stomachs but these are parasites of R. argentea (Wandera personal communication) and appeared only in stomachs in which their host were present indicating that they were ingested with their host. Among the major prey items, C. nilotica, anisoptera nymphs, R. argentea and Nile perch juveniles were most important in Nile perch of < 60 cm. Nile perch of >= 60 and < 100 cm ingested mainly R. argentea and Nile perch juveniles while those of >= 100 cm ate tilapiines and Nile perch juveniles.

The most important items eaten by Nile perch in Lake Nabugabo during 1991-93 were R. argentea, ephemeropterans (mainly Povilla adusta), anisopteran nymphs, tilapiines, juvenile Nile perch, and haplochromines (Fig. 4.1). Other prey which were occasionally encountered were mormyrids, P. eathiopicus, Clarias spp, Synodontis spp, Brycinus jacksoni (formerly _Alestes jacksoni_), _Shilbe intermedius_, chironomids, chaoborids, notonectids and corixids. Plant materials and gravel were also found in a few stomachs. Ephemeropterans, _R. argentea_, anisopteran nymphs and chironomids were the main prey in Nile perch of < 20 cm. Nile perch of >= 20 cm and < 60 cm mainly ate _R. argentea_, tilapiines, Nile perch juveniles, haplochromines and ephemeropterans while those of >= 60 cm and < 100 cm mainly ate _R. argentea_ and tilapiines. The few Nile perch specimens of >= 100 cm examined had ingested tilapiines, mormyrids and _P. aethiopicus_. _C. nilotica_ which became very important prey of Nile perch in lakes Victoria and Kyoga after haplochromines had been depleted, and which are important in Lake Albert and other native habitats of Nile perch (Hopson 1982) were not encountered in Lake Nabugabo and their place was filled by ephemeropterans.

Most Nile perch prey data available for Lake Kyoga during 1967-68 were for fish of >= 20 cm and < 100 cm total length. The types of prey eaten during this period are given in Table 4.1. Eight items were eaten. The major ones were anisopteran nymphs, _R. argentea_, tilapiines, _C. nilotica_, haplochromines and juvenile Nile perch. _P. aethiopicus_ and molluscs were found in a few stomachs.

During 1978-80, twelve different items were eaten by Nile perch in Lake Kyoga. The major prey items were _R. argentea_, anisopteran nymphs, _C. nilotica_, tilapiines, Nile perch juveniles, haplochromines and chironomids (Fig. 4.1).

Table 4.1. The frequency of occurrence of various items in stomachs of different size groups of L. niloticus in Lake Kyoga during the 1967-68 period.

Total length (cm)	<20:	>=20 <60:	>=60 <100:	>=100 :
Tilapiines		13	6	
L. niloticus		2	5	2
Haplochromines		9		
R. argentea		77	47	1
P. aethiopicus			2	
Anisopteran nymphs		86	37	1
Caridina nilotica		20		
Molluscs			1	
Number examined		207	98	4

Mormyrids, P. eathiopicus, molluscs and plant materials were found in a few stomachs. Nile perch of < 20 cm mainly ate C. nilotica, R. argentea, anisopteran nymphs and chironomids. Those of >= 20 cm and < 60 cm mainly ingested R. argentea, anisopteran nymphs, C. nilotica, tilapiines, juvenile Nile perch and haplochromines. Nile perch of >= 60 cm and < 100 cm mainly ate R. argentea, Nile perch juveniles, tilapiines and haplochromines while those of >= 100 cm depended almost solely on tilapiines.

The types of prey eaten by Nile perch in Lake Kyoga during 1988-90 were similar to those eaten during the 1978-80 period (Table 4.2). The major prey items were again, R. argentea, anisopteran nymphs, C. nilotica, tilapiines, Nile perch juveniles, and to a lesser extent haplochromines. The other types which were only occasionally found in the stomachs included Mastacembelus spp, chironomids, ephemeropterans, notonectids, corixids and molluscs. Cestodes, plant materials and gravel were found in a few stomachs. The types of prey again varied with the size of the Nile perch. There were no data for Nile perch of >= 100 cm for this period.

After 1988-90, there was a shift in the relative importance of the various prey items in Lake Kyoga. The major types of prey during 1991-93 were haplochromines, R. argentea, anisopteran nymphs, chironomids, tilapiines, Nile perch juveniles and C. nilotica. The only other item found in the stomachs of Nile perch during this period were

Table 4.2. The frequency of occurrence of various items in stomachs of different size groups of L. niloticus in Lake Kyoga during the 1988-90 period.

Total length (cm)	<20:	>=20 <60:	>=60 <100:	>=100:
Tilapiines	51	169	26	
L. niloticus	1	120	16	
Haplochromines	10	37	4	
R. argentea	118	696	17	
Mastacembelus spp	1	2		
Anisopteran nymphs	64	466	6	
Caridina nilotica	145	59		
Chironomids	5			
Ephemeroptera	2	13		
Notonectids	7	12		
Corixids		9		
Molluscs	2	10	1	
Cestodes		8		
Vegetation	6	16		
Gravel & stones		3		
Number examined	412	1621	70	

molluscs. The type of prey again varied with the size of the predator. During this period, haplochromine cichlids were the most important prey in all size groups of Nile perch < 100 cm. Nile perch of >= 100 cm mainly ate tilapiines and juvenile Nile perch. The haplochromines that were eaten by Nile perch in Lake Kyoga during this period were dominated by one species, Astatotilapia latifasciata (Regan) 1929 (Wandera and Namulemo, personal communication).

The most important prey eaten by Nile perch in Lake Albert during 1989-90 were Alestes spp, haplochromines, C. nilotica, anisopteran nymphs, Nile perch juveniles, tilapiines and Hydrocynus spp (Fig. 4.1). Other items ingested included mormyrids, Bagrus spp, Polypterus spp, Auchenoglanis spp and molluscs. C. nilotica and haplochromines were important in Nile perch of < 20 cm. Nile perch of >= 20 cm and < 60 cm ate Alestes spp, haplochromines, anisopteran nymphs, mollusc and C. nilotica while those of >= 60 cm and < 100 cm ate Alestes spp, haplochromines, Hydrocynus spp, Nile perch juveniles and tilapiines. Nile perch of >= 100 cm ate a variety of fish prey which included Alestes spp, juvenile Nile perch, Polypterus spp, mormyrids and Bagrus spp.

Therefore, the major prey of Nile perch in lakes Victoria, Kyoga, Nabugabo and Albert were C. nilotica, anisopteran nymphs, R. argentea or Alestes spp, haplochromine species, tilapiine species and Nile perch juveniles.

The relative importance of these prey to different size classes of Nile perch is illustrated in Figures 4.2. C. nilotica was the most important prey of Nile perch of < 20 cm total length. Its importance decreased in Nile perch of >= 20 cm and < 60 cm, and it was not eaten by larger Nile perch except in Lake Victoria during 1988-92 where they were eaten by fishes up to 100 cm. C. nilotica was not seen in stomachs of Nile perch in Lake Victoria between 1968-77 and it does not occur in Lake Nabugabo (Ogutu-Ohwayo 1993).

Anisopteran nymphs were eaten by Nile perch < 20 cm and reached their peak importance in fishes of >= 20 cm and < 60 cm. They were ingested by larger Nile perch in Lake Kyoga than in the other lakes.

R. argentea in lakes Victoria, Kyoga and Nabugabo, and Alestes spp in Lake Albert, were, in the absence of haplochromines, the most important prey species of Nile perch. R. argentea was very important in Nile perch of >= 20 cm and < 100 cm in lakes Victoria, Kyoga and Nabugabo, while in Lake Albert, Alestes spp were important in Nile perch of > 20 cm. Among Nile perch of >= 20 cm and < 100 cm a decline in the importance of haplochromines was accompanied by an increase in that of R. argentea and vice versa (Fig. 4.2). This indicates that Nile perch feed on R. argentea only when haplochromines are scarce and suggests that R. argentea was a less preferred prey compared to haplochromines.

Haplochromines were initially the most important prey

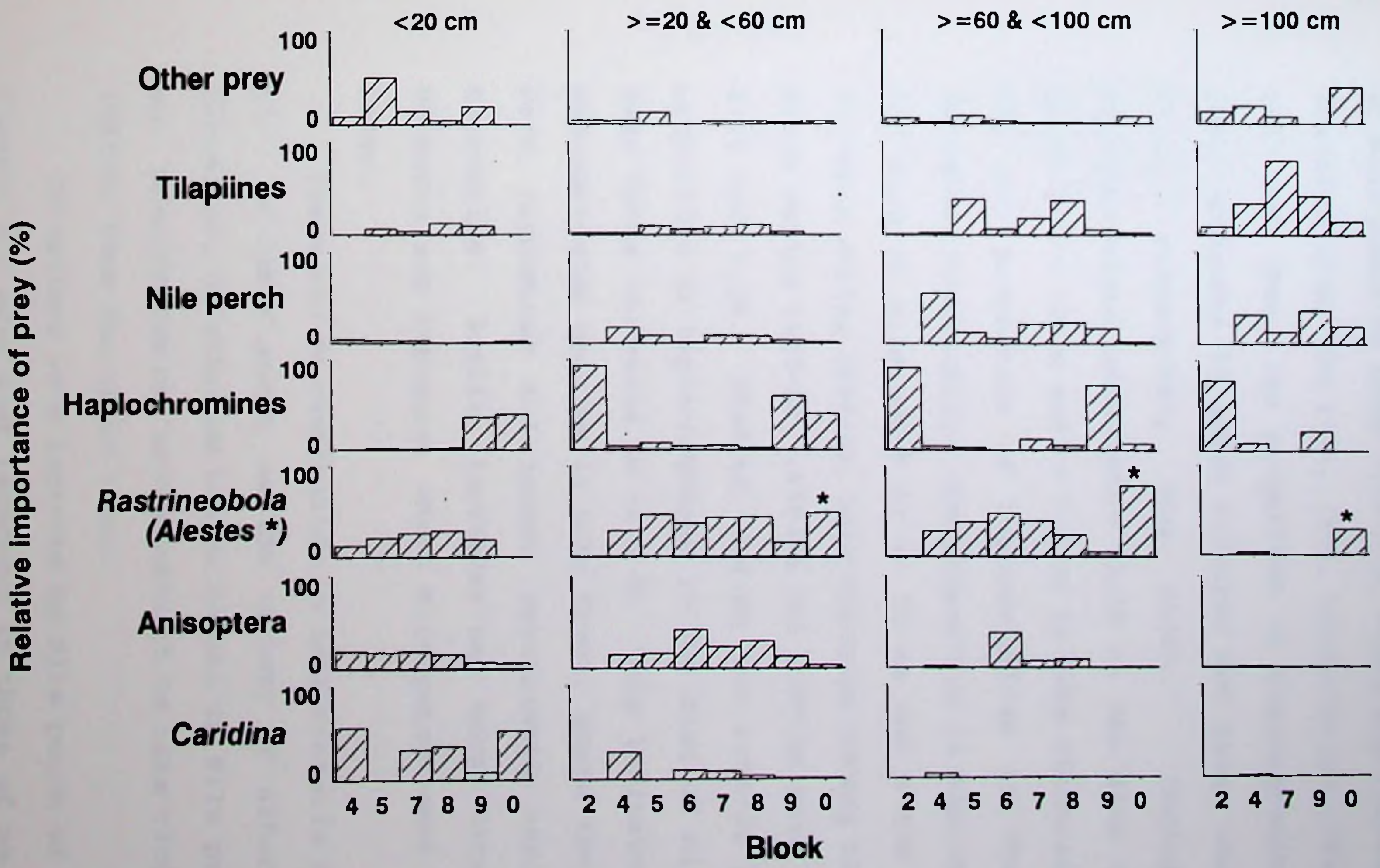


Figure 4.2. The relative importance of prey to Nile perch of different length classes in the lakes over different periods. Blocks represent:- 2 & 4: Victoria 1968-77 & 1988-92; 5: Nabugabo 1991-93; 6, 7, 8 & 9 Kyoga 1967-68, 1978-80, 1988-90 & 1991-93; 0: Albert 1989-92.

of Nile perch in lakes Victoria, Kyoga and probably Nabugabo (Hamblyn 1966, Gee 1964, 1969, Ogutu-Ohwayo 1993). Between 1963 and 1966, the proportion of haplochromines in Nile perch stomachs in lakes Victoria and Kyoga was 56.4% and 47.1%, respectively (Gee 1969). During 1968-77, haplochromines contributed 92.2% to the diet of the Nile perch of >= 20 cm and < 100 cm in Lake Victoria. By 1988-92, the proportion of haplochromines in the diet had decreased drastically. The proportion of haplochromines in the diet of Nile perch of >= 20 cm and < 100 cm in Lake Victoria during 1988-92, Lake Nabugabo during 1991-93, Lake Kyoga during 1967-68, 1978-80 and 1988-90 were all between 2.4% and 7.5%. However, during the 1991-93 period, the proportion of haplochromines in the diet of Nile perch in Lake Kyoga increased to 62.1 %. This indicated that some haplochromine species in Lake Kyoga, where the Nile perch were introduced and became established earliest, were recovering. Similar increases may occur later in lakes Victoria and Nabugabo, where Nile perch were established later.

There was no cannibalism in Lake Victoria during 1968-77. In later years, as the variety of alternative prey decreased, cannibalism became common in Nile perch of > 60 cm. Cannibalism was more prominent in Lake Victoria during 1988-92 than the other lakes.

Tilapiines were ingested by Nile perch of most length classes but were most important in those of >= 60 cm. The main tilapiine species found in all the lakes sampled was O. niloticus.

The length and numbers of prey ingested

The length and numbers of prey eaten have also changed since the Nile perch was introduced in lakes Victoria, Kyoga and Nabugabo. The changes in average length and numbers of prey eaten by Nile perch of different length classes are illustrated in Figure 4.3. The length of prey eaten by Nile perch in Lake Victoria during 1968-77 was linear over the entire length range of the predator. By 1988-92, the length of prey eaten in Lake Victoria increased evenly only in Nile perch of < 100 cm after which there was a shift to feeding on relatively larger prey. A similar pattern in the sizes of prey eaten was recorded in Lake Kyoga during 1978-80 and Lake Albert during 1989-92. However, during 1991-93 in Lake Kyoga, there was a shift in prey selection towards the sizes and numbers recorded in Lake Victoria during the 1968-77 period.

As for the length of prey, the numbers of prey in the gut of Nile perch in Lake Victoria during 1968-77 increased evenly over the entire size range of the predator. However, during 1988-92, this pattern had changed. The number of prey in the gut initially increased with predator only in Nile perch of < 60 cm and then decreased in larger fish. A similar pattern was observed in Lake Kyoga during the 1978-80 and 1991-93 periods and in Lake Albert during the 1989-92

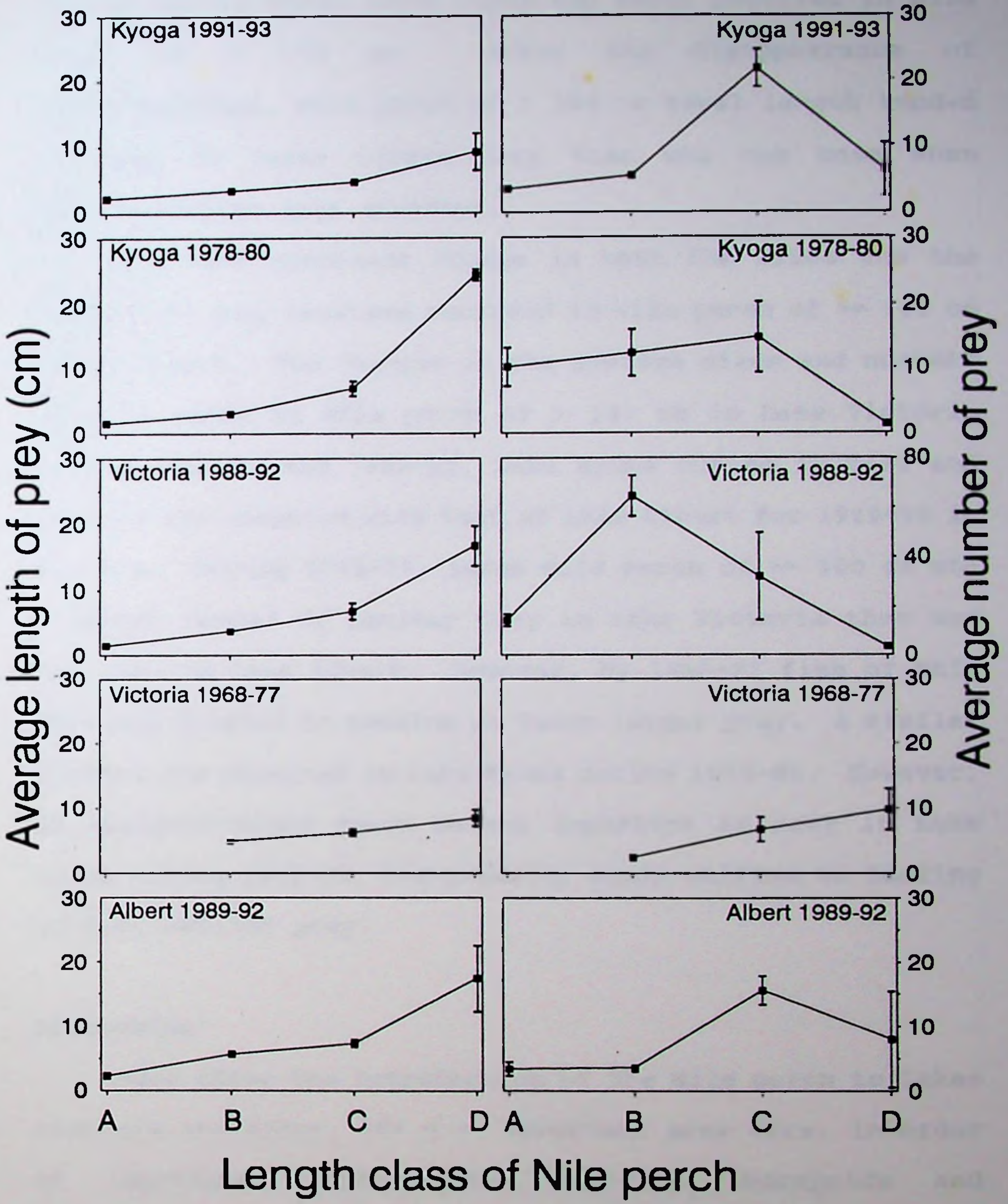


Figure 4.3. The average length and numbers of prey eaten by Nile perch of various length classes in lakes Victoria, Kyoga, and Albert during different periods. Vertical bars are 2 SE of mean. Length classes are as described in Figure 4.1.

period but in these later cases the shift occurred in Nile perch of > 100 cm. After the disappearance of haplochromines, Nile perch of > 100 cm total length tended to feed on fewer larger prey than was the case when haplochromines were abundant.

The most prominent change in both the sizes and the numbers of prey consumed occurred in Nile perch of >= 100 cm total length. The changes in the average sizes and numbers of prey eaten by Nile perch of > 100 cm in Lake Victoria during 1968-77 and 1988-92, Lake Kyoga during 1978-80 and 1991-93 are compared with that of Lake Albert for 1989-92 in Fig 4.4. During 1968-77, large Nile perch of >= 100 cm ate a larger number of smaller prey in Lake Victoria than was the case in Lake Albert. However, by 1988-92 fish of this size had shifted to feeding on fewer larger prey. A similar pattern was observed in Lake Kyoga during 1978-80. However, as haplochromines again became important as prey in Lake Kyoga during 1991-93, the predator again shifted to feeding on many smaller prey.

Discussion

Soon after the introduction of the Nile perch to lakes Victoria and Kyoga, its most important prey were, in order of importance haplochromine cichlids, mormyrids and tilapiine cichlids (Hamblyn 1966, Gee 1969). Although no historical data are available, similar prey seem to have been eaten in Lake Nabugabo since haplochromines, which were

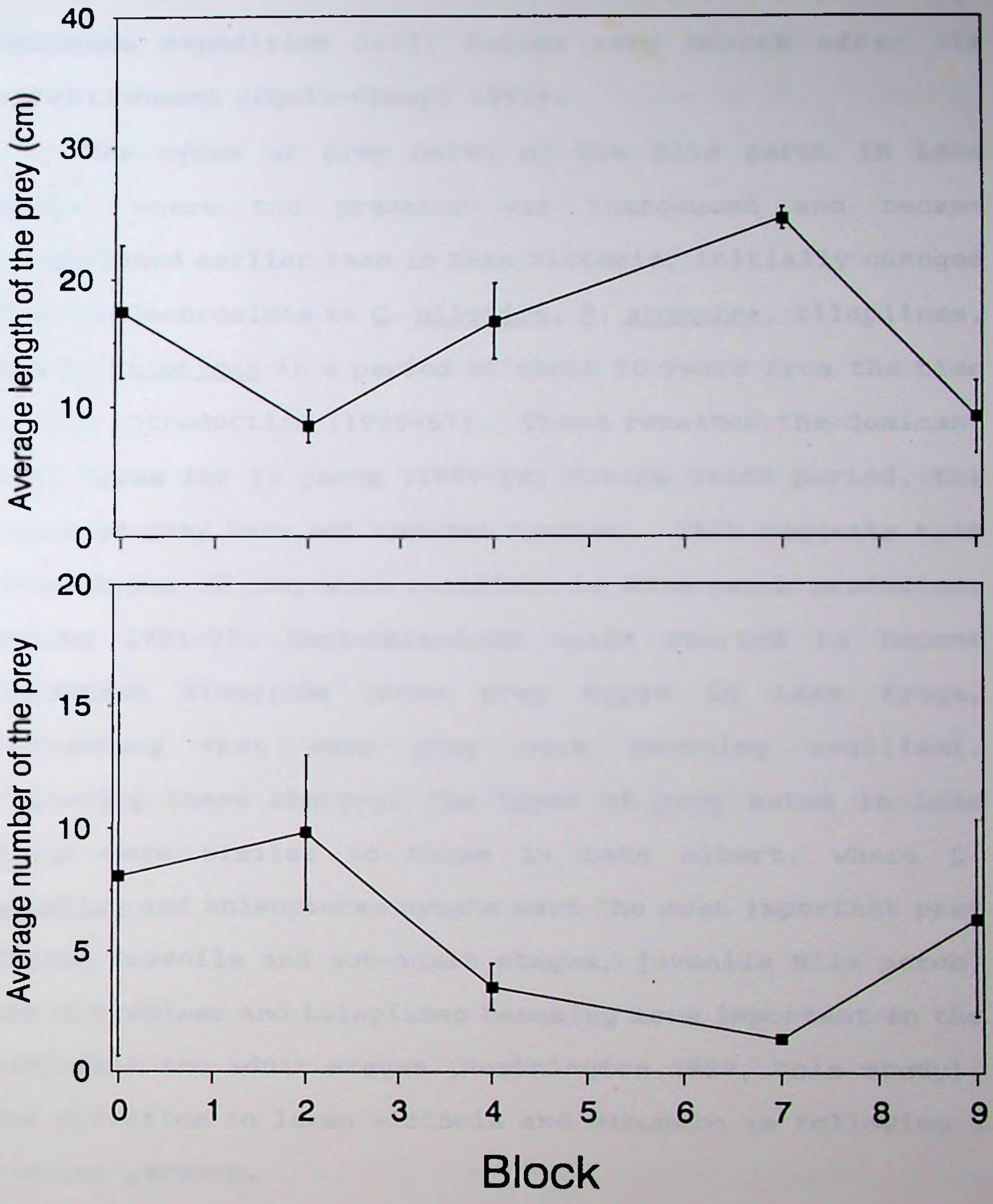


Figure 4.4. Changes in average lengths and numbers of prey eaten by Nile perch of >= 100 cm total length. The Vertival bars are 2 SE of mean.

abundant prior to establishment of Nile perch (Cambridge Nabugabo expedition 1962) became very scarce after its establishment (Ogutu-Ohwayo 1993).

The types of prey eaten by the Nile perch in Lake Kyoga, where the predator was introduced and became established earlier than in Lake Victoria, initially changed from haplochromines to C. nilotica, R. argentea, tilapiines, and L. niloticus in a period of about 10 years from the time of its introduction (1956-67). These remained the dominant prey types for 23 years (1967-90) during which period, the types of prey were not reduced further. This suggests that these types of prey were resilient to Nile perch predation. During 1991-93, haplochromines again started to become important alongside above prey types in Lake Kyoga, indicating that more prey were becoming resilient. Following these changes, the types of prey eaten in Lake Kyoga were similar to those in Lake Albert, where C. nilotica and anisopteran nymphs were the most important prey during juvenile and sub-adult stages, juvenile Nile perch, haplochromines and tilapiines becoming more important in the sub-adult and adult stages (Worthington 1929, this study). The situation in lakes Victoria and Nabugabo is following a similar pattern.

Earlier observations in Lake Albert (Worthington 1929, Hamblyn 1966, Gee 1969) showed that Nile perch of < 60 cm ate C. nilotica and anisopteran nymphs, and became piscivorous at larger sizes. During its piscivorous phase, the predator mainly ate pelagic characids Alestes spp and Hydrocynus spp. The data collected from Lake Albert during 1989-92 show that the types of prey eaten by Nile perch in Lake Albert has not changed for about 60 years (1928-1992). This indicates that these types of prey are resilient to predation by the Nile perch and are the types that can survive together with the predator.

The types of prey eaten by Nile perch in Lake Victoria during 1988-92, Lake Kyoga during all the periods between 1967-93 and in Lake Nabugabo during 1991-93 have similarities to those eaten in native habitats. In Lake Chad, prawns and small pelagic characids Alestes dageti Blache and Microalestes acutidens (Peters) were the most important prey in Nile perch up to 80 cm, beyond which Hydrocynus spp. became the most important (Hopson, 1972). In Lake Turkana, a pelagic cyprinid, Engraulicypris stellae, was important (Gee 1969, Hopson 1982).

Similarities between new and native habitats are also apparent in the sizes and numbers of prey eaten. Soon after introduction of the Nile perch, the average sizes and numbers of prey eaten increased evenly with predator size. After haplochromines had been depleted, the sizes and numbers of prey eaten, especially by large Nile perch (> 100 cm) in lakes Victoria, Kyoga and Nabugabo changed to those seen in lakes Albert and Chad (Hopson 1972). It can, therefore be concluded that the types, sizes and numbers of prey eaten in the new habitats have stabilized and are similar to what is eaten in native habitats of the Nile perch.

Nile perch in the new habitats seem to have adjusted both the size and numbers of prey ingested in order to optimize net energy gain. During the 1968-77 period, when haplochromines were abundant, Nile perch of >= 100 cm fed on a larger number of smaller prey than was even the case in Lake Albert. This was apparently because of the abundance of vulnerable haplochromine prey which had not previously been exposed to such a large predator. After haplochromines had been depleted, it was more profitable for large Nile perch (> 100 cm) to feed on a smaller number of larger prey. When the stocks of haplochromine increased, Nile perch shifted and again fed a larger number of smaller prey. Therefore, Nile perch has the capability to adjust both the numbers and sizes of prey eaten depending on the types and sizes available. The reason for the changes in the sizes and numbers of prey eaten especially in Nile perch of >= 100 cm may be related to energy requirements, especially for reproduction. Female Nile perch mature at around this size (Chapter 7).

Currently, the three dominant fish prey types of Nile perch, R. argentea, Nile perch itself and Nile tilapia are also heavily exploited commercially. C. nilotica is directly exploited as a by-catch in the R. argentea fishery in some parts of Lake Victoria (Ogari and Asila 1992). Sustainability of Nile perch stocks will depend upon a steady food supply which will be determined partly by the level of exploitation of the prey species. Human exploitation and Nile perch predation have already reduced the overall size of R. argentea in Lake Victoria (Wandera 1992). Heavy exploitation of juvenile perch using beach seines is suspected to have reduced stocks of Nile perch in Lake Kyoga during the mid 1980s (Twongo personal communication.). It is therefore important that exploitation of Nile perch prey should be regulated and, where possible, prohibited, if the species is to sustain commercial harvest.

Conclusion

The type, sizes and numbers of prey eaten by Nile perch in have changed in a similar fashion in several new habitats as the predator became established. Initially, haplochromine cichlids constituted the main prey in most sizes of Nile perch in lakes Victoria and Kyoga. Later, C. nilotica, anisopteran nymphs, Rastrineobola argentea, juvenile Nile perch and Oreochromis niloticus became the main prey. There were no further changes in the types of prey ingested for 23 years in Lake Kyoga but thereafter haplochromines again became important in addition to the above types. Similar pattern were recorded in lakes Victoria and Nabugabo. The sizes and numbers of prey ingested by Nile perch in the new habitats also followed a pattern similar to that in native habitats. Therefore since the types, sizes and number of prey eaten by Nile perch in the new habitats has converged on species that are resilient and have similarities to those eaten in native habitats, these prey types can sustain the Nile perch fishery.

Chapter 5

Deterioration in length-weight relationships of Nile perch, *Lates niloticus* L. in lakes Victoria, Kyoga and Nabugabo

Abstract

Length-weight relationships of Nile perch in lakes Victoria, Kyoga and Nabugabo were examined to see how they had changed following depletion in haplochromine prey, and how the situation in the new habitats compared with that in Lake Albert and other native habitats of the Nile perch. The length to weight ratios in the new habitats were initially higher than in Lake Albert and other native habitats. After haplochromines had been depleted, they declined to values below those of Lake Albert and most native habitats to the lowest level known in any native habitat. They have remained at this level for at least 15 years in Lake Kyoga, where Nile perch were introduced and got well established earliest and can be considered to have stabilized. A similar pattern is developing in lakes Victoria and Nabugabo. However, further stress on the prey population could depress the weight to length ratios below the lowest level known and this could affect the health of Nile perch stocks and make its fishery unviable. Therefore, human over-exploitation of Nile perch prey should be avoided.

Introduction

The types, sizes and numbers of prey taken by the Nile perch in lakes Victoria, Kyoga and Nabugabo have changed since the predator was introduced and became established (Gee 1964, 1969, Hamblyn 1966, Hughes 1986, Ogutu-Ohwayo 1985, 1990a, b, Ogari & Dadzie 1988, Ligtvoet & Mkumbo 1990). These lakes originally had diverse fish faunas with many species in common. Haplochromines formed at least 80% by weight of the demersal ichthiomass in Lake Victoria up to the time when the Nile perch stocks started increasing rapidly (Kudhongania & Cordone 1974, Okaronon et al 1985). They were also abundant in lakes Kyoga and Nabugabo prior to introduction and establishment of the Nile perch (Worthington 1929, Cambridge Nabugabo expedition 1962, Ogutu-Ohwayo 1985, 1993).

Soon after introduction of the Nile perch, its condition factor (K) in lakes Victoria and Kyoga was higher than in most natural habitats (Worthington 1929, Kenchington 1939, Gee 1964, 1969, Hopson 1972, 1982 Okedi 1971). This was attributed to the high feeding intensity of the predator in the new habitats due to the greater abundance of suitably sized and vulnerable haplochromine prey (Gee 1964, 1969). At that time, haplochromines were the main prey of most sizes of Nile perch in lakes Victoria and Kyoga (Hamblyn 1966, Gee 1964, 1969, Okedi 1971) and apparently Nabugabo (Ogutu-Ohwayo 1993). Following rapid increases in Nile perch stocks, stocks of haplochromines, and those of most native fish species in these lakes declined and some completely disappeared due to predation by the Nile perch (Ogutu-Ohwayo 1985, 1990a, b, Ogari & Dadzie 1988, Ligtvoet & Mkumbo 1990, Witte *et al*. 1992a, b). Nile perch then shifted to feed on other prey comprising prawns, *Caridina nilotica* Roux, anisopteran nymphs, *Rastrineobola argentea* Pellegrin, its own juveniles and *Oreochromis niloticus* L. This was accompanied by changes in sizes and numbers of prey eaten. These changes may have resulted in a decrease in the quantity and quality of food taken by the Nile perch, an increase in the amount of energy expended in collecting the food and a fall in condition factor of the predator.

The nutritional status of a fish can be assessed by examining length-weight relationships (Le Cren 1951, Weatherly 1972, Nikolsky 1963). Heavier fish of a given length are regarded as being in better condition. Length-weight relationship and condition factor K were used to assess the effects of the changes in types and sizes of prey eaten by the Nile perch on its condition in the new habitats and to find out if these changes had stabilized and were within expected values as reported from those habitats where the Nile perch has remained in balance with its prey population for a long time.

The changes in length-weight relationship and K since introduction and establishment of the Nile perch in lakes Victoria, Kyoga and Nabugabo were examined and compared with the situation in Lake Albert and elsewhere to see if the condition of the predator in the new habitats was the same, higher or lower than in native habitats. It was assumed that in order for the condition of the Nile perch in the new habitats to be regarded as being healthy, the weight and K for fish of specific length classes should be higher or at least not significantly lower than those of Lake Albert and other native habitats. The hypothesis examined was that there were no significant differences in length-weight relationships and K of Nile perch within and between the new habitats over specific periods and that this was not significantly different from that of Lake Albert and other native habitats.

Materials and Methods

The information was obtained by comparing data which were collected over different periods from Lake Victoria between 1964 and 1992, Lake Kyoga between 1967 and 1993, and Lake Nabugabo between 1991 and 1993 with that collected from Lake Albert between 1989 and 1992. Comparative information for lakes Victoria and Kyoga came from reports of Gee (1964, 1969) and Asila and Ogari (1987) and that for other native habitats from Worthington (1929) for Lake Albert, Kenchington (1939) for the Blue Nile at Sennar and Hopson (1972, 1982) for lakes Chad and Turkana.

Nile perch specimens were obtained from commercial catches, experimental gill nets, seines and trawls. The total length and standard length of the fish were measured

Results

Comparisons of length-weight relationships between the lakes were confined to Nile perch of >= 20 cm and < 100 cm because it was this size range which had sufficient samples in all the lakes. There were also no data for Nile perch smaller than this for the periods before 1982 when haplochromines were still abundant in Lake Victoria.

The parameters of length-weight relationships of Nile perch of >= 20 cm to < 100 cm in lakes Albert, Victoria, Nabugabo and Kyoga during the different periods are given in Table 5.1 and those quoted in literature in Table 5.2. Generally, the weight was proportional to the cube of the length. However, the exponents of the length weight relationship varied slightly between the habitats and within habitats over different periods.

Length-weight relationships of Nile perch in lakes Victoria, Kyoga, Nabugabo and Albert are illustrated in Figures 5.1. Length-weight relationships varied between lakes and within lakes over different periods. The length weight relationships of Lake Victoria for the periods 1968-77 and 1982 were higher than those of the same lake for the 1988-92 period, of lakes Albert and Nabugabo and of Lake Kyoga for all the periods examined. The length weight relationship of Lake Kyoga for all the periods were lower than those of Lake Albert. Length-weight relationships recorded in Lake Kyoga during the periods 1978-80 and 1991-93, that of Lake Albert and those of other native habitats

Table 5.1. The parameters of length-weight relationships of Nile perch of >= 20 and < 100 cm in lakes Victoria, Kyoga, Nabugabo and Albert during different periods ($W = aL^b$).

Block, Lake & Period:	Parameter:					
	a	SE_a	b	SE_b	R^2	N
0: Albert 1989-92	.0087	.038	3.10	.008	.995	645
1: Victoria 1964-67	.0051	.045	3.26	.008	.980	2938
2: Victoria 1968-77	.0062	.039	3.22	.014	.992	419
3: Victoria 1982	.0035	.042	3.34	.022	.947	658
4: Victoria 1988-92	.0079	.042	3.12	.004	.994	2876
5: Nabugabo 1991-93	.0076	.035	3.12	.009	.995	602
6: Kyoga 1967-68	.0059	.045	3.15	.020	.989	272
7: Kyoga 1978-80	.0098	.033	3.05	.005	.996	1288
8: Kyoga 1988-90	.0115	.032	3.01	.006	.993	1807
9: Kyoga 1991-93	.0104	.039	3.03	.004	.966	2081

Table 5.2. Parameters of length-weight relationships of Nile perch reported in some other native habitats and in the Kenyan region of Lake Victoria.

Water body	Parameter		Source of data
	a	b	
Blue Nile at Sennar	0.0055	3.21	Kenchington 1939
Lake Chad	0.0125	3.00	Hopson 1972
Lake Turkana	0.0078	3.13	Hopson 1982
Victoria (Kenya)	0.0078	3.12	Asila & Ogari 1978

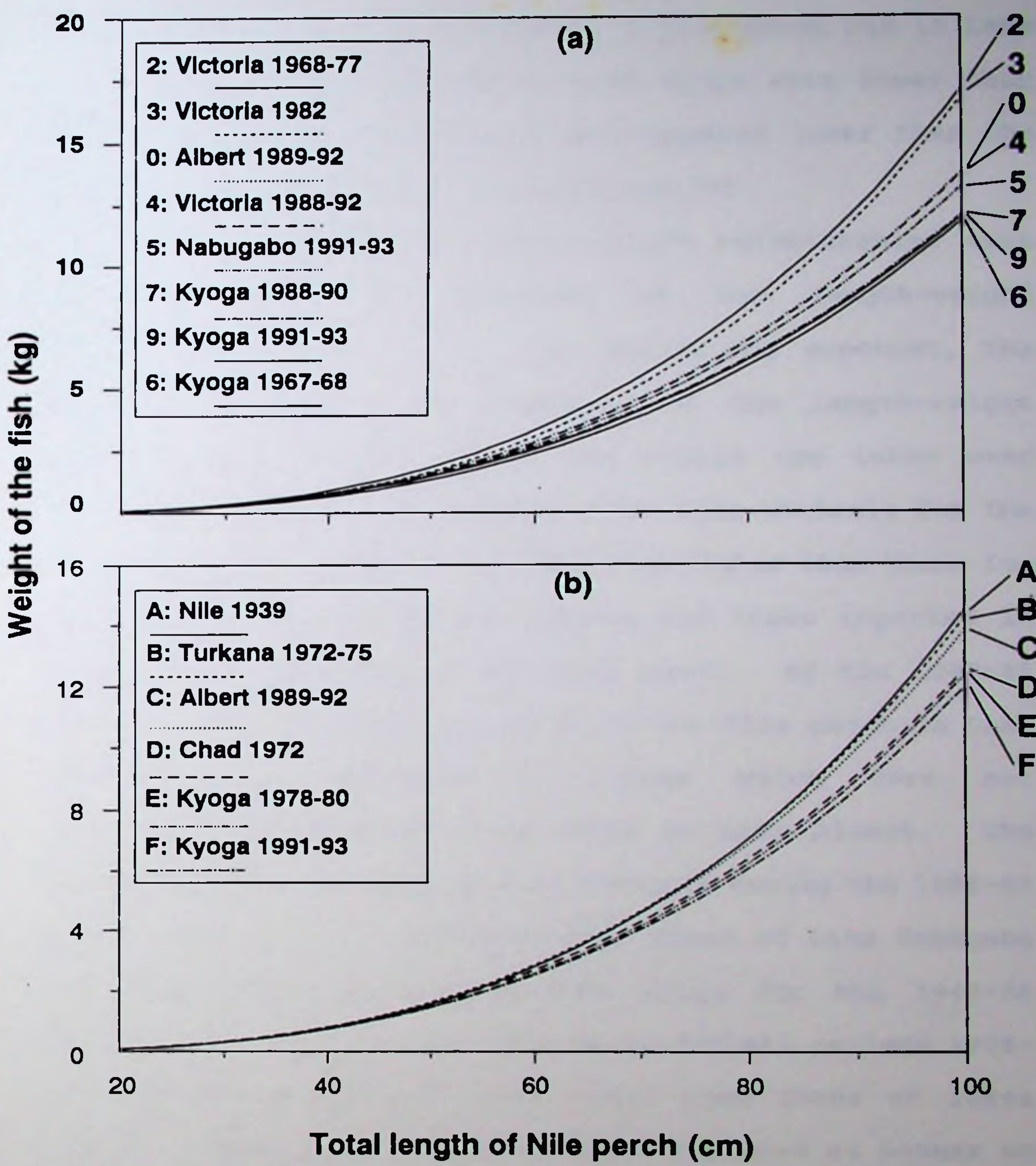


Figure 5.1. (a) Length-weight relationships of Nile perch of >= 20 cm and < 100 cm in lakes Victoria, Kyoga, Nabugabo and Albert during different perids and (b) A comparison of length-weight relationships of Nile perch of Lake Kyoga with that of several native habitats.

were also compared(Fig. 5.1b). The lowest length-weight relationship in a native habitat of Nile perch was in Lake Chad. The values attained in Lake Kyoga were lower than those of most native habitats and appeared lower than the lowest level recorded in a native habitat.

The differences in length-weight relationships were compared using the exponents of the length-weight relationships (Fig. 5.2). The higher the exponent, the heavier the fish. The exponents of the length-weight relationships varied between and within the lakes over different periods. The exponents for Lake Victoria for the periods 1964-67, 1968-77 and 1982 were higher than those for Lake Albert for the period 1989-92 and those reported in other native habitats of the Nile perch. By the 1988-92 period, the length-weight ratios of the Nile perch in Lake Victoria had decreased to values which were not significantly different from those of Lake Albert. The exponents for Nile perch in Lake Victoria during the 1988-92 period were also not different from those of Lake Nabugabo for the 1991-93 period and Lake Kyoga for the 1967-68 period. The exponents for Lake Kyoga for all periods 1978-80, 1988-90 and 1991-93 were lower than those of lakes Albert, Victoria and Nabugabo, those reported at Sennar on the Blue Nile (Kenchington 1939) and on Lake Turkana (Hopson 1982). However, the values for Lake Kyoga have not fallen below that of Lake Chad which is the lowest values reported in a native habitat of the Nile perch and have remained at

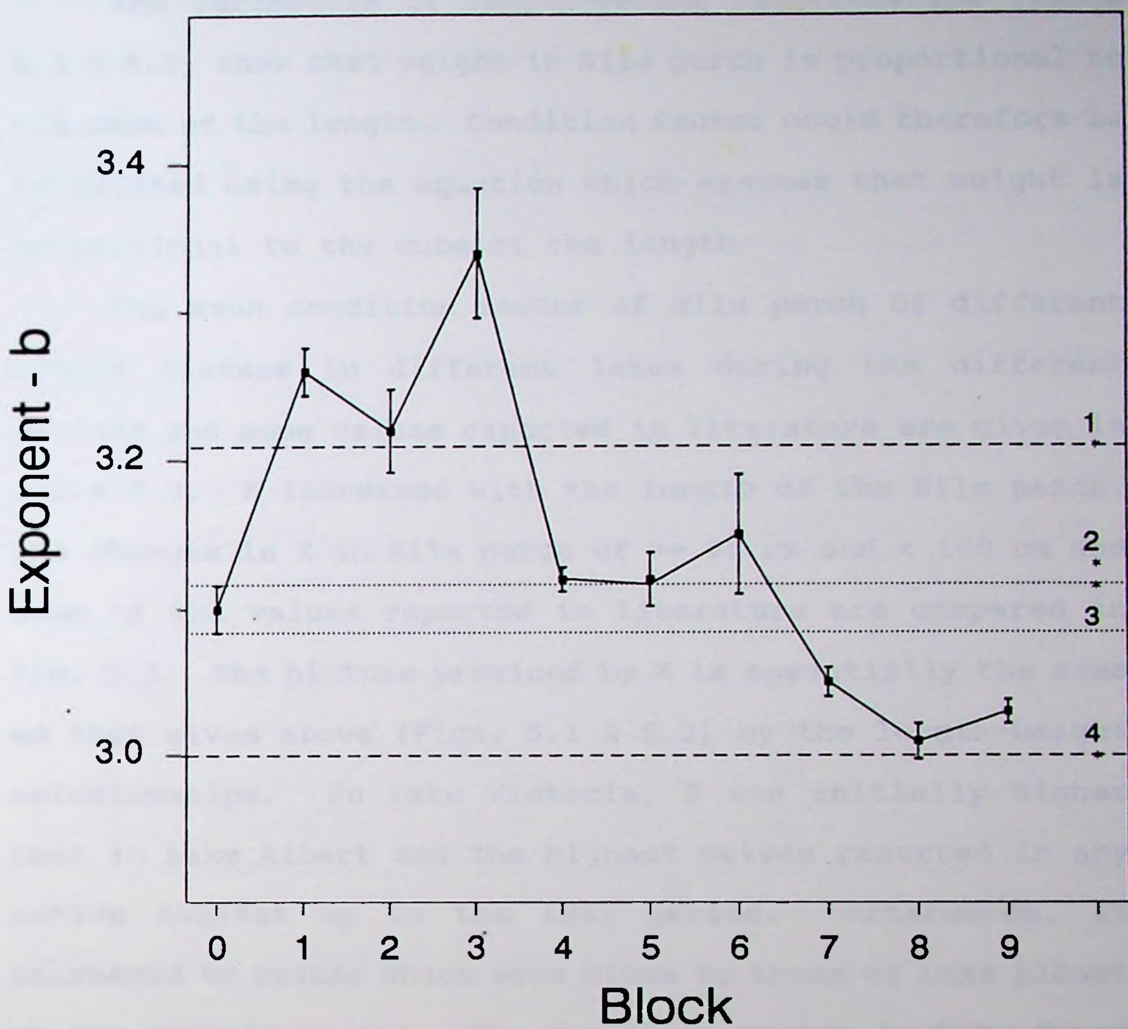


Figure 5.2. A comparison of the exponents of the length - weight relationships of Nile perch in the new habitats over different periods with that in Lake Albert and other native habitats of the predator. Vertical bars are 2 SE of respective values. The dotted lines mark the Lake Albert 2 SE range and the dashed lines the maximum and minimum values reported in literature for native habitats of Nile perch. Asterisks are values reported in literature (1 = Nile at Sennar, 2 = Turkana, 3 = Victoria - Kenya, 4 = Chad). The exponents obtained in this study are joined by a solid line.

this level for at least 15 years.

The parameters of length-weight relationships (Table 5.1 & 5.2) show that weight in Nile perch is proportional to the cube of the length. Condition factor could therefore be calculated using the equation which assumes that weight is proportional to the cube of the length.

The mean condition factor of Nile perch of different length classes in different lakes during the different periods and some values reported in literature are given in Table 5.3. K increased with the length of the Nile perch. The changes in K in Nile perch of >= 20 cm and < 100 cm and some of the values reported in literature are compared in Fig. 5.3. The picture provided by K is essentially the same as that given above (Figs. 5.1 & 5.2) by the length-weight relationships. In Lake Victoria, K was initially higher than in Lake Albert and the highest values reported in any native habitat up to the 1982 period. Afterwards, it decreased to values which were close to those of Lake Albert by the 1988-92 period. The condition factor in Lake Kyoga for the periods 1978-80, 1988-90 and 1991-93 were again lower than that of Lake Albert and approximated to the lowest value recorded in a native habitat.

Table 5.3. The mean condition factor of Lates niloticus in lakes Albert, Victoria, Nabugabo and Kyoga during different periods. Some values found in literature are also given.

Block, Lake & Period:	Length Class (Total length cm)				
	<20:	>=20 & <60:	>=60 & <100:	>=100:	>=20 & <100 :
0: Albert 1989-92	1.24	1.21	1.35	1.40	1.28
1: Victoria 1964-67	1.22	1.24	1.61	1.78	1.43
2: Victoria 1968-77:		1.34	1.58	1.61	1.46
3: Victoria 1982:		1.35	1.51	1.5	1.43
4: Victoria 1988-92:	1.23	1.17	1.30	1.28	1.24
5: Nabugabo 1991-93:	1.11	1.11	1.27	1.35	1.19
6: Kyoga 1967-68:		1.00	1.12	1.34	1.06
7: Kyoga 78-80:	1.19	1.13	1.21	1.37	1.17
8: Kyoga 1988-90:	1.12	1.17	1.22		1.20
9: Kyoga 1991-93:	1.15	1.15	1.21	1.24	1.18

Some values reported in literature:

Nile (Kenchington 1939)	1.25	1.42	1.51	1.40
Chad (Hopson 1972)				1.20
Turkana (Hopson 1982)	1.14	1.25	1.33	1.22
Albert (Worthington 1929)				1.25
Victoria (Gee 1964, 1969)				1.6
Kyoga (Gee 1964, 1969				1.4

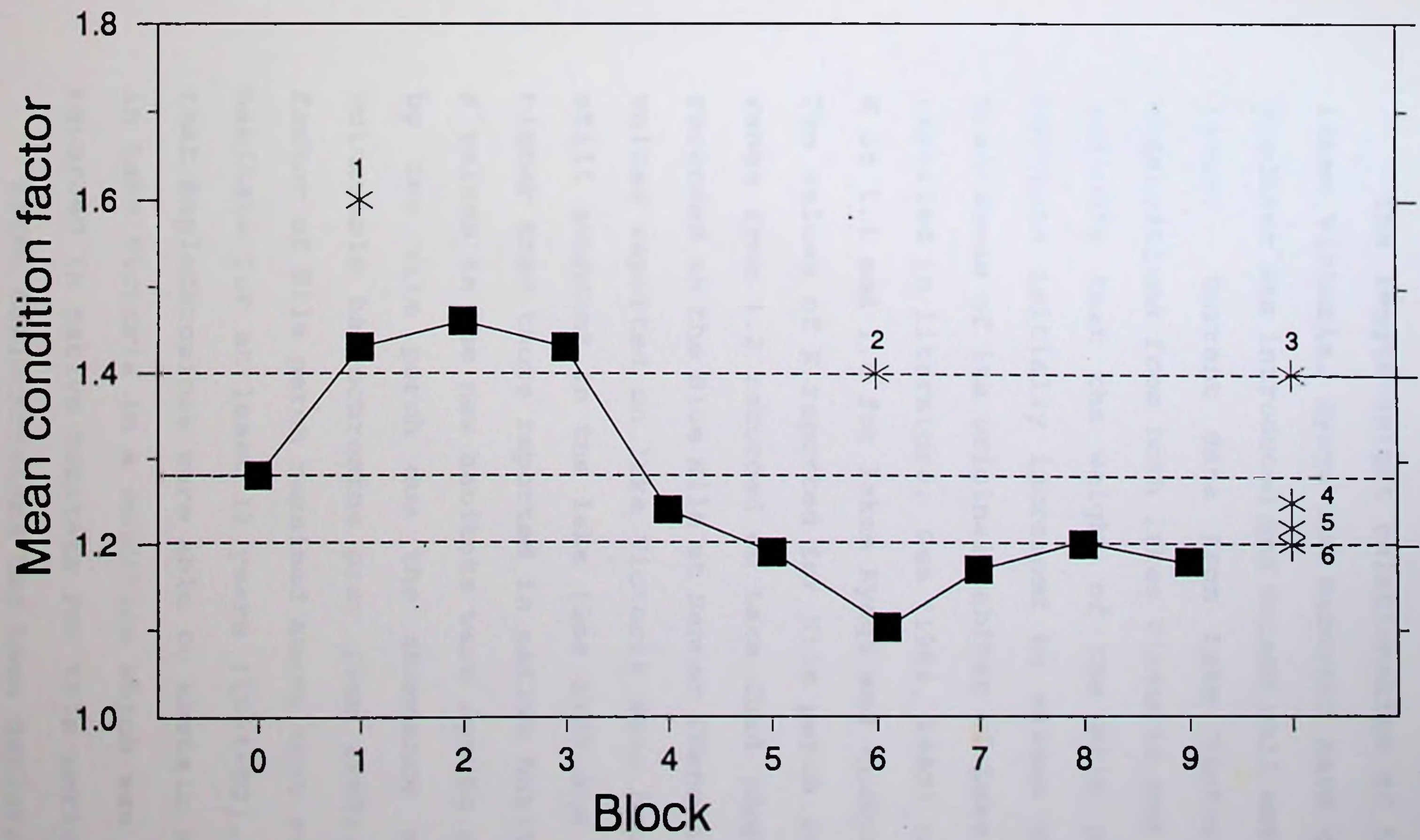


Figure 5.3. The mean condition factor of Nile perch of >= 20 cm and < 100 cm. The dashed lines give the Lake Albert value, the maximum and minimum values reported in native habitats. Asterisks are values reported in literature [1 = Victoria & 2 = Kyoga (Gee 1969), 3 = Nile at Sennar (Kenchington 1939), 4 = Albert (Worthington 1929), 5 = Turkana & 6 = Chad (Hopson 1972, 1982) The values obtained in this study are joined by a solid line. SE were too small too be included in the illustration.

Discussion

The length-weight relationships of the Nile perch in lakes Victoria, Kyoga and Nabugabo have changed since the predator was introduced and became well established in these lakes. Current data from Lake Victoria and previous observations from both lakes Victoria and Kyoga (Gee 1969) indicate that the weight of the Nile perch in the new habitats initially increased to values which were higher than those of its original habitat of Lake Albert and those reported in literature. Gee (1964, 1969) reported values of K of 1.4 and 1.6 for lakes Kyoga and Victoria respectively. The values of K reported for Nile perch in native habitats range from 1.2 recorded on Lake Chad (Hopson 1972) to 1.4 recorded on the Blue Nile at Sennar (Kenchington 1939). The values reported on lake Victoria when haplochromines were still abundant in the lake (Gee 1969 and this study) were higher than those reported in native habitats. The higher K values in the new habitats were due to excessive feeding by the Nile perch due the abundance at that time of vulnerable haplochromine prey (Gee 1969). The condition factor of Nile perch remained above that recorded in native habitats for at least 18 years (1964-82). This indicates that haplochromines were able to sustain Nile perch stocks in Lake Victoria in a condition which was higher than that recorded in native habitats for this period.

After haplochromines had been depleted, the weight of Nile perch in Lake Victoria decreased from the high levels recorded up to about 1982 to a level which were not significantly different from that of Lake Albert. However, the values recorded in Lake Kyoga indicate that K in lakes Victoria and Nabugabo may decline further. Nile perch was introduced and got established earlier in Lake Kyoga than lakes Victoria and Nabugabo. Depletion in haplochromine stocks in Lake Victoria and probably Lake Nabugabo occurred later than that of Lake Kyoga. In each of the lakes invaded by the Nile perch, the predator switched to the same types of prey after haplochromines had been depleted. These comprised C. nilotica, anisopteran nymphs, R. argentea, Nile perch juveniles and O. niloticus. The only exception is in Lake Nabugabo where C. nilotica is absent (Ogutu-Ohwayo 1993). Therefore, it is reasonable to assume that although K in lakes Victoria and Nabugabo are within the values seen in Lake Albert, the lower values recorded and sustained in Lake Kyoga for at least 15 years suggest that further decline in K in lakes Victoria and Nabugabo is possible. Also, since Nile perch switched to the above types of prey in Lake Kyoga, there has been no further depletion in prey, instead some previously important prey like the haplochromines have started to recover in Lake Kyoga (Chapter 3) and have again started to become important as prey of Nile perch (Chapter 4). Therefore, further depression in K in Lake Kyoga is unlikely.

The differences in K between the new habitats and Lake Albert seem to arise out of the types and sizes of the dominant fish prey. Whereas R. argentea is the main fish prey of the Nile perch in the new habitats for the size ranges of fish compared, this size of Nile perch in Lake Albert mainly feed on Alestes nurse. R. argentea is much smaller in size than A. nurse and Nile perch would have to consume a larger number of R. argentea to meet its food requirements. It will, therefore spend more energy collecting R. argentea than A. nurse for the same amount of food intake. In Lake Victoria, Wanink & Goudswaard (1994) have suggested that R. argentea is less valuable to Nile perch compared to haplochromines which grew to a similar size range as A. nurse partly because of size differences. It therefore seems, based on energetic considerations, that K values of the Nile perch in the new habitats will remain and probably stabilize at values which are lower than those of Lake Albert.

The situation in lakes Victoria, Kyoga and probably later Nabugabo is complicated further by human exploitation of Nile perch prey. Whereas dominant prey like A. nurse and C. nilotica are not commercially exploited in Lake Albert, R. argentea is currently heavily exploited by humans in lakes Victoria and Kyoga and this is likely to spread to Lake Nabugabo. Even C. nilotica is already being exploited in some regions of Lake Victoria (Ogari & Asila 1992). Since K values in some of the new habitats have hit the lowest values recorded anywhere, further stress on the food base of the Nile perch such as that which may arise through heavy human exploitation of the prey could depress the condition of the fish further and may have undesirable consequences. As Holling (1973) has put it, once a character has been forced to the boundary of the domain, it can crash or be displaced by even a slight additional disturbance. Therefore, over-exploitation of Nile perch prey should be avoided.

Conclusion

The condition factor of the Nile perch in the new habitats was initially higher than that in Lake Albert and other native habitats due to the abundance in these lakes of vulnerable haplochromine prey. After haplochromines were depleted K decreased to values below those in lake Albert and most native habitats and approached the lowest value recorded anywhere. It has remained at this level for at least 15 years in some of the new habitats and can be considered stable. However, further reduction in Nile perch prey through human exploitation can depress the condition of the fish to levels that would affect the health of its stocks. It is therefore recommended that human over-exploitation of Nile perch prey in the new habitats should be discouraged.

Chapter 6

Growth rates of juvenile Nile perch, Lates niloticus L. in lakes Victoria, Kyoga and Nabugabo

Abstract

The growth rates of Nile perch, Lates niloticus L. of 20 cm to 40 cm total length were estimated in lakes Victoria and Kyoga in 1991 and 1992 and Nabugabo in 1992 and 1993 by tagging. Fish grew faster in Lake Kyoga (mean growth rate 28.7 ± 1.3 cm per year, N = 49) than in Lake Victoria (18.9 ± 1.4 cm per year, N = 20) and Lake Nabugabo (19.0 ± 0.7 cm per year, N = 43). There were significant differences in growth rates between the lakes ($F_{2,109} = 24.037$, $p < 0.001$). Growth rates in Lake Kyoga were significantly higher than those of lakes Victoria and Nabugabo ($p < 0.001$) but those of lakes Victoria and Nabugabo were not significantly different from each other ($p = > 0.05$). The faster growth rates in Lake Kyoga were attributed to improvement in food supply due to increases in stocks of haplochromine prey. Growth rates in Lake Kyoga were significantly higher than, but those of lakes Victoria and Nabugabo were within the ranges of those reported in several native habitats of Nile perch.

Introduction

Growth among fish is affected by environmental conditions such as temperature, salinity, and food supply (Brown 1957). However, food supply is the most important factor affecting growth rates in the tropics where water temperatures are high and vary little. Fish growth is plastic and can increase or decrease according to food supply (Matuszer et al 1990, Kempinger & Carline 1977, Wootton 1989). It can be affected by the quantity, quality and size of prey. The higher the quality of the food the faster the growth rate.

Food eaten by an organism is invested into growth, reproduction and maintenance. Among immature individuals, most of the energy intake is channelled to growth and most rapid growth in length occurs before the onset of maturity (Nikolsky 1963). After maturity, much of the food is invested in gonadal products although most fishes continue to grow slowly after maturity. Before attainment of maturity, the rate of growth is closely related to food supply and varies according to the type, quality and quantity of the food (Nikolsky 1963). Therefore, the effects of changes in food supply on growth can be seen best before the onset of maturity.

Since the rate of growth is influenced by the quality and quantity of food (Parker & Larkin 1959), it can be accelerated through improvement in food supply or retarded through its reduction. Growth rates may also vary with different food types. In addition foraging efficiency varies with type and abundance of prey. However, fish can survive for long periods with little or no food but this will lower the growth rate and affect reproduction. Growth patterns can also change with the type of prey. Changes in growth pattern following changes in prey have been observed in <u>Esox lucius</u> and <u>Perca fluviatilis</u> (Hunt & Carbine, 1951, Le Cren, 1958).

The type, size and numbers of prey eaten by the Nile perch <u>Lates niloticus</u> L. in lakes Victoria, Kyoga and Nabugabo have changed since it was introduced and became established in these lakes (Ogutu-Ohwayo 1985, 1990a, b, Ogari & Dadzie 1988, Ligtvoet & Mkumbo 1990, and this study). These changes may have affected growth rates of the Nile perch. In Lake Chad, growth pattern of the Nile perch changed as the predator shifted from prawns and small fish to large fish prey (Hopson, 1972). Changes in the abundance of clupeid prey have also been associated with changes in growth rate of <u>Lates mariae</u> in Lake Tanganyika (Coulter 1965). This study was partly intended to show how the changes in the type, size and numbers of prey eaten may have affected growth rate of the Nile perch in the new habitats and how the situation in the habitats invaded by the Nile perch compared with that in native habitats where Nile perch has remained in balance with its prey for a long time.

There are virtually no historical data upon which comparisons of changes in growth rate of Nile perch in lakes

Victoria, Kyoga and Nabugabo can be based. Acere (1985) and Asila and Ogari (1987) estimated growth rates of Nile perch only in Lake Victoria and their data suggest that originally, both here and probably in other non-native habitats growth rates were higher than in native habitats (Jensen 1957, Hopson 1972). At that time, haplochromines were the most abundant fish in Lake Victoria (Kudhongania and Cordone 1974) and formed the main prey of the Nile perch (Gee 1964, 1969, Hamblyn 1966). These were rapidly depleted by Nile perch predation following rapid increases in its stocks (Ogutu-Ohwayo 1985, 1990a, b, Ogari & Dadzie 1988, Ligtvoet and Mkumbo 1990) after which the predator shifted to other probably less profitable prey. Haplochromine populations have recently increased and become more important as prey in Lake Kyoga (Chapter 4: Fig. 4.3). This change in the type of prey can be manifested in growth rate of the predator in Lake Kyoga as compared to lakes Victoria and Nabugabo and may give an idea of how fast the predator grew when haplochromines were still abundant and whether depletion in haplochromines may have resulted in reduction in growth rate of Nile perch.

Unlike in temperate regions, estimation of age and growth of fish in the tropics using growth marks on bony structures is difficult due to lack of distinct checks and a means of interpreting them where they do occur. Because of this, previous attempts to estimate growth parameters of Nile perch in Lake Victoria have been based on modal length progression analysis (Acere 1985, Asila & Ogari 1987) and to a limited degree on tagging (Ligtvoet & Mkumbo 1990). There are, however problems of estimating age and growth of long-lived species like Nile perch from modal length progression analysis because length frequency analyses become unreliable when the distributions merge or overlap following changes in growth rate (Beamish & MacFarlane 1987). Length progression analyses are thought to be unsuitable for ageing Nile perch (Hopson 1972). The data presented here will, therefore, be useful in estimation of age and growth of the Nile perch and for comparison with previous results which were based on other methods.

Growth rates of Nile perch in lakes Victoria, Kyoga and Nabugabo were examined and compared. The hypothesis tested was that there were no significant differences in growth rates of the fish between the three lakes and that the growth rates in these lakes were not significantly different from those in habitats where Nile perch occurs naturally.

Materials and methods

Growth rates were estimated by tagging Nile perch on lakes Victoria, Kyoga and Nabugabo. In lakes Kyoga and Nabugabo, the fish were caught in seines and in Lake Victoria by trawling in shallow waters. Fish trawled from deep waters appeared fatigued and some had everted stomachs apparently due to expansion of the gas bladder following rapid changes in depth. Live fish were placed in tanks and transported to the place of release. The total length of the fish was measured to the nearest 0.1 cm, the number on the tag was recorded, the tag was injected in the dorsal musculature using a tagging gun and the fish released. The site of capture and that of release were also recorded.

Tagged fish on lakes Victoria and Kyoga were recovered by commercial fishermen but those in Lake Nabugabo were recovered in experimental seines and wherever possible measured and released again. Advertisements for report of tagged fish were made verbally at fish landings, by posters placed at different places, and in radio broadcasts. Fishermen were requested to pass to the nearest fisheries official or bring to our laboratory either the tagged fish or a stick equal to the total length of the fish plus information on the date and place of capture. A reward which included a refund of transport costs incurred was to be given. Initially, some fishermen who recovered immature fish which were not permitted by law tended to bring sticks which were longer than the fish they had recovered for fear of being prosecuted. This problem was overcome by requesting the fishermen, who could not bring the fish fresh, to gut and sun dry it without removing the tag and later bring it together with the stick to our laboratory to facilitate comparison with the stick. It is the measurement on the stick which were recorded, dry fish were only used to verify whether the length of the stick had been a fair estimate of that of the fish.

Growth rates were estimated for fishes tagged in lakes Victoria and Kyoga in 1991 and 1992 and in Lake Nabugabo in 1992 and 1993. In order to make the data comparable between the lakes, fishes of the same length range were tagged during approximately the same time of the year. A total of 1842 Nile perch were tagged on Lake Victoria, 1766 on Lake Kyoga and 700 on Lake Nabugabo. Most were within the 20 to 60 cm length class. Most of these would, according to previous results of Hopson (1972), Jensen (1957) and Acere (1985) be in their first year of life. These were mainly immature individuals but also represented the size range just before recruitment into the harvestable stock. The data therefore gave an idea of how fast the Nile perch grew before it matured and was recruited into the fishery.

Growth rates were estimated using the equation:

$$GR=\frac{(L_2-L_1)}{D}\times 365$$

Where GR = annual growth increment in cm, L_1 = total length in cm at release, L_2 = total length in cm at recapture and D = number of days between release and recapture.

Results and discussion

One hundred and ten tagged fish were recovered on Lake Kyoga, 27 on Lake Victoria and 43 on Lake Nabugabo.

Comparisons of growth rate between lakes were confined to Nile perch of 20 to 40 cm because most of the fish recovered on the three lakes were within this size range. This also reduced the effect of maturity on growth rate because many fish especially males start maturing after about this size (Holden 1963, Hopson 1972, 1982, Ogutu-Ohwayo 1988). Also, in order to minimize errors due to inaccurate measurements on the stick only measurements made on actual fish were used in comparison of growth rates.

Mean annual growth rates of Nile perch for each of the three lakes are illustrated in Figure 6.1. Nile perch grew faster in Lake Kyoga (N = 49, mean = 28.7 ± 1.3 cm per year) than in Lake Victoria (N = 20, mean = 18.9 ± 1.4 cm per year) and Lake Nabugabo (N = 43, mean = 19.0 ± 0.7 cm per year). ANOVA showed that there were significant differences in growth rates between lakes ($F_{2,109} = 24.037$, $p < 0.001$). A multiple comparison of means test between the lakes (see also Fig. 6.1) showed that growth rates in Lake Kyoga were significantly higher than those of lakes Victoria and Nabugabo ($p < 0.05$) but those of lakes Victoria and Nabugabo were not significantly different ($p > 0.05$).

The size at first maturity of Nile perch in lakes Victoria, Kyoga and Nabugabo is currently similar (Chapter 7, Fig. 7.3). Faster growth rate of Nile perch in Lake Kyoga as compared with lakes Victoria and Nabugabo can be explained in terms of differences in the type and size of prey eaten. Haplochromines were the most important and

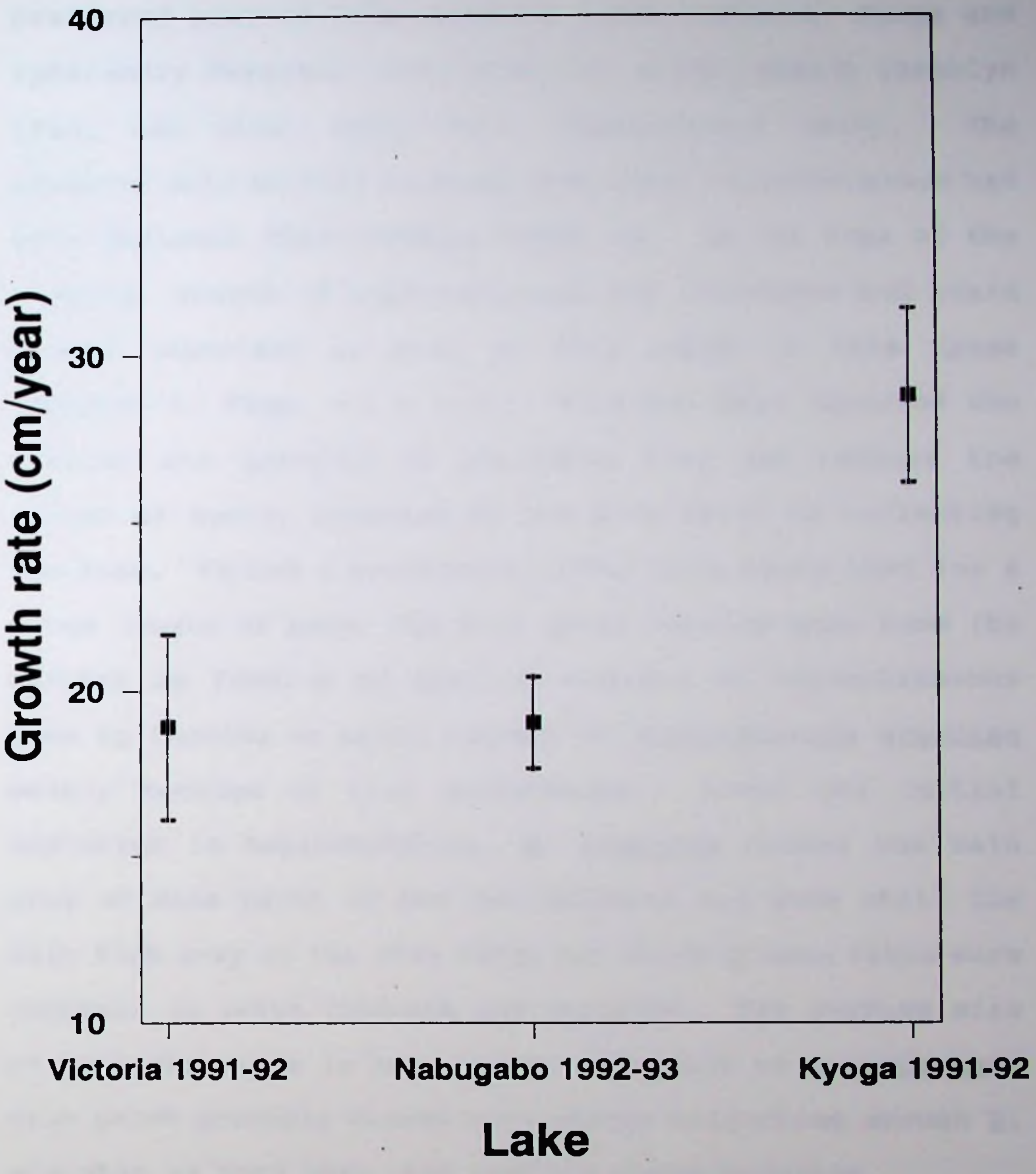


Figure 6.1. Growth rate of Nile perch of 20 to 40 cm in lakes Victoria, Nabugabo and Kyoga. Vertical bars are 2 SE of mean growth rate. Growth rates of Lake Kyoga were significantly higher than those of lakes Victoria and Nabugabo but those of lakes Victoria and Nabugabo were not significantly different.

preferred prey of Nile perch in lakes Victoria, Kyoga and apparently Nabugabo, soon after its establishment (Hamblyn 1966, Gee 1969, Okedi 1971, Ogutu-Ohwayo 1993). The predator only shifted to other prey after haplochromines had been depleted (Ogutu-Ohwayo 1990a, b). At the time of the tagging, stocks of haplochromines had increased and again become important as prey of Nile perch in Lake Kyoga (Chapter 4; Figs. 4.1 & 4.2). This may have improved the quality and quantity of available food and reduced the amount of energy expended by the Nile perch in collecting the food. Wanink & Goudswaard (1994) have shown that for a given length of prey, the Nile perch obtains more food (by weight) by feeding on specific numbers of haplochromines than by feeding on equal numbers of Rastrineobola argentea mainly because of size differences. After the initial depletion in haplochromines, R. argentea became the main prey of Nile perch in the new habitats and were still the main fish prey of the size range for which growth rates were compared in lakes Victoria and Nabugabo. The average size of haplochromines is much higher than that of R. argentea. Nile perch probably expend more energy collecting enough R. argentea as prey than when hunting haplochromines.

The current mean growth rates of Nile perch in lakes Victoria and Nabugabo are close to the mean values reported for several native habitats of Nile perch. L. niloticus attained a length of 19.5 cm to 23.9 cm at the end of the first year in Lake Mariout (Jensen 1957) and a mean length of 21.1 cm in Lake Chad (Hopson 1972). The higher values currently recorded for Lake Kyoga suggest that Nile perch has the capacity to adjust its growth rate as food supply changes and apparently grew faster when haplochromines were still abundant in the new habitats.

Acere (1985) estimated the growth rate of Nile perch in Lake Victoria using data collected when haplochromines were still its main prey and observed that at that time, it attained a mean total length of 52 cm at the end of the first year of life. This value is much higher than the current estimates for Lake Victoria and other non-native habitats. Hughes (1992) has questioned the accuracy of Acere's estimates because he pooled length frequency data collected over many years without taking into account the time of the year that the fish were collected, which invalidates use of length frequency analysis. Most of Acere's specimens also came from gill net catches which due to their selectivity can give biased estimates using modal length progression analysis.

Hughes (1992) estimated growth rate of Nile perch in the Nyanza Gulf of Lake Victoria in 1983 and recorded growth of 23 cm total length in 287 days. This indicates that the fish achieved a length of about 29 cm by the end of the first year of life. This value, which corresponds to the period when haplochromines were just disappearing from the Nyanza Gulf, is comparable to the current estimates for Lake Kyoga.

There were no growth estimates for Lake Albert. However, if the values for lakes Mariout and Chad are representative of native habitats, then the current growth rates of immature Nile perch in lakes Victoria and Nabugabo are comparable to those in native habitats. The prediction that growth rate of the Nile perch in the new habitats has attained a level which is not different from that of native habitats can be accepted in respect to lakes Victoria and Nabugabo. The currently higher values for Lake Kyoga seem to be due to the recent increases in haplochromine prey.

Chapter 7

Reproductive tactics of the Nile perch, Lates niloticus L. and stability of its stocks in lakes Victoria, Kyoga and Nabugabo

Abstract

The size at first maturity, fecundity and sex ratios of L. niloticus in lakes Victoria, Kyoga and Nabugabo over different periods were examined to see how these traits had adjusted to changes in prey by comparing the situation in the new habitats over different periods with that in Lake Albert. Initially, Nile perch in the new habitats adjusted its size at first maturity from levels recorded in Lake Albert (40-50 cm for males and 80 - 100 cm for females) to smaller sizes (30 - 40 cm for males and 50 - 59 cm for females). Afterwards the size at first maturity adjusted upwards and remained at levels recorded in Lake Albert. The species is very fecund with fecundity being proportional to the cube of the length. Sex ratios were initially not significantly different between new habitats and Lake Albert (85 - 110 females : 100 males) but later became and have remained male biased (23 - 65 females : 100 males). Reproductive potential of the Nile perch does not seem threatened by changes in prey as the species has very high reproductive potential and can adjust its size at first maturity under changing feeding regimes in a manner that promotes reproductive success. However, the reasons and implications of male biased sex ratios are obscure and need further investigations.

Introduction

Stearns (1976, 1980) has defined life history tactics as a set of co-adapted traits developed by natural selection to solve a particular ecological problem. The reproductive traits that have been referred to in the literature include the age or size at maturity, fecundity, survival rates, size and nature of gametes, timing and frequency of breeding and size of the offspring (Stearns, 1976, 1980, Stearns & Crandall 1989, Wootton 1989) and to a less extent sex reversal (Shapiro 1989). Tactics are the ways these traits are adjusted to promote reproductive success. This is possible because life history characteristics are not fixed but fall within a range which is determined by genetic and environmental conditions (Stearn & Crandall 1989).

The types, sizes and numbers of prey eaten by Nile perch have changed since it was introduced and became well established in lakes Victoria, Kyoga and Nabugabo (Ogutu-Ohwayo 1990a, b, Ogari & Dadzie, 1988, Witte et al 1992a, b and this study). At the time of the introduction, haplochromines were abundant and formed at least 80% of the demersal fish biomass in Lake Victoria (Kudhongania & Cordone 1974). They were the main prey of the Nile perch soon after its establishment in the new habitats (Hamblyn 1966, Gee 1964, 1969) but were rapidly depleted by Nile perch predation as its stocks increased (Witte et al 1992a, b). This reduction in prey has causes uncertainty of the future of the Nile perch fishery. It is feared that as prey are depleted, stocks of the Nile perch will decline until the fishery becomes unviable.

Changes in the quality and quantity of food can affect reproduction by affecting the onset of maturity and fecundity (Stearns 1976, Stearns & Crandall 1989, Wootton 1989). Fish fed intensively mature earlier than those fed insufficiently. Improvement in food supply can accelerate maturity while reduction in food supply can delay maturity in fish (Scott 1962, Nikolsky 1963, Bagenal 1969, Wootton 1973). An organism subjected to environmental changes such as the reduction in food supply discussed above may adjust its reproductive traits in a manner that will promote fitness. This is usually achieved by delaying maturity to a larger size in order to gain fecundity (Stearns 1976, 1980, Stearns & Crandall 1989).

The changes in the type, size and abundance of prey available to the Nile perch in lakes Victoria, Kyoga and Nabugabo are likely to have affected the size at first maturity of the fish. Sex ratios may also vary when food is limiting and different amounts of energy are required to maintain one sex than the other especially where there is sexual size dimorphism (Charnov 1979, Charnov & Bull 1989, Frank 1990, Holtby & Healey 1990). The possibility that environmental conditions, especially changes in food supply, can affect reproduction in Nile perch is suggested by differences in some aspects of reproductive biology of the species between new and native habitats (Kenchington 1939, Holden 1963, Okedi 1971, Hopson 1972, 1982). Nile perch in lakes Victoria and Kyoga initially matured at a smaller size than in the native habitats (Okedi 1971, Hopson 1972). Sex ratios and fecundity of the species were also different between native and new habitats (Okedi 1971, Kenchington 1939). Examination of how reproductive traits of the Nile perch especially the size at first maturity have adjusted to changes in prey supply was used as one of the ways of seeing whether the Nile perch stocks would stabilize and sustain production.

Size at first maturity, fecundity and sex ratios of the Nile perch in lakes Victoria, Kyoga and Nabugabo over different periods before and after establishment of the predator were examined. It was predicted that these traits would adjust to changes in food supply, and finally stabilized. Stability was expected to occur at levels which approximate to those of Lake Albert and other native habitats or that are unique to the new habitats. In a stable state, there would be no significant changes in these traits.

Materials and Methods

The information was obtained by comparing data collected from Lake Victoria between 1964 and 1992, Lake Kyoga between 1967 and 1993, Lake Nabugabo between 1991 and 1993 and Lake Albert between 1989 and 1992. Comparative information for other native habitats were obtained from the reports of Worthington (1929) and Holden (1963) for Lake Albert, Kenchington (1939) for the Blue Nile, Hopson (1972, 1982) for lakes Chad and Turkana.

Nile perch specimens were obtained from commercial catches, experimental gill nets and seines. The total length, standard length and the weight of each specimen were measured and the gonads assigned to the maturity stages recognised by Hopson (1972); Immature - I; Developing - II; Maturing (and/or recovering for females) - III; Mature (and/or recovering for males) - IV; Ripe V; Ripe running - VI; Spent (for females only) - VII. Males were graded into six stages because their gonads contained running milt most of the time and the spent condition was not distinct. The females go through a well defined stage of recovery. Recycling females were designated as IIIR.

The gonads were removed and weighed. Gilson's fluid has often been used to separate eggs from connective tissue during fecundity studies (Bagenal & Braum 1978) but this method was abandoned during the present study after several trials had resulted in dissolution of eggs and tissue. Ripe ovaries for fecundity studies were therefore preserved in 10 percent formalin solution as used by Okedi (1971).

The preserved ova were washed in tap water, most of the adhering moisture removed with blotting paper, and the total weight recorded. Examination of ova under a binocular dissecting microscope revealed that in some cases, a ripening ovary (particularly Stage V) had some eggs still at different stages of development. Only those ovaries with ova which had developed to uniform size were used in estimations of fecundity. About 0.1 gm samples were taken from different parts of the ovary. The number of ova in at least five weighed replicate sub-samples was counted under a binocular microscope. The mean number of ova from these samples was used to estimate the total number of ova in each pair of ovaries.

Because Nile perch shed all ripe ova at each spawning, fecundity was defined according to Nikolsky (1963) and Bagenal and Braum (1978) as the number of ripening eggs in the ovary prior to the next spawning season.

Sex ratios were analyzed using a binomial test (Siegel 1956). Size at first maturity and sex ratios were compared as detailed in Chapter 2.

Results

Size at first maturity

The sizes at first maturity were only estimated for Nile perch of more than 20 cm total length because sexes were not clearly distinguishable below this size. Gonadal Stages I and II consisted of immature fish. Stage III was the transitional stage between immature and mature fish. In both sexes, the fish were mature at gonadal stage IV i.e. when the milt or the oocytes were discernible for the first time. Size at first maturity is defined according to Beverton and Holt (1957) as the size at which 50% of the fish are mature.

There were variations in size at first maturity between the blocks (Figs. 7.1a & b). The size at first maturity of male Nile perch in Lake Victoria between 1964 and 1967 was between 30 cm and 34 cm total length (Fig. 7.1a). It then adjusted over time such that by the 1988-92 period they were maturing at between 60 cm and 64 cm. The size at first maturity of males in Lake Kyoga between 1967 and 1993, Lake Nabugabo between 1991 and 1993 and Lake Albert between 1989 and 1993 were all between 50 cm and 59 cm total length. Therefore, the equilibrium size at first maturity of male Nile perch were estimated to lie between 50 cm and 59 cm total length.

The size at first maturity of female Nile perch in Lake Victoria during the 1964-77 period was at between 40 and 59 cm total length (Fig. 7.1b). As in the males, size at first maturity increased over the years and by the 1988-92 period females were attaining maturity at between 90 cm and 99 cm. The sizes at first maturity of female Nile perch in Lake Kyoga during the 1967-93 period, Lake Nabugabo during the 1991-93 period and Lake Albert during the 1989-93 period were between 80 cm and 99 cm total length. The size range within which the size at first maturity of female Nile perch might stabilize was estimated to lie between 80 cm and 99 cm total length.

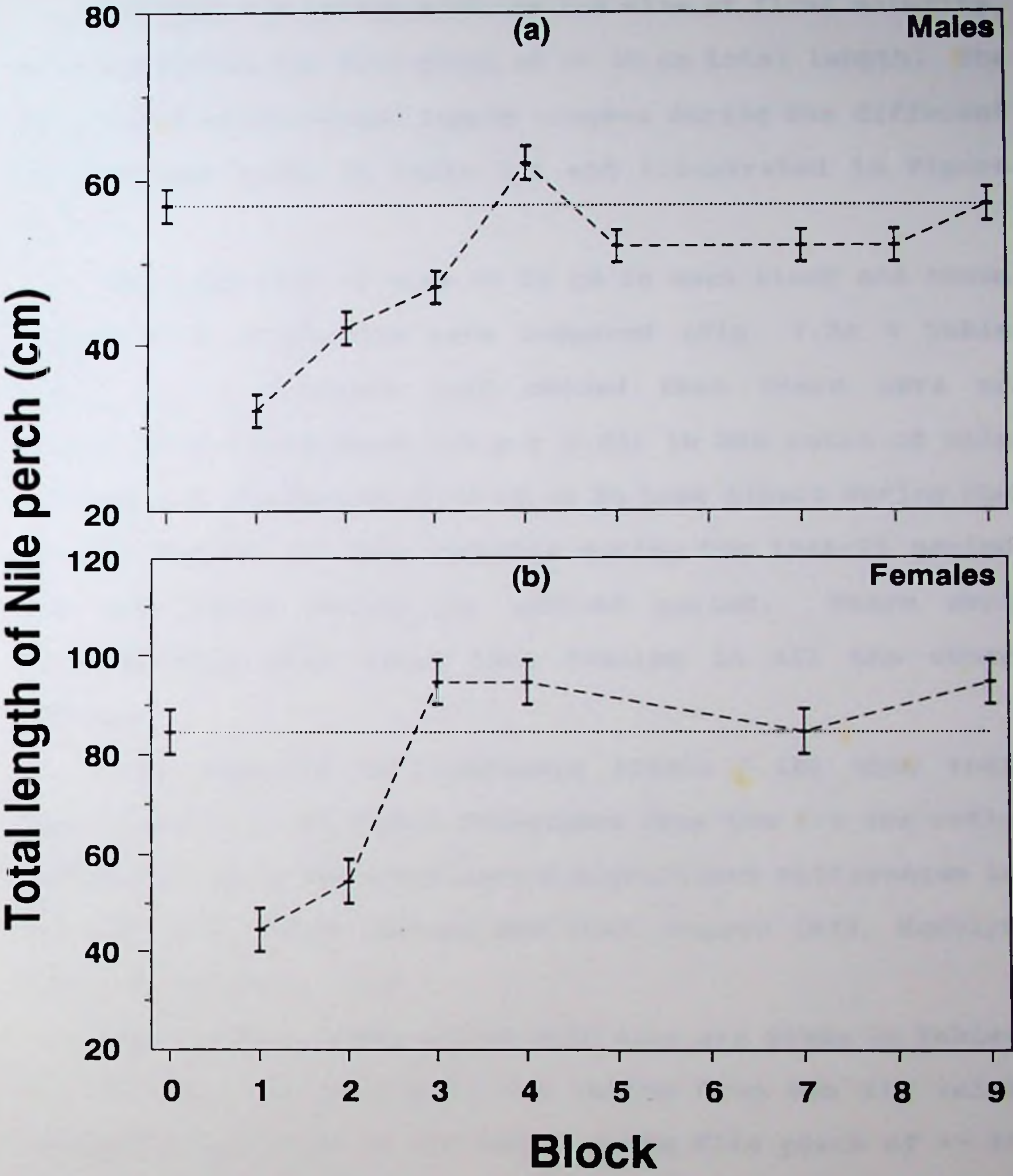


Figure 7.1. The size class within which 50% of male and female Nile perch matured in lakes Albert, Victoria, Nabugabo and Kyoga during different periods. The mid values for the new habitats are joined by a dashed line. The Lake Albert level is indicated by a dotted line.

Sex ratios

Primary sex ratios were, as for size at first maturity, only estimated for Nile perch of >= 20 cm total length. The sex ratios of different length classes during the different periods are given in Table 7.1 and illustrated in Figure 7.2.

When all fish of more >= 20 cm in each block and those reported in literature were compared (Fig. 7.2a & Table 7.1a, b), a binomial test showed that there were no significant differences (at $p \leq 0.05$) in the ratio of male to female L. niloticus of >= 20 cm in Lake Albert during the period 1989-92, in Lake Victoria during the 1968-77 period and Lake Kyoga during the 1967-68 period. There were significantly more males than females in all the other blocks.

Data reported in literature (Table 7.1b) show that there were no significant deviations from the 1:1 sex ratio in the Blue Nile but there were a significant differences in sex ratios in lakes Turkana and Chad (Hopson 1972, Hamblyn 1960, Kenchington 1939).

The changes in sex ratios with size are given in Tables 7.2 to 7.4. Deviations in sex ratios from the 1:1 value increased with size of the fish. Among Nile perch of >= 20 cm and < 60 cm (Table 7.2), there were significantly more males than females in all the blocks with the exception of Lake Kyoga between 1967 and 1968. In Nile perch of 60 cm to 100 cm (Table 7.3), there were no difference in sex ratios

Table 7.1. (a). A comparison of sex ratios of *L. niloticus* in different water bodies using a binomial test.

Block, Lake & Period	Fish size	No ♂	No ♀	z value	p value
0: Albert	>=20	350	391	1.54	0.062
1: Victoria 1964-67	>=20	2482	2110	5.47	0.000
2: Victoria 1968-77	>=20	231	255	1.13	0.129
3: Victoria 1982	>=20	397	285	4.25	0.000
4: Victoria 1988-92	>=20	3040	702	47.51	0.000
5: Nabugabo 1991-93	>=20	326	104	10.65	0.000
6: Kyoga 1967-68	>=20	129	114	0.898	0.184
7: Kyoga 1978-80	>=20	1131	593	12.93	0.000
8: Kyoga 1988-90	>=20	1299	818	10.43	0.000
9: Kyoga 1991-93	>=20	1551	834	14.66	0.000

(b). Some values reported in literature

Water body	Fish size	No ♂	No ♀	z value	p value	Source of information
Chad	>30	2779	1694	16.21	0.000	Hopson 1972
Turkana	>20	499	425	2.40	0.008	Hamblyn 1960
Blue Nile	<107	59	69	0.97	0.166	Kenchington 1939
Kyoga		435	282	5.68	0.000	Okedi 1971
Victoria		935	944	0.23	0.230	Okedi 1971

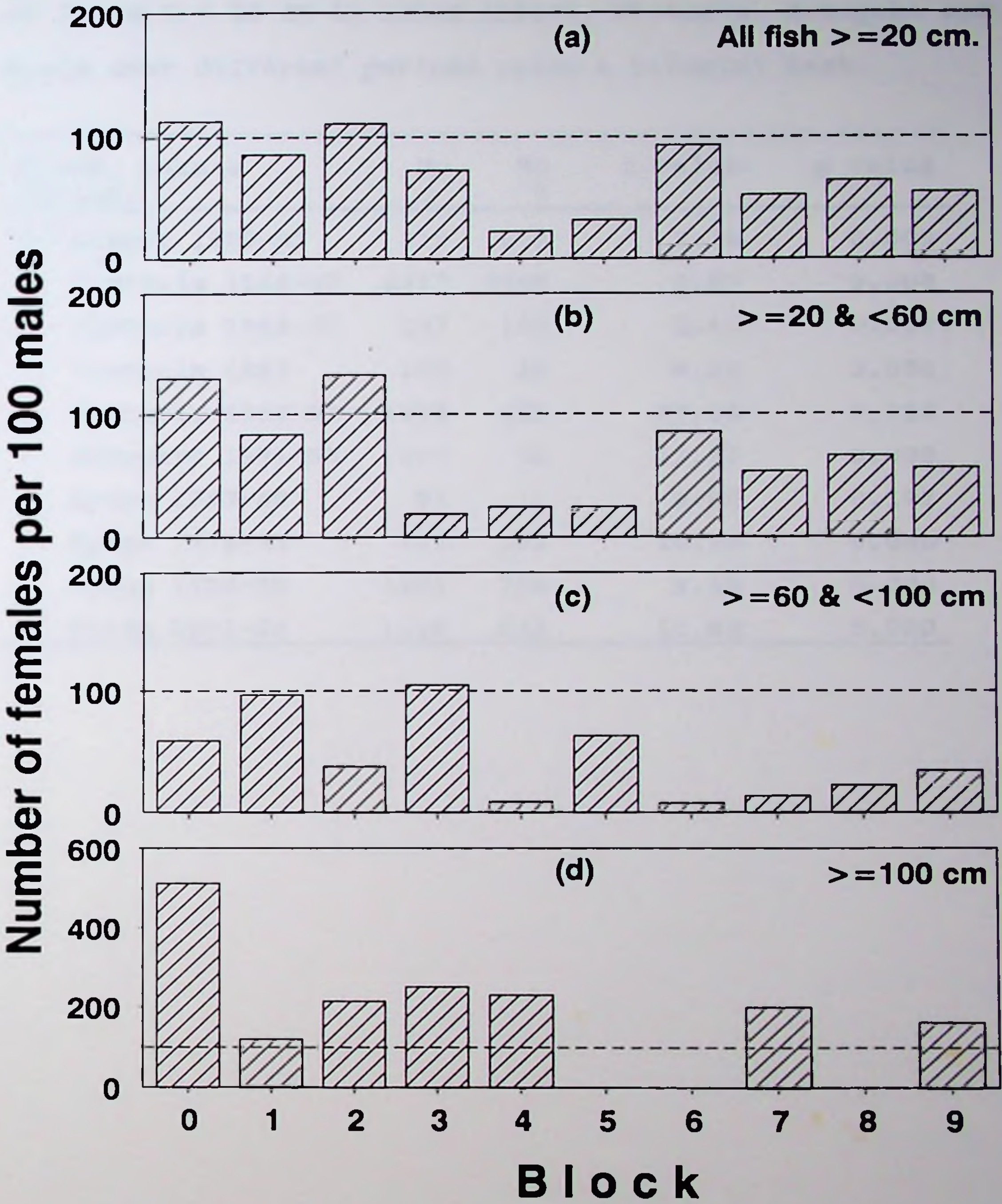


Figure 7.2. Sex ratios of Nile perch of different length categories in lakes Albert, Victoria, Nabugabo and Kyoga during different periods. The horizontal dashed line marks the level at which sex ratios would be the same.

Table 7.2. A comparison of sex ratios of L. niloticus of >= 20 cm & < 60 cm in lakes Albert, Victoria, Nabugabo and Kyoga over different periods using a binomial test.

Block, Lake & Period:	No ♂	No ♀	z value	p value
0: Albert 1989-92	210	272	2.78	0.003
1: Victoria 1964-67	2447	2065	5.67	0.000
2: Victoria 1968-77	137	182	2.46	0.007
3: Victoria 1982	155	29	9.22	0.000
4: Victoria 1988-92	1825	485	27.86	0.000
5. Nabugabo 1991-93	288	72	11.33	0.000
6. Kyoga 1967-68	83	71	0.87	0.192
7. Kyoga 1978-80	737	393	10.20	0.000
8. Kyoga 1988-90	1204	796	9.10	0.000
9. Kyoga 1991-93	1116	623	11.80	0.000

Table 7.3. A comparison of sex ratios of L. niloticus of >= 60 cm and < 100 cm in lakes Albert, Victoria, Nabugabo and Kyoga over different periods using a binomial test.

Block, Lake & Period:	No ♂	No ♀	z value	p value
0: Albert 1989-92	132	78	3.10	0.001
1: Victoria 1964-67	34	33	0.00	0.500
2: Victoria 1968-77	73	28	4.38	0.000
3: Victoria 1982	240	251	0.54	0.298
4: Victoria 1988-92	1168	109	29.61	0.000
4. Nabugabo 1991-93	38	24	1.65	0.049
6. Kyoga 1967-68	46	38	0.76	0.224
7. Kyoga 1978-80	317	45	14.24	0.000
8. Kyoga 1988-90	95	22	6.66	0.000
9. Kyoga 1991-93	389	136	11.00	0.000

for Lake Victoria during the 1964-67 and 1982 periods and in Lake Kyoga during the 1967-68 period. The other blocks again had significantly more males. In contrast to the smaller size groups, Nile perch of >= 100 cm (Table 7.4) had significantly more females in all the blocks with the exception of Lake Victoria during 1982.

Secondary sex ratios using only mature Nile perch were also compared (Table 7.5 & Fig. 7.3). In all cases, there were significantly more mature males than females. A comparison between the new habitats and Lake Albert (Fig. 7.3) showed that in blocks 1 and 2, the proportion of mature females in Lake Victoria was significantly higher than in Lake Albert but by block 3, the proportion of mature females had decreased to a significantly lower level than in Lake Albert. The proportion of mature females in all the other blocks of the new habitats was significantly lower than that for Lake Albert.

Fecundity

The number of ripe ovaries available for fecundity determination from different habitats was too small to permit comparisons of fecundity among blocks. Detailed analysis of the relationship between fecundity and size of the fish was done using data collected from Lake Kyoga during the 1978-80 period. The relationship between fecundity and size is shown in Figure 7.4. Fecundity increased with length and weight of the fish. The

Table 7.4. A comparison of sex ratios of <u>L. niloticus</u> of >= 100 cm in lakes Albert, Victoria, Nabugabo and Kyoga over different periods using a binomial test.

Block, Lake & Period:	No ♂	No ♀	z value	p value
0: Albert 1989-92	8	41	4.57	0.000
1: Victoria 1964-67	1	12	2.77	0.003
2: Victoria 1968-77	21	45	2.83	0.002
3: Victoria 1982	2	5	0.76	0.224
4: Victoria 1988-92	47	108	4.82	0.000
5: Nabugabo 1991-93	0	8	2.47	0.007
6: Kyoga 1967-68	0	5	1.79	0.037
7: Kyoga 1978-80	77	155	5.05	0.000
8: Kyoga 1988-90				
9: Kyoga 1991-93	46	75	2.55	0.005

Table 7.5. A comparison of sex ratios of mature *L. niloticus* in lakes Albert, Victoria, Nabugabo and Kyoga over different periods using a binomial test. Sex ratios were in all cases significantly different from the 1:1 ratio (at 5% level of significance).

Block, Lake & Period:	No ♂	No ♀	z value	p value
0: Albert 1989-92	183	75	6.66	0.000
1: Victoria 1964-67	1483	812	13.98	0.000
2: Victoria 1968-77	164	97	4.09	0.000
3: Victoria 1982	324	76	12.35	0.000
4: Victoria 1988-92	1326	108	32.14	0.000
5: Nabugabo 1991-93	78	14	6.57	0.000
6: Kyoga 1967-68	34	9	3.65	0.000
7: Kyoga 1978-80	537	156	14.44	0.000
8: Kyoga 1988-90	135	8	10.54	0.000
9: Kyoga 1991-93	476	108	15.18	0.000

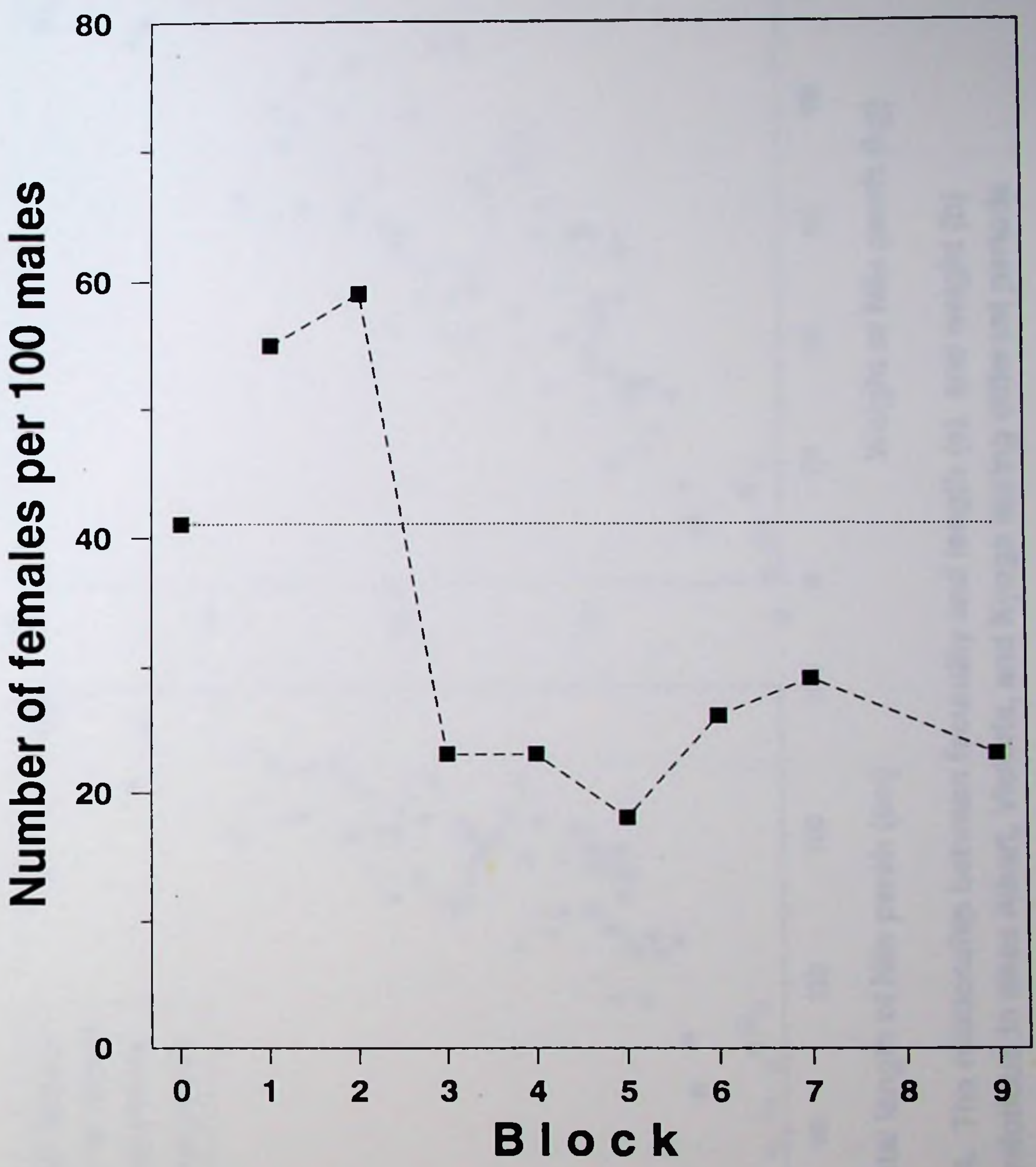


Figure 7.3. The ratios of mature females to mature male Nile perch in lakes Albert, Victoria, Kyoga and Nabugabo over different periods. The values for the new habitats are joined by a dashed line. The Lake Albert level is indicated by dotted line.

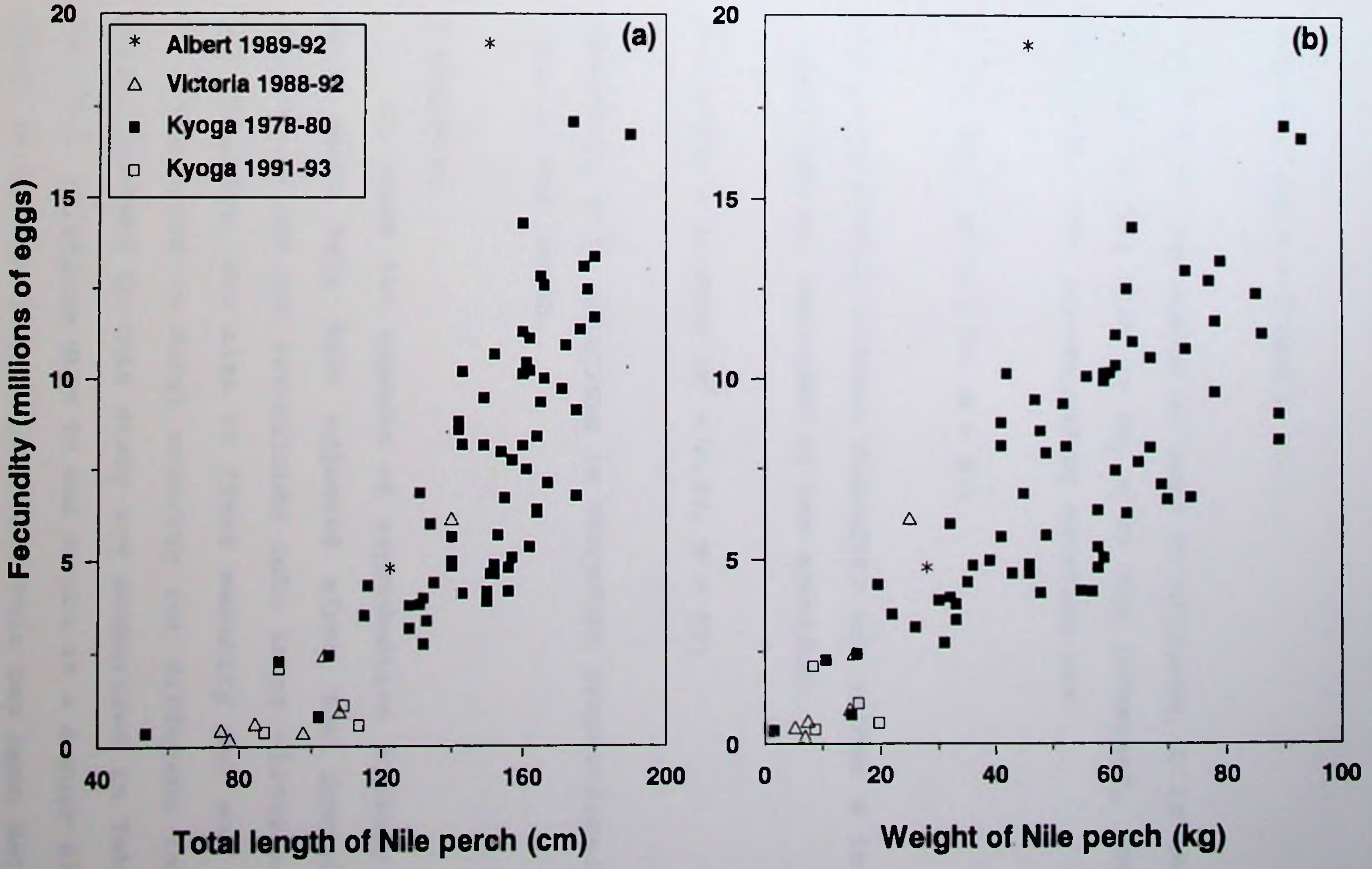


Figure 7.4. The relationship between fecundity and length (a) and weight (b) of *Lates niloticus* in lakes Albert, Victoria, and Kyoga during different periods

relationship between fecundity and length was of the form:

$$\text{Log } F = \text{Log } a + b \text{ Log } L$$

where F is the number of eggs in millions, L is the total length of the fish in cm, a is the intercept, and b the exponent. The corresponding equation was:

$$F = 1.99L^3 \quad (R^2 = 0.75,\ N = 67)$$

The relationship between fecundity and weight W in kg was linear and was described by the equation:

$$F = 24900 + 141800W \quad (R^2 = 0.62,\ N = 67)$$

Fecundity in L. niloticus is therefore proportional to the cube of the length.

Discussion

At least two aspects of reproductive biology of the Nile perch have been adjusted since the predator was introduced and got established into lakes Victoria, Kyoga and Nabugabo; the size at first maturity and sex ratios.

The sizes at first maturity for different lakes and those recorded in this study are summarized in Table 7.6. Female L. niloticus grow to and mature at a larger size than males in all the localities where this has been determined

Table 7.6. The size at first maturity, (in cm total length) of L. niloticus in different habitats and during different periods within the same habitat.

Water body	Males	Females	Source of information
Lake Chad	50	60-65	Hopson (1972)
Lake Turkana	65	90	Hopson (1982)
Lake Albert	60	85	Holden (1963)
Lake Albert 1989-92	55-59	80-89	Present study
Blue Nile	60	60	Kenchington (1939)
Lake Victoria & Kyoga	30-33	33-35	Okedi (1971)
Lake Victoria	54	68	Acere (1985)
Lake Victoria 1964-67	30-34	40-49	Present study
Lake Victoria 1968-77	40-44	50-59	Present study
Lake Victoria 1982	45-49	90-99	Present study
Lake Victoria 1988-92	60-64	90-99	Present study
Lake Nabugabo 1991-93	50-54		Present study
Lake Kyoga 1978-80	50-54	80-89	Present study
Lake Kyoga 1988-92	50-54		Present study
Lake Kyoga 1991-93	55-59	90-99	Present study

(Kenchington 1939, Holden 1963, Okedi 1971, Hopson 1972, 1982 and this study). The reasons for maturation at larger sizes were not been investigated. However, among other organisms, sexual size dimorphism in adults is thought to be due to sexual selection, parental investment or niche separation (Holtby & Healey 1990). Size is thought to be an important component of fitness and is related to differential investment and resource partitioning between the sexes (Holtby and Healey 1990, Carothers 1984, Roff 1981). Maturation is affected by food supply and competition for it (Randall et al 1986). Under abundant food supply, fish will grow rapidly and mature once they have acquired enough energy to do so (Policansky 1983, Randall 1986). When males mature at a smaller size than females, the energy costs for females is higher than that for males. Large body size confers selective advantage on females. Among Nile perch, there is rapid increase in the size of prey ingested at about the size that females reach their size at first maturity. Larger size enables females to increase their energy intake by enabling them to feed on larger prey. A similar requirement may not be necessary in males.

If we can assume that the size at first maturity recorded in Lake Albert is the equilibrium size at first maturity for the species, then Nile perch in the new habitats initially matured at a smaller size than in its original habitat and then increased to comparable sizes (Fig

7.1). These changes were concurrent with the decrease in the abundance of haplochromines from the new habitat and their importance as food of the Nile perch (see Chapter 4). This suggests that food supply is a major environmental condition affecting maturity in Nile perch. Changes in the size at first maturity following changes in the abundance of prey has been demonstrated in rainbow trout (Scott 1962, Nikolsky 1963, Bagenal 1969, Wootton 1973).

Nile perch ova contain many fat globules (Kenchington 1939, Okedi 1971) and clearly require much food for their formation. Formation of ova is accompanied by gradual disappearance of mesenteric fat and loss of plumpness (Kenchington 1939). Since fecundity in the Nile perch increases with size, maturity at a larger size would increase fecundity as predicted by Stearns (1980), Stearns and Crandall (1989) and Wootton (1989). The phenomenon that large size was important because it enables the organism to produce a vast number of ova was also recognized by Darwin (1874). If the size at first maturity increased due to reduction in food supply, then size at first maturity should be concurrent with improved food supply. Current observations (Chapter 4) show that Nile perch shifts from feeding on many small prey to feeding on a few large prey at about the size that females attain sexual maturity. Maturity seem may be delayed to a size when the Nile perch has the capability to obtain enough food to support reproduction.

The increases in the size at first maturity occurred after haplochromines had been depleted from lakes Victoria and Kyoga. The changes can therefore be attributed to the reduction in the originally most abundant and vulnerable prey. Between 1964 and 1977, when haplochromines were still abundant, males in Lake Victoria matured at a smaller size than was the case between 1988 and 1992. The sizes at first maturity of the males increased from 30-34 cm between 1968-1977 to 40-45 cm between 1988 and 1992. The values in Lake Victoria for 1988-92 approximate to those of different periods of Lake Kyoga between 1967 and 1993 and Lake Albert between 1989 to 1992. They are also similar to those recorded previously from lakes Albert (Worthington 1929, Holden 1963) and Turkana (Hopson 1982) but higher than those recorded in Lake Chad (Hopson 1972) and the Blue Nile (Kenchington 1939). The size at first maturity of Nile perch in the new habitats has remained at this level for as long as 15 years in some of the new habitats. It therefore seems to have stabilized.

Nile perch produce pelagic eggs that are shed freely (Okedi 1971). Reproductive potential will be determined by the number of eggs that are produced, the proportion of eggs that are fertilized and hatch, the survival rate of the offspring, environmental conditions to which the eggs are exposed and the growth rate of the offspring. Since Nile perch does not take care of its eggs or young, it has to produce numerous eggs. Because of this, L. niloticus is very fecund. The relationship between fecundity and length (which has an exponent of 3.0) is similar to that of fishes which produce many eggs relative to their size. Such fish include the mormyrids and cyprinids where the exponent is close to three, but different from those that produce fewer eggs and offspring which are cared for, such as the cichlids where the exponent is close to two (Lowe 1955, Cadwalladr 1965, Welcomme 1967, Okedi 1970). But L. niloticus grows to a larger size and therefore produces many more eggs than mormyrids and cyprinids.

The sex ratios were male biased especially among mature Nile perch (Table 7.5). The reasons for the males biased sex ratios are obscure but the overall pattern is such that when haplochromines were still abundant in the new habitats, the proportion of mature females in the new habitats was higher than is currently the case (Fig. 7.3). This suggests that food may have a role to play. Although natural selection favours organisms with a 1:1 sex ratio (Fisher 1958), Charnov and Bull (1989) have indicated that biased sex ratios do occur but are common in species where individuals change sex during their adult life or those where sex is determined by environmental conditions experienced during pre-adult development.

One possible explanations for the male biased sex ratios in L. niloticus would, therefore be sex reversal. Hermaphrodite gonads have been detected and sex reversal reported in Lates calcarifer (Bloch) an Indo-pacific species of the same genera as L. niloticus where sex ratios are also males biased with a secondary sex ratio of 3.8:1 in favour of males (Moore 1979, Davis 1982). L. calcarifer is a protandrous hermaphrodite and protandrous hermaphrodites normally have male biased sex ratios (Charnov & Bull 1989). However, no hermaphrodite gonads were encountered in L. niloticus specimens examined macroscopically during this study and both sexes were encountered at all sizes for which sex ratios were determined. In species which undergo sex reversal, one sex appears first followed by the other (Shapiro 1989). Microscopic examination of Nile perch gonads may, in future throw more light on this.

The male biased sex ratios may also result from environmental conditions experienced by the species during pre-adult development. Charnov & Bull (1989), Charnov et al 1981 and Frank (1990) have indicated that sex ratios can deviate from the 1:1 ratio if resources are limiting. Under such circumstances, the sex which requires less resources to produce and maintain would be produced in greater proportions (Randall et al 1986, Ricklefs 1990, Frank 1990). Male Nile perch grow to a smaller size than females and need less energy for maintenance and gonadal development. This type of situation would favour a male biased sex ratio.

Holtby and Healey (1990) have suggested that biased sex ratios can result from sampling techniques or the gear used. The sex which is more active would be taken up more than the one which is more sedentary. Although a comparison between fishing gears was not made during this study, this was not apparent from the range of gears used. Hopson (1972, 1982) attributed difference in sex ratio to a higher mortality rate of males than females especially among the larger fish. Female Nile perch grow to and mature at a larger size than males. Selective fishing may contribute to males biased secondary sex ratios. Fishing mortality in Nile perch seems to be heaviest in fish < 100 cm. This would mean that more female Nile perch than males are cropped before they mature and this would result in male biased sex ratios. However, this does not explain the variations in sex ratio within the same lakes over time. Further research is therefore required to elucidate on biased sex ratio in this species.

Conclusion

Initially, Nile perch in the new habitats adjusted its size at first maturity from levels recorded in its original habitat to a smaller size apparently due to excessive food supply provided by vulnerable haplochromine prey. After these prey were depleted, size at first maturity adjusted upwards and stabilized at levels recorded in its original habitat. The species is very fecund with fecundity being proportional to the cube of the length. Reproductive potential of the Nile perch does not seem threatened by depletion of haplochromines and the species seems to have the capability to adjust its size at first maturity under changing feeding regimes in a manner that promotes reproductive success. However, sex ratios which were initially not significantly different between new habitats and the original habitat later became and have remained male biased. The implications of male biased sex ratios on reproductive success of the species is uncertain and needs further investigations.

Chapter 8

Can the fisheries of lakes Victoria, Kyoga and Nabugabo stabilize and sustain production in the presence of Nile perch ?

Abstract

Evidence for re-stabilization of the fish stocks in lakes Victoria, Kyoga and Nabugabo following establishment of Nile perch was sought by comparing changes in fish species diversity, prey selection and life history characteristics of the predator before and after its establishment with that in Lake Albert. The diversity of exploited fish species initially decreased from a level that was similar to that in Lake Albert to one that was significantly lower and then persisted. Afterwards, stocks of some species began to recover. Prey selection by Nile perch in the new habitats changed from predominance of haplochromines to types, sizes and numbers similar to those eaten in Lake Albert and other native habitats. The condition, factor which was initially higher in the new habitats, decreased and remained at values which although lower than in Lake Albert, are not below the lowest values recorded in a native habitat. Size at first maturity shifted from smaller to larger sizes, which are similar to those in Lake Albert; this increases overall reproductive potential because fecundity is proportional to the cube of the length. Since these characteristics have converged and persisted on values found in habitats where Nile perch is in balance with its prey, the fisheries of the lakes invaded by Nile perch can remain viable in its presence.

Introduction

Prior to the introduction of Nile perch, lakes Victoria, Kyoga and Nabugabo had similar and very diverse fish faunas (Graham 1929, Greenwood 1965, 1966, Worthington 1929, Cambridge expedition 1962, Fryer & Iles 1972). After Nile perch were introduced and became well established, stocks of most of the native species declined rapidly, and some completely disappeared (Hughes 1983, 1986, Ogutu-Ohwayo 1990a, b, Ogari & Dadzie 1988, Ligtvoet and Mkumbo 1990, Witte et al 1992a, b). Although human over-exploitation of the fish stocks (Jackson 1971), competition between introduced and native tilapiines (Welcomme 1984), and environmental degradation (Hecky & Bugenyi 1992, Hecky 1993, Mugidde, 1992, 1993, Hecky et al 1994) have contributed to changes in fish stocks, predation by the Nile perch is believed to be the main factor that has caused these rapid declines in fish stocks (Barel et al 1975). This has raised fears that fish stocks will be depleted to a level where the fisheries of these lakes will become unviable (FAO 1985). Also, Nile perch is the most important commercial species in these lakes and stability of its stocks is important to the overall viability of the fisheries.

Theoretically, when a force such as that due to Nile perch predation disturbs a character (such as populations of the prey), that character will be forced out of its normal range of variance (Holling 1973, May 1973, Connell & Sousa 1983). Stability can occur only when the character attains a new steady persistent state (May 1973, Goodman 1975). However, a perturbed character can have multiple stable points, i.e. it can return to one or more equilibria (Lewontin 1969, Sutherland 1974, 1981, 1990). In all cases, the force has to be resisted if the character is to stabilize (Connell & Sousa 1983). Alternatively, the character can be forced to a point where it crashes. Therefore, for stability to occur, there must be resistance or resilience to the perturbation, i.e. the character must have the capability to absorb the disturbance. Ideally for stability to occur, resilience should be equal and opposite to perturbation. However, for the system not to crash due to the perturbation, resilience should be equal to or exceed perturbation. Therefore, for the fisheries of lakes Victoria, Kyoga and Nabugabo to be prevented from collapsing due to Nile perch predation, some of the prey species should be or become resilient to predation by the Nile perch. This resilience should be equal to or greater than the force due predation pressure, i.e. resilience should be seen to be overcoming predation pressure due to Nile perch.

Evidence for re-stabilization of the fish stocks in lakes Victoria, Kyoga and Nabugabo after establishment of the Nile perch was obtained from examination of changes that occurred in the number and diversity of fish taxa, prey selection by the Nile perch and in life history characteristics of the Nile perch before and after establishment of the predator.

Changes in number and diversity of fish taxa

Stocks of the Nile perch started to increase rapidly in 1965 in Lake Kyoga and in 1977, 1982 and 1983 in the Kenyan, Ugandan and Tanzanian regions of Lake Victoria (Ogutu-Ohwayo 1985, Hughes 1983, Okaronon et al 1985, Goudsward & Witte 1985). Initially, haplochromines were the most abundant fishes in Lake Victoria (Kudhongania & Cordone 1974); they formed the main food of the predator soon after its introduction into lakes Victoria, Kyoga and apparently Nabugabo (Hamblyn 1966, Gee 1969, Ogutu-Ohwayo 1985, Ogutu-Ohwayo 1993).

The changes in fish species diversity just before and after the rapid increases in Nile perch stocks are best illustrated by the changes in fish species diversity in the Kenyan region of Lake Victoria (Fig. 8.1). As Nile perch stocks increased, there was a rapid decline in fish species diversity and in the contribution of haplochromines to the commercial catches. The decline in haplochromines was not due to a shift in fishing effort. Experimental trawling in the same part of the lake confirmed that as the catch rates of the Nile perch increased, those of haplochromines declined drastically (Okemwa 1984, Okaronon et al 1985, Goudswaard & Ligtvoet 1987, Ogutu-Ohwayo 1990a). However, by 1990, haplochromines started to reappear in commercial catches. This suggests that some haplochromines species had become resilient and could persist alongside the Nile perch. Increases in stocks of a few haplochromine species were

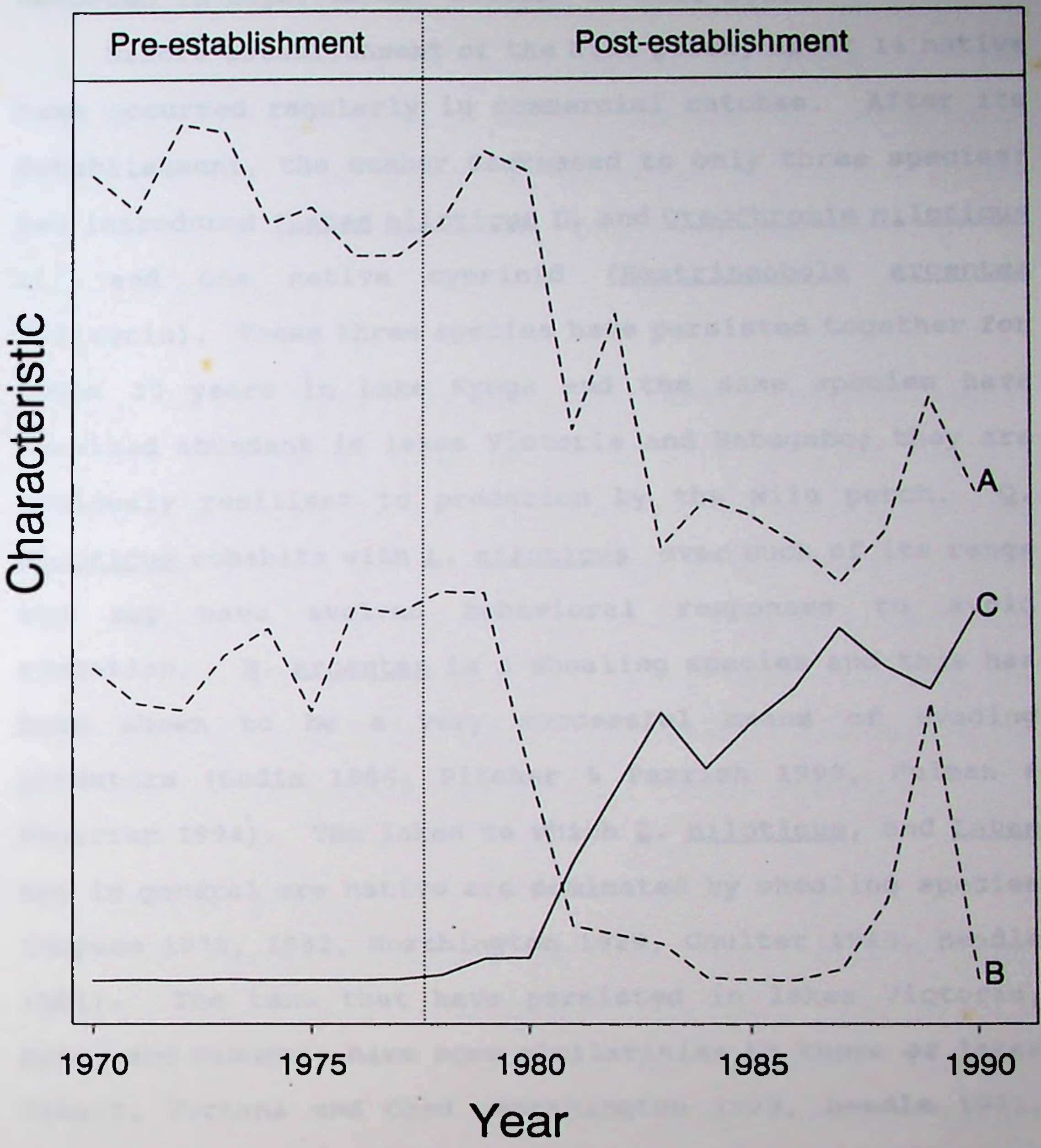


Figure 8.1. Changes in fish species diversity (A) and in the contribution of haplochromines (B) with increases in the contribution of the Nile perch (C) to commercial catches in the Kenyan region of Lake Victoria. Lines are drawn to scale as given in parts of the thesis where the respective graphs occur. The vertical dotted line divided the pre- and post-establishment periods.

recorded in experimental catches in Lake Kyoga.

Before establishment of the Nile perch, about 14 native taxa occurred regularly in commercial catches. After its establishment, the number decreased to only three species: two introduced (Lates niloticus L. and Oreochromis niloticus L.) and one native cyprinid (Rastrineobola argentea Pellegrin). These three species have persisted together for about 30 years in Lake Kyoga and the same species have remained abundant in lakes Victoria and Nabugabo; they are obviously resilient to predation by the Nile perch. O. niloticus cohabits with L. niloticus over much of its range and may have evolved behavioral responses to avoid predation. R. argentea is a shoaling species and this has been shown to be a very successful means of evading predators (Godin 1986, Pitcher & Parrish 1993, Fuiman & Magurran 1994). The lakes to which L. niloticus, and Lates spp in general are native are dominated by shoaling species (Hopson 1972, 1982, Worthington 1929, Coulter 1965, Beadle 1981). The taxa that have persisted in lakes Victoria, Kyoga and Nabugabo have some similarities to those of lakes Albert, Turkana and Chad (Worthington 1929, Beadle 1981, Hopson 1972, 1982). Both L. niloticus and O. niloticus are among the dominant species in all these lakes: Alestes spp. and Hydrocynus spp., the remaining major components of the fish community in lakes Albert, Turkana and Chad and can be regarded as ecologically analogous to R. argentea as far as resilience to predation is concerned. It can therefore be concluded that the species composition of the fish fauna in lakes Victoria, Kyoga and Nabugabo has converged on types that are resilient to Nile perch predation and can persist alongside it. The important question is whether these species can support both the fishery and provide food for the Nile perch.

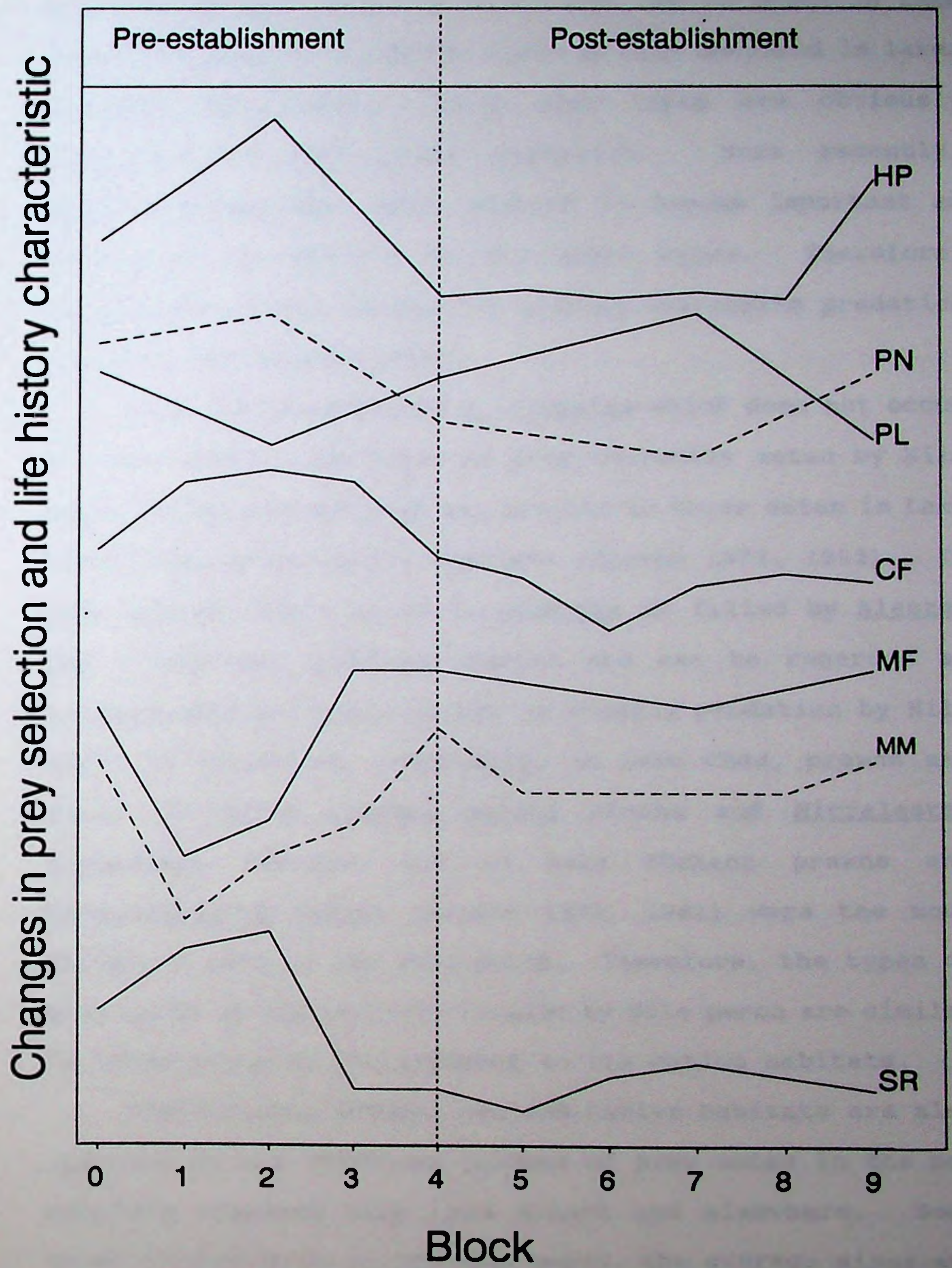
Changes in prey selection and life history characteristics

The changes in prey selection and in life history characteristics of the Nile perch in the new habitats during the period before and after the rapid increases in Nile perch stocks and that for its native habitat of Lake Albert are illustrated in Figure 8.2. There were distinct and consistent changes in the various characteristics during the pre- and post-establishment periods of the predator.

The types of prey

Soon after introduction of the Nile perch, haplochromine cichlids constituted the main prey of Nile perch in lakes Victoria, Kyoga and probably Nabugabo (Hamblyn 1966, Gee 1969, Okedi 1971, Ogutu-Ohwayo 1993). Following the rapid increases in Nile perch stocks, haplochromine cichlids were depleted and became unimportant as prey. <u>Caridina</u> <u>nilotica</u> Roux and anisopteran nymphs then became the dominant prey of juveniles while <u>R</u>. <u>argentea</u>, juvenile Nile perch and <u>O</u>. <u>niloticus</u> became the food of larger Nile perch. The only exception was the absence of <u>C</u>.

Figure 8.2. A comparison of changes in prey selection and in life history characteristics of Nile perch in the invaded lakes and that of Lake Albert. Blocks are for lakes: 0 - Albert 1989-92; 1, 2, 3, & 4 - Victoria 1964-67, 1967-77, 1982 & 1988-92; 5 - Nabugabo; 6, 7, 8 & 9 - Kyoga 1967-68, 1978-80, 1988-90 & 1991-93. HP = Importance of haplochromines as prey in fish of >= 20 cm and < 100 cm; PN & PL = Mean number and mean length of prey eaten by fish of >= 100 cm; CF = mean condition factor in fish of >= 20 & < 100 cm; MM = Size at first maturity of males and MF = Size at first maturity of females. SR = Sex ratios of mature fish. Sex ration is given as the number of females per 100 males. Individual lines are drawn to scale.


Pre-establishment
Post-establishment
Changes in prey selection and life history characteristic
HP
PN
PL
CF
MF
MM
SR
0
1
2
3
4
5
6
7
8
9
Block

nilotica in Lake Nabugabo. There were no further changes in the type of prey eaten by Nile perch for 23 years in Lake Kyoga and similar changes in types of prey occurred in lakes Victoria and Kyoga. These prey types are obviously resilient to Nile perch predation. More recently, haplochromines have again started to become important as Nile prey in addition to the above types. Therefore, resilience of prey seems have started overcoming predation pressure due to Nile perch.

With the exception of *R. argentea* which does not occur in Lake Albert, the types of prey currently eaten by Nile perch in the new habitats are similar to those eaten in Lake Albert and other native habitats (Hopson 1972, 1982). In Lake Albert, the role of *R. argentea* is filled by *Alestes* spp.; both are shoaling species and can be regarded as ecologically analogous as far as evading predation by Nile perch is concerned. Similarly, in Lake Chad, prawns and small characids *Alestes dageti* Blache and *Micralestes acutidense* (Peters) and in Lake Turkana prawns and *Engraulicypris stelae* (Hopson 1972, 1982) were the most important prey of the Nile perch. Therefore, the types of prey eaten in the habitats invaded by Nile perch are similar to those eaten by the predator in its native habitats.

Similarities between new and native habitats are also apparent in the sizes and numbers of prey eaten in the new habitats compared with Lake Albert and elsewhere. Soon after introduction of the Nile perch, the average sizes and numbers of prey eaten increased evenly with predator size. After haplochromines had been depleted, the sizes and numbers of prey eaten, especially by large Nile perch, in lakes Victoria, Kyoga and Nabugabo changed to those seen in lakes Albert and Chad (Hopson 1972). It can, therefore be concluded that the types, sizes and numbers of prey eaten in the new habitats have stabilized and are similar to what is eaten in native habitats of the Nile perch. The major question is whether these prey types and sizes can sustain Nile perch stocks in the new habitats.

Length-weight relationships

The nutritional status of a fish can be assessed from the relationships between length and weight (Le Cren 1951, Nikolsky 1963); heavier fish of a given length are said to be in better condition. Before the rapid increases in Nile perch stocks and when haplochromines were still abundant, the condition factor K of Nile perch in the new habitats were significantly higher than those in Lake Albert and other native habitats (Worthington 1929, Kenchington 1939, Hamblyn 1966, Gee 1969, Hopson 1972, 1982, and this study). After haplochromines had been depleted, Nile perch K decreased to levels which were lower than those of lake Albert but not different from those of Lake Chad. The K in Lake Kyoga has not decreased further for 26 years; this suggests that the available types and sizes of prey can sustain K at this level. K values recorded in lakes

Victoria and Nabugabo after depletion of haplochromines are still higher than those of Lake Kyoga. Although K in Lake Kyoga seems to have stabilized, values are lower than in Lake Albert, and several native habitats (Kenchington 1939) and similar only to that of Lake Chad, which has the lowest values for a native habitat. The lower values recorded in Lake Kyoga suggest that Nile perch in this lake may be food limited and similar levels can be expected in lakes Victoria and Nabugabo since the types of prey eaten in the three lakes are similar. Further stress on Nile perch prey e.g. through human over-exploitation, could depress K of Nile perch.

There has as yet been no improvement in K following the recent increases in haplochromine stocks in Lake Kyoga. The nutritional gain that may have accrued from improved food supply appears to have been invested in growth. During this period, Nile perch grew faster in Lake Kyoga, where the haplochromines were recovering than in lakes Victoria and Nabugabo (Chapter 6; Fig. 8.1).

Reproductive fitness

Stearns (1976) and Stearns & Crandall (1989) noted that organisms subjected to an environmental stress such as a reduction in food supply may adjust reproductive traits in a manner that promotes fitness. Most commonly, maturity is delayed to a larger size in order to gain fecundity. Nile perch in the new habitats did adjust size at first maturity when prey changed. When haplochromines were abundant, male and female Nile perch matured at a smaller size (30-45 cm for males and 40-50 cm for females). After haplochromines were depleted, males and females matured at larger sizes, (50-59 cm for males and 80-100 cm for females). The size at first maturity has since remained at this level, suggesting that they have stabilized. These values are similar to those for Lake Albert, where males matured at 50-59 cm total length and females at 80 - 100 cm (Worthington 1929 and this study). Adjustment of the size at first maturity upwards increases overall fitness because fecundity in Nile perch is proportional to the cube of the length.

Conclusion

The diversity of exploited stocks in the lakes invaded by the Nile perch decreased rapidly following establishment of the predator and stopped declining when only resilient species remained. Thereafter some species started recovering. The types and sizes of prey eaten by the Nile perch changed alongside the changes in diversity and converged on those species that were resilient. These types and sizes of prey were similar to those eaten in native habitats of the Nile perch. The K of Nile perch which was initially higher decreased to values similar to those recorded in native habitats. Nile perch adjusted its size at first maturity with changes in the types and sizes of prey to values found in native habitats; this would increase overall fitness because fecundity is proportional to the cube of the length. Since these factors have converged and persisted on values similar to those in native habitats where Nile perch is in balance with its prey, the fisheries of the lakes invaded by Nile perch can remain viable.

Literature cited

Acere, T.O. 1985. Observations on the biology, age and growth and sexuality of Nile perch _Lates niloticus_ (Linne) and the growth of its fishery in the northern waters of Lake Victoria. FAO Fish. Rep. 335:42-61

Anderson, A.M. 1961. Further observations concerning the proposed introduction of Nile perch into Lake Victoria. E. Afr. Agric. J. 26: 195-201.

Asila, A. & J. Ogari 1987. Growth parameters and mortality rates of Nile perch (_Lates niloticus_) estimated from length-frequency data in the Nyanza Gulf (Lake Victoria). FAO Fish. Rep. 389: 272-287.

Bagenal, T.B. 1969. The relationship between food supply and fecundity in brown trout, _Salmo trutta_ L. J. Fish. Biol. 1: 167-182.

Bagenal, T.B. & E. Braum 1978. Eggs and early life history, 165-201. In T.B. Bagenal (ed.) Methods of Assessment of Fish Production in Freshwaters. IBP Handbook No.3. Blackwell Scientific Publications. Oxford London.

Barel, C.D.N., R. Dorit, P.H. Greenwood, G. Fryer, N. Hughes, P.B.N. Jackson, H. Kawanabe, R.H. Lowe-McConnell, F. Witte & K. Yamaoka, 1985. Destruction of fisheries in Africa's lakes. Nature 315: 19-20.

Beadle, L.C. 1962. The evolution of species in Lakes of East Africa. Uganda Journal 26:44-54.

Beadle, L.C. 1981. The inland waters of tropical Africa. An introduction to tropical limnology. 2nd edition. Longman, London. England. 475pp.

Beamish, R.J. & G.G. McFarlane 1987. Current trends in age determination methodology. pp 15-42. In: Summerfelt R.C & G.E. Hall (eds.). Age and Growth in Fish. Iowa State University Press.

Beverton, R.J.H. & S.J. Holt 1957. On the Dynamics of Exploited Fish Populations. Ministry of Agriculture, Fisheries and Food. Fishery Investigation Series II. Vol XIX. Her Majesty's Stationery Office: London 533 pp.

Bolger, T. & P.L. Connolly 1989. The selection of suitable indices for the measurement and analysis of fish condition. J. Fish. Biol. 34:171-182.

Bootsma, H.A. & R.E. Hecky. 1993. Conservation of the African Great Lakes: A Limnological Perspective. Conserv. Biol. 7:644-656.

Brooks, J.L., & Dobson 1965. Predation, body size and the composition of plankton. Science 150: 26-35.

Brown M.E. 1957. Experimental studies on growth. pp 361- 400. In: M.E. Brown (ed.). The Physiology of Fishes. Academic press, New York and London.

Bwathondi, O.P.J. 1987. The state of Lake Victoria fisheries, Tanzanian sector, FAO Fish. Rep. 388:35-39.

Cadwalladr, D.A. 1965. Notes on breeding biology and ecology of Labeo victorianus Boulenger (Pisces:

Cyprinidae) of Lake Victoria. Rev. Zool. Bot. afric. 72:109-134.

Cadwalladr, D.A. & A.J. Stoneman. 1966. A review of the Fisheries of the Ugandan waters of Lake Albert, East Africa, 1928-1965/66, with data mainly from 1953. E. A. Freshwat. Fish. Res. Org. Suppl. Publ. Government Printers, Entebbe, Uganda.

Cambridge Nabugabo Biological Expedition 1962. Preliminary Report (mimeographed), Makerere University, Kampala, 21p.

Carothers, J.H. 1984. Sexual selection and sexual dimorphism in some herbivorous lizards. Am. Nat. 124: 244-254.

Charnov, E.L. 1979. The genetical evolution of patterns of sexuality: Darwinian Fitness. Am. Nat. 113: 465-480.

Charnov, E.L. & J.J. Bull. 1989. Non-fisherian sex ratios with sex change and environmental sex determination. Nature 338: 148-150.

Charnov, E.L., R.L. Los-den Hartogh, W.T. Jones & J. van den Assem. 1981. Sex ratio evolution in a variable environment. Nature 289: 27-33.

Cone, R.S. 1989. The need to reconsider the use of condition indices in fishery science. Trans. Amer. Fish. Soc. 118:510-514.

Connel, J.H., & W.P. Sousa. 1983. On the evidence needed to judge ecological stability or persistance. Am. Nat.

121:789-824.

Coulter, G.W. 1965. The biology of the Nile perch in Lake Tanganyika. J. appl. Ecol. 2:409. FAO, 1985.

Darwin, C.R. 1874. The descent of man, and selection in relation to sex. 2nd ed. Appleton, New York.

Davis, T.L.O. 1982. Maturity and sexuality in barramundi, Lates calcarifer (Bloch), in the nothern territory and south-eastern gulf of Carpentaria. Aust. J. Mar. Freshwater Res. 33: 529-544.

FAO/CIFA. 1985. Introduction of species and conservation of genetic resources. Committee for Inland Fisheries of Africa (CIFA). Sixth Session, Lusaka, Zambia, 7-11 October, 1985. CIFA/85/13. FAO. Rome. 18pp

Fisher, R.A., The genetic theory of natural selection. Dover, New York, 2nd. ed. 158pp

Frank, S.A. 1990. Sex allocation theory for birds and mammals. Annu. Rev. Ecol. Syst. 21:13-55.

Fryer, G. 1960. Concerning the proposed introduction of Nile perch into Lake Victoria. E. Afr. Agric. J. 25: 267-270.

Fryer, G. 1961. Observations on the biology of the cichlid fish Tilapia variabilis Boulenger in the northern waters of Lake Victoria (East Africa) Revue Zool. Bot. afr. 64:1-33.

Fryer, G. 1973. The Lake Victoria fisheries: some facts and fallacies. Biol. Conserv. 5:305-308

Fryer, G., & T.D. Iles. 1972. The cichlid fishes of the

Great Lakes of Africa: their biology and evolution. Oliver and Boyd, London. 641 pp.

Fuiman, L.E., & A.E. Mugurran. 1994. Development of predator defences in fishes. Reviews in Fish Biology and Fisheries, 4: 145-183.

Garrod, D.J. & J.W. Horwood 1989. Reproductive Strategies and Response to Exploitation, 367-384. In G.W. Potts & R.J. Wootton (eds.). Fish Reproduction: Strategies and Tactics. Harcourt Brace Jovanovich, Publishers, Academic Press, London

Gee, J.M. 1964. Nile perch Investigations. Ann. Rep. E. Africa. Freshwat. Res. Org. (1962/63): 14-24.

Gee, J.M. 1969. A comparison of certain of aspects of the biology of Lates niloticus (Linne) in some East African lakes. Rev. Zool. Bot. afr. 80: 244-262.

Gerking, S.D. 1962. Production and food utillization in a population of bluegill sunfish. Ecol. Monogr. 32: 31-78.

Gerking, S.D., & D.V. Plantz, Jr. 1980. Size-biased predation by the Gilla topminnow Poeciliopsis occidentalis (Baird and Girard). Hydrobiologia 72: 179-191.

Godin, J.-G.J. 1986. Antipredator function of shoaling in teleost fishes: a selective review. Naturaliste can. 113: 241-50

Goeltenboth, F. & A. Kristyanto. 1987. Ecological studies on the Rawa Pening Lake (Central Java): some biotic parameters of the semi-natural lake. Trop. Ecol. 28:101-116.

Goodman, D. 1975. The theory of diversity-stability relationships in ecology. Annu. Rev. Biol. 50:237-266

Goudswaard, P. & F. Witte 1985. Observations on Nile perch Lates niloticus (L) in Tanzanian waters of Lake Victoria. FAO. Fish. Rep. No. 335: 62-67.

Gourdswaard, P. & W. Ligtvoet 1987. Recent developments in the fishery for haplochromines (Pisces: Cichlidae) and the Nile perch, Lates niloticus (Pisces: Centropomidae) in Lake Victoria. FAO Fish. Rep. No. 388:101-112.

Graham, M. 1929. The Victoria Nyanza and its Fisheries. A report on the Survey of Lake Victoria 1927-1928 and appendices - Crown Agents for Colonies, London 255 pp.

Greenwood, P.H. 1965. The cichlid fishes of Lake Nabugabo, Uganda. Bull. Brit. Mus. Nat. Hist. (Zool.) 12:313-357

Greenwood, P.H. 1966. The fishes of Uganda. The Uganda Society, Kampala. 131pp.

Greenwood, P.H. 1974. The Haplochromis species (Pisces: Cichlidae) of Lake Rudolf, East Africa. Bull. Brit. Mus. (Nat.l Hist.), Zool. Ser. 27: 141-175.

Griffiths, G.K. 1989. Statistical process control methods for long and short runs. A.S.Q.C. Quality press. Milwankee. Wisconsin.

Hamblyn, E.L. 1966. The food and feeding habits of the

Nile perch, Lates niloticus (Linne) (Pisces: Centropomidae). Rev. Zool. Bot. afr. 74:1-28.

Harley, K.L.S. 1990. The role of biological control in the management of the water hyacinth, Eichhornia crassipes. Biological News and Information 11:11-22.

Hecky, R.E. 1993. Peter Kilham Memorial Lecture. The eutrophication of Lake Victoria. Verh. Int. Verein. Limnol. 25:39-48.

Hecky, R. & F.W.B. Bugenyi 1992. Hydrology and chemistry of the African Great Lakes and water quality issues: Problems and solutions. Mitt. Verein. Int. Limnol. 23:45-54.

Hecky, R.E., Bugenyi, F.W.B., Ochumba, P., Talling, J.F., Mugidde, R., Gophen, M. & Kaufman L. 1984. Deoxygenation of the deep water of Lake Victoria, East Africa. Limnol. Oceonograph., 39:1476-1481.

Holden, M. 1963. Report on the Fisheries of Lake Albert. Uganda Fisheries Department Entebbe. 112 pp.

Holling, C.S. 1973. Resilience and stability of ecological systems. Ann. Rev. Ecol. Syst. 4:1-23.

Holtby, L.B. & M.C. Healey. 1990. Sex-specific life history tactics and risk taking in Coho salmon. Ecology. 71: 678-690.

Hopson, A.J. 1972. A study of the Nile perch (Lates niloticus (L.), Pisces: Centropomidae) in Lake Chad. Overseas Research Publication, Commonwealth Office, Overseas Development Administration, No. 19. 93 pp.

Hopson A.J. 1982. The Biology of *Lates niloticus* in Lake Turkana, pp 1285-1299. In A.J. Hopson (ed.) Lake Turkana. A report on the findings of the Lake Turkana project 1972-1975. Vol 5. Overseas Development Administration London.

Hrbacek, J., M. Dvarokova, V. Korinek, & L. Prochaakova. 1961. Demonstration of the effect of the fish stock on the species composition of zooplankton and the intensity of the metabolism of the whole plankton association. Verh. Int. Limnol. 14: 192-195.

Hughes, N.F. 1983. A study of the Nile perch, an introduced predator, in Kavirondo Gulf of Lake Victoria. A report of the Oxford University Nile perch project 1983. 16pp.

Hughes, N.F. 1986. Changes in the feeding biology of the Nile perch, *Lates niloticus* (L) (Pisces: Centropomidae) in Lake Victoria, East Africa, since its introduction in 1960, and its impact on the native fish community in the Nyanza Gulf. J. Fish. Biol. 29:541-548.

Hughes, N.F. 1992. Growth and reproduction of the Nile perch, *Lates niloticus*, an introduced predator, in the Nyanza Gulf, Lake Victoria, East Africa. Envir. Biol. Fishes. 33:299-305.

Hunt, B.P. & W.F. Carbine. 1951. Food of the young pike *Esox lucius* L. and associated fishes in Peterson's ditches, Houghton Lake, Michigan. Trans. Amer. Fish. Soc. 80:67-83.

Jackson, P.B.N. 1960. On the desirability or otherwise of introducing fishes to waters that are foreign to them. Publ. Cons. Sci. Afr. S. Sahara, 63:157-164.

Jackson, P.B.N 1971. The African Great Lakes Fisheries: past, present and future. Afr.J. Trop. Hydrobio. Fish. 1:35-49.

Jensen, K.W. 1957. Determining age and growth in Tilapia nilotica, T. galilaea, T. zillii and Lates niloticus by means of their scales. K. norske Vidensk. selsk. Forh. 30:150-157.

Kenchington, F.E. 1939. Observations on the Nile perch (Lates niloticus) in Sudan. Proc. Zool. Soc. Lond. (Ser. A) 109:157-168.

Kempinger, J.J. & R.F. Carline. 1977. Dynamics of the walleye (Stizostedion vitreum vitreum) populations in Lake Wisconsin, 1955-72. J.Fish. Res. Board Can. 34:1800-1811.

Kudhongania, A.W. & E.J. Cordone. 1974. Batho-spatial distribution patterns and biomass estimates of the major demersal fishes in Lake Victoria. Afr. J. Trop. Hydrobiol. Fish. 3(1), 15-31.

Lazzaro, X. 1987. A review of planktivorous fishes: Their evolution, feeding behaviors, selectivities, and impacts. Hydrobiologia 146: 97-167.

Le Cren, E.D. 1958. Observation on the growth of perch (Perca fluviatilis L) over twenty-two years with special reference to the effects of temperature and changes in population density. J. Anim. Ecol. 27:287-334.

Ligtvoet, W., & O.C. Mkumbo. 1990. Stock Assessmant of Nile perch in Lake Victoria. FAO Fisheries Report 430:35-74.

Lowe (McConnell), R.M. 1955. The fecundity of Tilapia species. E. Afric. Agric. For. J. 21:45-52.

Lowe-McConnell, R.H. 1988. Broad characteristics of the ichthyofauna. pp 93-110. In: C Leveque, M.N. Bruton & G.W. Sentongo (eds.). Biologie des Poissons d'eau Douce Africains/ Biology and Ecology of African Freshwater Fishes, ORSTOM. Paris.

Lewontin, R.C. 1969. The meaning of stability. Brookhaven Symp. Biol. 22:13-24.

Mwebaza-Ndawula, L. 1994. Changes in relative abundance of zooplankton in northern Lake Victoria, East Africa. Hydrobiologia 272:259-264.

Mugidde, R., 1992. Changes in phytoplankton primary productivity and biomass in Lake Victoria (Uganda). MSc. Thesis, University of Manitoba. 84 pp.

Mugidde, R., 1993. The increase in phytoplankton production and biomass in Lake Victoria (Uganda). Verh. Int. Verein. Limnol. 25: 846-849.

Matuszer J.E., B.J. Shuter & J.M. Casselman. 1990. Changes in Lake Trout Growth and Abundance after Introduction of Cisco into Lake Opeongo, Ontario. Trans. Amer. Fish. Soc. 119:718-729.

May, R.M. 1973. Stability and Complexity in Model Ecosystems. Princeton, New Jersey, Princeton University Press. 229 pp

Moore, R. 1979. Natural sex inversion in the giant perch (Lates calcarifer). Aust. J. Mar. Freshwater. Res. 30:803-813.

Moreau, J., J. Arrignon & R.A. Jubb. 1988. Introduction of foreign fishes in African inland waters, 395-426. In C. Leveque, M.N. Bruton & G.W. Sentongo (eds.). Biology and Ecology of African Inland Freshwater Fishes. Orstom, Paris.

Nikolsky, G.V. 1963. The ecology of fishes. Academic Press, London and New York. 352 pp.

Ochumba, P.B.O. & D.I. Kibara. 1989. Observations on the blue-green algal blooms in the open waters of Lake Victoria, Kenya. Afr. J. Ecol. 27:23-34.

Ogari, J. 1985. Distribution, food and feeding habits of Lates niloticus in the Nyanza Gulf of Lake Victoria (Kenya). FAO Fish. Rep. No 335: 68-80.

Ogari, J. & S. Dadzie 1988. The food of the Nile perch, Lates niloticus (L.), after disappearance of the haplochromine cichlids in the Nyanza Gulf of Lake Victoria (Kenya). J. Fish. Biol. 32:571-577.

Ogari, J. & A. Asila. 1992. Status of fisheries of Lake Victoria Kenya Sector. FAO Fish. Rep. 475: 15-23.

Ogutu-Ohwayo, R. 1985. The effects of predation by the Nile perch, Lates niloticus (Linne) introduced into

Lake Kyoga (Uganda) in relation to the fisheries of Lake Kyoga and Lake Victoria. FAO Fish. Rep. 335, 18-41.

Ogutu-Ohwayo, R. 1990a. The decline of the native fishes of Lakes Victoria and Kyoga (East Africa) and the impact of the introduced species, especially the Nile perch, Lates niloticus and the Nile tilapia, Oreochromis niloticus. Env. Biol. Fish. 27:81-96.

Ogutu-Ohwayo, R. 1990b. Changes in the prey ingested and the variations in Nile perch and other fish stocks in Lake Kyoga and the northern waters of Lake Victoria (Uganda). J. Fish Biol. 37:55-63.

Ogutu-Ohwayo, R. 1990c. The reduction in fish species diversity in Lakes Victoria and Kyoga (East Africa) following human exploitatin and introduction on non-native fishes. J. Fish. Biol. 37(Supp. A):207-208.

Ogutu-Ohwayo, R., 1993. The effects of predation by the Nile perch, Lates niloticus L., on the fishes of Lake Nabugabo, with suggestions for conservation of endangered endemic cichlids. Conserv. Biol. 7: 701-711.

Ogutu-Ohwayo, R. & R.E. Hecky 1991. Fish introductions in Africa and some of their implications. Can. J. Fish. Aquat. Sci. 48(Suppl. 1): 8-12.

Oijen. M.J.P. van, F. Witte & E.L.Witte-Mass, 1981. An introduction to ecological and taxonomic investigations on the haplochromine cichlids from the Mwanza Gulf of

Lake Victoria. Neth. J. Zool. 31:149-174.

Okaronon, J., J. Acere, & D. Ocenodongo. 1985. The current state of the fisheries in the northern portion of Lake Victoria (Uganda). FAO Fish. Rep. (335): 89-98.

Okedi, J.Y. 1970. A study of the fecundity of some mormyrid fishes from Lake Victoria. E. Afric. For. J. 35:436-442.

Okedi, J.Y. 1971. Further observations on the ecology of the Nile perch (Lates niloticus Linne) in Lake Victoria and Lake Kyoga. Ann. Rep. E. Afr. Freshwat. Fish. Res. Org. (1970): 42-55.

Okemwa, E. 1984. Potential fishery of Nile perch, Lates niloticus (L.) (Pisces: Centropomidae) in the Nyanza Gulf of Lake Victoria. Hydrobiologia 108:121-126.

Parker, R.R & P.A. Larkin 1959. A concept of growth in fishes. J. Fish. Res. Bd. Can. 16:721-744.

Pielou, E.C. 1969. An introduction to mathematical ecology. Wiley, Interscience.

Pike, G.H., 1984. Optimal foraging theory: A critical review. Ann. Ecol. Syst. 15:523-75.

Pitcher, T.J. & Parrish, J.K. 1993. Functions of shoaling behavior in teleosts. pp 363-439. In Pitcher, T.J. (ed.). Behavior of Teleost Fishes, 2nd edn. London. Chapman and Hall.

Policansky, D. 1983. Size, age and dermography of metamorphosis and sexual maturation in fishes. Am.

Zool. 23:57-63.

Randall R.G., J.E. Thorpe, R.J. Gibson & D.G. Reddin. 1986. Biological factors affecting age at maturity in Atlantic salmon (Salmo solar), p. 90-96. In D.J. Meerburg Salmonid age at maturity. Can. Spe. Publ. Fish. Aquat. Sci. 89.

Reif, C.B., & D.W. Tappa. 1966. Selective predation: Smelt and cladocerans in Harveys lake. Limnol. Oceanogr. 11: 437-438.

Ricklefs, R.E. 1990. Ecology. W.H. Freeman and Company, New York. 895 pp.

Roff, D. 1981. On being the right size. Am. Nat. 118:405-422.

Scott, D.P. 1962. Effects of food quality on Fecundity of rainbow trout, Salmo gairdneri. J. Fish. Res. Bd. Canada. 19: 715-731.

Shapiro, D.Y. 1989. Sex reversal and sociodemographic processes in coral reef fishes. 103-118. In. G.W. Potts & R.J. Wootton (eds.). Fish reproduction: strategies and tactics.

Shoener, T.W. 1969. Model of optimal size of solitary predators. Am. Nat. 103: 277-313.

Shoener, T.W. 1971. Theory of feeding strategies. Ann. Rev. Ecol. Sys. 2: 369-404

Siddiqui, A.Q. 1977. Lake Naivasha fishery and its management together with a note on the food habits of fishes. Biol. Conserv. 12:217-227.

Siegel, S. 1956. Non parametric statistics for behavioral scientists. McGraw Hill 312 pp.

Skelton, P.H. 1988. The distribution of African Freshwater fishes. In: C Leveque, M.N. Bruton & G.W. Sentongo (ed.). Biologie des Poissons d'eau Douce Africains/ Biology and Ecology of African Freshwater Fishes, ORSTOM. Paris.

Smith, S.H. 1968. Species succession and fishery exploitation in the Great Lakes. J. Fish Res. Bd. Can. 25:667-93.

Stearns, S.C. 1976. Life history tactics: A review of ideas. Q. Rev. Biol. 51:3-47

Stearns, S.C. 1980. A new view of life-history evolution. Oikos 35:266-281

Stearns, S.C. & R.E. Crandall 1989. Plasticity for Age and Size at Sexual Maturity: A Life-history Response to Unavoidable Stress, 13-34. In G.W. Potts & R.J. Wootton (eds.). Fish Reproduction: Strategies and Tactics. Harcourt Brace Jovanovich, Publishers, Academic Press, London

Stoneman J. & J.F. Rogers. 1970. Increase in fish production achieved by stocking exotic species (Lake Kyoga, Uganda). Uganda Fisheries Department, Occassional Paper (3):16-19.

Sutherland J.P. 1974. Multiple stable points in natural communities. Am. Nat. 108:859-873.

Sutherland, J.P. 1981. The fouling community at

Beaufort, North Carolina: a study in stability. Am. Nat. 118:499-519.

Sutherland, J.P. 1990. Perturbations, resistance, and alternative views of the existence of multiple stable points in nature. Am. Nat. 136:270-275

Talling, J.F., 1963. Origin of stratification in the African Rift valley lakes. Limnol. Oceonogr. 8:68-78.

Trewavas, E. 1933. Scientific results of the Cambridge Expedition to East African Lakes, 1930-31, II. The cichlid fishes. J. Lin. Soc. (Zoology) 38:309-341.

Tumwebaze, J.A. & E. Coenen. 1991. Report on the frame survey conducted in the Ugandan part of Lake Victoria (Sept 3rd - Dec 20th 1990). Fisheries Department, Entebbe, Uganda. 13pp

Turner, J.L., 1977a. Some effects of demersal trawling in Lake Malawi (Nyasa) from 1968 to 1974. J. Fish. Biol. 10:261-271.

Turner, J.L. 1977b. Changes in the size structure of cichlid populations of Lake Malawi resulting from bottom trawling. J. Fish Res. Board Can. 34: 232-238.

Twongo, T. 1991. Implications of the water hyacinth infestation for fisheries, with particular reference to Lake Kyoga. pp 19-23. In Thompson, K. (Ed.). The Water Hyacinth in Uganda. FAO F1:TCP/UGA/9153/A.

Wanink, J.H & P.C. Goudswaard 1994. Effects on Nile perch (Lates niloticus) introduction into Lake Victoria, East Africa on the diet of the Pied

Kingfishers (Ceryle rudis). Hydrobiol. 279/280:367-376.

Wandera, S.B. 1992. The effect of Nile perch predation and human exploitation on the population structurte of Rastrineobola argentea in Lake Victoria, Kyoga and Nabugabo. FAO Fish. Rep. 475:48.

Weatherall, J.A. 1972. Catch Assessment Survey (CAS) of Lake Victoria. EAFFRO Occasional paper No. 14.

Weatherly. A.H. 1972. Growth and Ecology of Fish populations. Academic press, London and New York. 293 pp.

Welcomme, R.L. 1966. Recent changes in the stocks of Tilapia in Lake Victoria. Nature 212:52-54.

Welcomme, R.L. 1967. Observations on the biology of the introduced Tilapia in Lake Victoria. Rev. Zool. Bot. afr. 76:249-279.

Welcome, R.L. 1984. International transfer of inland fish species. pp. 22-40. In: W.R. Courtenay, Jr. & J.R. Stauffer, Jr. (eds.). Distribution, Biology and Management of Exotic Fishes. Johns Hopkins University Press, Baltimore. MD.

Werner, E.E. & D.J. Hall. 1974. Optimal foraging and the size selection of prey by the bluegill sunfish (Lepomis macrochirus). Ecology 55: 1042-1052.

Willoughby N.G., I.G. Watson, S. Lauer & I.F. Grant. 1993. An investigation into the effects of water hyacinth on the biodiversity and abundance of fish and invertebrates in Lake Victoria, Uganda. Technical Report. Natural Resources Institute. Overseas Development Administration, U.K. 26p.

Witte, F., & M.J.P. van Oijen. 1990. Taxonomy, ecology and fishery of haplochromine trophic groups. Zool. Verh. Leiden 262: 1-47.

Witte, F., T. Goldschmidt, J. Wanink, M.J.P van Oijen, K. Goudswaard, E. Witte-Maas & M. N. Bouton. 1992a. The destruction of an endemic species flock: quantitative data on the decline of haplochromine cichlids of Lake Victoria. Env. Biol. Fishes 34:1-28.

Witte, F., T. Goldschmidt, P.C. Goudswaard, W. Ligtvoet, M.J.P. van Oijen & J.H. Wanink. 1992b. Species extinction and concomitant ecological changes in Lake Victoria. Neth. J. Zool. 42:214-232.

Wootton, R.J. 1973. The effects of size of food ration on egg production in the three-spined stickleback, Gasterosteus aculeatus L. J. Fish. Biol. 5:89-96.

Wootton, R.J. 1989. Introduction: Tactics and Strategies in Fish Reproduction, 1-12. In G.W. Potts & R.J. Wootton (eds.). Fish Reproduction: Strategies and Tactics. Harcourt Brace Jovanovich, Publishers, Academic Press, London

Worthington, E.B. 1929. A report of the fishing survey of Lakes Albert and Kyoga, March-July 1929. Crown agents for Colonies, London. 136 pp.

Worthington, E.B. 1932. A report on the fisheries of

Uganda investigated by the Cambridge Expedition to the East African Lakes, 1931-1932. Crown Agents for colonies, London. England.

Zaret, T.M., & R.T. Paine 1973. Species introduction in a tropical lake. Science. 182:449-455.

Appendices

Appendix 3.1. Shannon-Weaver indices of diversity H' for Lake Albert and the Kenyan, Ugandan and Tanzanian regions of Lake Victoria between 1970 and 1990.

Year	Lake Albert	Lake Victoria		
		Kenya	Uganda	Tanzania
1970		1.99	1.46	1.99
1971	1.33	1.90	1.62	1.65
1972	1.60	2.12	1.75	1.72
1973	1.43	2.10	1.79	1.77
1974	1.72	1.87	1.73	1.69
1975	1.62	1.91	1.42	2.03
1976	1.57	1.79	1.67	1.82
1977	1.51	1.79	1.87	1.67
1978	1.51	1.87	1.87	2.07
1979	1.55	2.05	1.72	2.05
1980	1.54	2.00	1.53	2.03
1981	1.78	1.35	1.63	2.19
1982	1.81	1.64	1.42	2.15
1983	1.91	1.05	0.66	2.03
1984	1.94	1.17	0.96	2.03
1985	1.94	1.13	0.79	2.14
1986	1.77	1.06	0.84	1.68
1987	1.86	0.96	0.70	1.55
1988	1.80	1.09	0.50	
1989	1.78	1.43	0.80	
1990		1.19		

Appendix 4.1. The frequency of occurrence of various items in stomachs of different size groups of *L. niloticus* in Lake Victoria during the 1968-77 period.

Total length (cm)	<20:	>=20 <60:	>=60 <100:	>=100:
Tilapiines		7	1	5
Haplochromines		270	87	42
R. argentea		1	1	
Mormyrids		2		
P. aethiopicus			1	
Clarias spp		7	5	6
Synodontis spp				1
Molluscs		3		
Vegetation		1		
Gravel & stones		1		
Number examined		292	95	54

Appendix 4.2. The frequency of occurrence of various items in stomachs of different size groups of *L. niloticus* in Lake Victoria during the 1988-92 period.

Total length (cm)	<20:	>=20 <60:	>=60 <100:	>=100:
Tilapiines	2	78	15	20
L. niloticus	55	600	328	19
Haplochromines	8	145	28	5
R. argentea	155	975	166	2
Mormyrids				3
P. aethiopicus		2		
Clarias spp		19	1	
Synodontis spp		1		2
Mastacembelus spp		1	1	
Anisopteran nymphs	246	507	14	1
Caridina nilotica	723	1007	30	1
Chironomids	87	36	2	
Chaoborids	3	2		
Ephemeroptera	8	10		
Notonectids	1			
Molluscs	8	58	8	
Crubs	3	2	2	6
Cestodes	3	40	7	
Vegetation		1	1	
Gravel & stones	4	5	1	
Number examined	1306	3487	603	59

Appendix 4.3. The frequency of occurrence of various items in stomachs of different size groups of L. niloticus in Lake Kyoga during the 1978-80 period.

Total length (cm)	<20:	>=20 <60:	>=60 <100:	>=100:
Tilapiines	12	64	30	42
L. niloticus	8	62	36	7
Haplochromines	4	37	21	
R. argentea	75	331	67	
Mormyrids		1		1
P. aethiopicus	1	1	1	3
Anisopteran nymphs	55	180	12	
Caridina nilotica	92	66	1	
Chironomids	39	9		
Molluscs		14	1	
Vegetation		2		
Gravel & stones	4	1		
Number examined	290	777	169	53

Appendix 4.4. The frequency of occurrence of various items in stomachs of different size groups of L. niloticus in Lake Kyoga during the 1991-93 period.

Total length (cm)	<20:	>=20 <60:	>=60 <100:	>=100:
Tilapiines	68	55	22	17
L. niloticus	6	60	64	15
Haplochromines	250	957	286	9
R. argentea	130	251	20	
Mastacembelus spp		2	4	
Anisopteran nymphs	47	210	2	
Caridina nilotica	59	24		
Chironomids	126	38		
Molluscs	3	6		
Number examined	689	1603	398	41

Appendix 4.5. The frequency of occurrence of various items in stomachs of different size groups of *L. niloticus* in Lake Nabugabo during the 1991-93 period.

Total length (cm)	<20:	>=20 <60:	>=60 <100:	>=100:
Tilapiines	21	41	13	2
L. niloticus	12	38	4	
Haplochromines	8	35	1	
R. argentea	71	207	13	
Mormyrids				1
P. aethiopicus			1	1
Clarias spp		2		
Synodontis spp	1		1	
Mastacembelus spp		2		
B. jacksoni		1		
S. intermedius			1	
Anisopteran nymphs	61	70		1
Chironomids	34	4		
Chaoborids	11	1		
Ephemeroptera	119	38		
Notonectids	1	7		
Corixids	5			
Vegetation		1		
Number examined	344	443	34	5

Appendix 4.6. The frequency of occurrence of various items in stomachs of different size groups of *L. niloticus* in Lake Albert during the 1989-92.

Total length (cm)	<20:	>=20 <60:	>=60 <100:	>=100:
Tilapiines		2	3	3
L. niloticus	1	7	3	4
Haplochromines	19	157	10	
Alestes spp		189	105	6
Hydrocynus spp			8	
Mormyrids				2
Bagrus spp			1	1
Auchenoglanis spp			1	1
Polypterus spp				4
Anisopteran nymphs	3	16	1	
Caridina nilotica	25	5		
Molluscs		11	1	
Vegetation		1		
Number examined	48	388	133	21

Appendix 4.7. The average length of prey ingested by Nile perch of different size groups in Lakes Albert, Victoria, Nabugabo and Kyoga during different periods.

Block, Lake & Period		Length Class (Total length cm)			
		<20	>=20 <60	>=60 < 100	>=100
0: Albert 89-92:	Mean	2.28	5.6	7.34	17.41
	2 SE	0.44	0.16	0.56	5.18
	N	37	315	95	13
1: Victoria 64-67:		-	-	-	-
2: Victoria 68-77:	Mean		4.88	6.22	8.46
	2 SE		0.24	0.50	1.26
	N		114	58	33
3: Victoria 1982:		-	-	-	-
4: Victoria 88-92:	Mean	1.46	3.72	6.82	16.67
	2 SE	0.10	0.20	1.26	3.00
	N	217	903	273	33
5: Nabugabo 91-93:	Mean	2.77	4.57	7.27	25.7
	2 SE	0.32	0.34	0.44	17.4
	N	96	183	22	2
6: Kyoga 67-68:		-	-	-	-
7: Kyoga 78-80:	Mean	1.60	3.00	6.93	24.51
	2 SE	0.16	0.30	1.20	0.84
	N	118	248	67	22
8: Kyoga 88-90:	Mean	1.86	2.90	5.53	
	2 SE	0.10	0.08	1.32	
	N	248	1172	49	
9: Kyoga 91-93:	Mean	2.21	3.41	4.66	9.18
	2 SE	0.14	0.10	0.24	2.78
	N	191	794	259	19

Appendix 4.8. The average number of prey ingested by Nile perch of different size groups in Lakes Albert, Victoria, Nabugabo and Kyoga during different periods.

Block, Lake & Period		Length Class (Total length cm)			
		<20	>=20 <60	>=60 & 100:	>=100
0: Albert 89-92:	Mean	3.44	3.63	15.63	
	2 SE	1.08	0.32	2.24	7.44
	N	36	332	98	16
1: Victoria 64-67:		-	-	-	-
2: Victoria 68-77:	Mean		2.42	6.76	9.82
	2 SE		0.22	1.88	3.14
	N		257	72	44
3: Victoria 1982:		-	-	-	-
4: Victoria 88-92:	Mean	14.48	64.57	32.05	3.51
	2 SE	2.54	8.24	17.6	0.97
	N	229	967	297	37
5: Nabugabo 91-93:	Mean	2.24	3.76	6.79	5.5
	2 SE	0.70	1.30	1.96	6.26
	N	103	208	24	2
6: Kyoga 67-68:		-	-	-	-
7: Kyoga 78-80:	Mean	10.24	12.38	14.77	1.37
	2 SE	3.02	3.60	5.48	0.15
	N	162	376	92	35
8: Kyoga 88-90:	Mean	2.47	8.52	7.17	
	2 SE	0.56	0.60	2.14	
	N	293	982	53	
9: Kyoga 91-93:	Mean	3.47	5.48	21.72	6.32
	2 SE	0.40	0.40	2.90	4.02
	N	481	1177	315	38

Appendix 6.1. The growth rate of Nile perch of 20 cm to 40 cm total length during the first year of life in lakes Victoria, Nabugabo and Kyoga during different periods. Data obtained by tagging fish.

Parameter	Lake and period:		
	Victoria 1991-92	Nabugabo 1992-93	Kyoga 1991-92
Mean	18.94	18.97	28.4
2 SE	2.8	1.42	1.90
Number	20	43	80

Appendix 7.1. The percentage of mature L. niloticus in different length classes of fish in Lake Victoria between 1964 and 1967. Males of >=20 cm and <100 cm were grouped in 5 cm classes and females in 10 cm classes. All fish of >=100 cm were grouped in 20 cm length classes (immat. = immature and mat. = mature).

Length class (cm)	Males			Females		
	No. immat.	No. mat.	% mat.	No. immat.	No. mat.	% mat.
20 - 24	37	3	7.5			
25 - 29	212	105	33.1	250	76	23.3
30 - 34	532	599	53.0			
35 - 39	178	367	67.3	871	583	40.1
40 - 44	28	240	89.6			
45 - 49	6	111	94.9	160	119	42.6
50 - 54	1	13	92.7			
55 - 59	1	14	93.3	4	2	
60 - 64		7				
65 - 69	2	9		9	6	
70 - 74	2	3				
75 - 79		2		1	7	
80 - 84		5				
85 - 89				2	3	
90 - 94		3				
95 - 99		1			5	
100 - 119		1		1	11	
120 - 139						
140 - 159						
>= 160						

Appendix 7.2. The percentage of mature L. niloticus in different length classes of fish in Lake Victoria between 1968 and 1977. Males of >=20 cm and <100 cm were grouped in 5 cm classes and females in 10 cm classes. All fish of >=100 cm were grouped in 20 cm length classes (immat. = immature and mat. = mature).

Length class (cm)	Males No. immat.	Males No. mat.	Males % mat.	Females No. immat.	Females No. mat.	Females % mat.
20 - 24						
25 - 29	3	4	25	4		
30 - 34	32	39	18.0			
35 - 39	28	44	36.4	116	7	5.7
40 - 44	4	14	71.4			
45 - 49		4		24	4	14.3
50 - 54		4				
55 - 59		28		9	18	66.7
60 - 64		36				
65 - 69		13		2	7	
70 - 74		4				
75 - 79		8			5	
80 - 84		4				
85 - 89		2			4	
90 - 94		3				
95 - 99		3			10	
100 - 119		16		1	16	
120 - 139		5		1	10	
140 - 159				1	14	
>= 160					2	

Appendix 7.3. The percentage of mature L. niloticus in different length classes of fish in Lake Victoria in 1982. Males of >=20 cm and <100 cm were grouped in 5 cm classes and females in 10 cm classes. All fish of >=100 cm were grouped in 20 cm length classes (immat. = immature and mat. = mature).

Length	Males			Females		
class (cm)	No. immat.	No. mat.	% mat.	No. immat.	No. mat.	% mat.
20 - 24						
25 - 29						
30 - 34						
35 - 39						
40 - 44	5					
45 - 49	11	11	50	4	1	
50 - 54	16	41	71.9			
55 - 59	18	53	74.7	21	3	12.5
60 - 64	16	69	81.2			
65 - 69	6	58	90.3	42	5	10.6
70 - 74		58	100			
75 - 79	1	20	95.2	81	27	25
80 - 84		7				
85 - 89		4		55	26	32.1
90 - 94						
95 - 99		1		5	10	66.7
100 - 119				1	1	
120 - 139		2				
140 - 159					2	
>= 160					1	

Appendix 7.4. The percentage of mature L. niloticus in different length classes of fish in Lake Nabugabo between 1991 and 1993. Males of >=20 cm and <100 cm were grouped in 5 cm classes and females in 10 cm classes. All fish of >=100 cm were grouped in 20 cm length classes (immat. = immature and mat. = mature).

Length class (cm)	Males			Females		
	No. immat.	No. mat.	% mat.	No. immat.	No. mat.	% mat.
20 - 24	37	1	2.6			
25 - 29	45	2	4.3	19		
30 - 34	44	2	4.3			
35 - 39	41	3	6.8	35		
40 - 44	38	5	12.2			
45 - 49	21	8	27.6	16		
50 - 54	8	10	55.6			
55 - 59	11	14	56	2		
60 - 64	3	5	62.5			
65 - 69	2	10	83.3	1		
70 - 74		8				
75 - 79		6		8	4	
80 - 84		2				
85 - 89				3	4	
90 - 94						
95 - 99		2		1	3	
100 - 119				5	3	
120 - 139						
140 - 159						
>= 160						

Appendix 7.5. The percentage of mature L. *niloticus* in different length classes of fish in Lake Victoria between 1988 and 1992. Males of >=20 cm and <100 cm were grouped in 5 cm classes and females in 10 cm classes. All fish of >=100 cm were grouped in 20 cm length classes (immmat. = immature and mat. = mature).

Length	Males			Females		
class (cm)	No. immat.	No. mat.	% mat.	No. immat.	No. mat.	% mat.
20 - 24	203					
25 - 29	253			180		
30 - 34	240	2	0.8			
35 - 39	296	6	2.0	151	2	1.3
40 - 44	244	10	3.9			
45 - 49	168	32	16	91	1	1.1
50 - 54	135	75	35.7			
55 - 59	96	65	40.4	56		
60 - 64	58	287	83.2			
65 - 69	16	192	94.8	46	5	9.8
70 - 74	3	182	98.4			
75 - 79	1	105	99.1	25	7	21.9
80 - 84		95	100			
85 - 89		60	100	9	4	30.7
90 - 94	1	37	97.4			
95 - 99		31	100	5	8	61.5
100 - 119		53	100	23	26	53.1
120 - 139		4		23	15	39.5
140 - 159					17	100
>= 160					1	

Appendix 7.6. The percentage of mature L. niloticus in different length classes of fish in Lake Kyoga between 1967 and 1968. Males of >=20 cm and <100 cm were grouped in 5 cm classes and females in 10 cm classes. All fish of >=100 cm were grouped in 20 cm length classes (immat. = immature and mat. = mature).

Length class (cm)	Males			Females		
	No. immat.	No. mat.	% mat.	No. immat.	No. mat.	% mat.
20 - 24	1	1				
25 - 29	6			3		
30 - 34	9					
35 - 39	11			14		
40 - 44	16	1				
45 - 49	12			41		
50 - 54	10	1				
55 - 59	10	5		13		
60 - 64	7	4				
65 - 69	3	4		22	1	
70 - 74	5	7				
75 - 79	2	6		9	3	
80 - 84	2	2				
85 - 89	1	3		1	2	
90 - 94						
95 - 99						
100 - 119				3	2	
120 - 139				1	1	
140 - 159				1		
>= 160						

Appendix 7.7 The percentage of mature *L. niloticus* in different length classes of fish in Lake Kyoga between 1978 and 1980. Males of >=20 cm and <100 cm were grouped in 5 cm classes and females in 10 cm classes. All fish of >=100 cm were grouped in 20 cm length classes (immat. = immature and mat. = mature).

Length class (cm)	Males			Females		
	No. immat.	No. mat.	% mat.	No. immat.	No. mat.	% mat.
20 - 24	87					
25 - 29	84			114	1	0.9
30 - 34	107	3	2.7			
35 - 39	108	9	7.7	137	1	0.7
40 - 44	108	54	33.3			
45 - 49	56	52	48.2	108	1	0.9
50 - 54	19	28	59.6			
55 - 59	4	18	81.2	26	5	16.1
60 - 64	12	26	68.4			
65 - 69	4	31	88.6	6	8	57.1
70 - 74		28	100			
75 - 79	1	33	97.1	7	4	36.6
80 - 84	1	57	98.3			
85 - 89	1	58	98.3	3	5	62.5
90 - 94	1	43	97.7			
95 - 99	1	20	95.2	7	2	32.5
100 - 119		39	100	17	13	
120 - 139		32	100	4	33	89.2
140 - 159		7	100	2	39	95.1
>= 160				1	31	96.9

Appendix 7.8. The percentage of mature L. niloticus in different length classes of fish in Lake Kyoga between 1988 and 1990. Males of >=20 cm and <100 cm were grouped in 5 cm classes and females in 10 cm classes. All fish of >=100 cm were grouped in 20 cm length classes (immat. = immature and mat. = mature).

Length class (cm)	Males			Females		
	No. immat.	No. mat.	% mat.	No. immat.	No. mat.	% mat.
20 - 24	143					
25 - 29	217	1	0.5	219		
30 - 34	268	9	3.3			
35 - 39	260	34	11.6	392	4	
40 - 44	124	40	24.4			
45 - 49	47	30	39.0	155	3	
50 - 54	6	9	60			
55 - 59	4	12	75	22	1	
60 - 64	1	17	94.4			
65 - 69		22	100	6	4	
70 - 74		19	100			
75 - 79		19	100	4	4	
80 - 84		11	100			
85 - 89		2		1	2	
90 - 94		3				
95 - 99		1				
100 - 119						
120 - 139						
140 - 159						
>= 160						

Appendix 7.9. The percentage of mature L. niloticus in different length classes of fish in Lake Kyoga between 1991 and 1993. Males of >=20 cm and <100 cm were grouped in 5 cm classes and females in 10 cm classes. All fish of >=100 cm were grouped in 20 cm length classes (immat. = immature and mat. = mature).

Length	Males			Females		
class (cm)	No. immat.	No. mat.	% mat.	No. immat.	No. mat.	% mat.
20 - 24	201					
25 - 29	188	1	0.5	289	1	0.3
30 - 34	160					
35 - 39	169	1	.06	187	1	0.5
40 - 44	120	3	2.4			
45 - 49	164	10	5.8	106	3	2.8
50 - 54	28	13	31.7			
55 - 59	23	35	60.3	35	1	2.7
60 - 64	6	24	80			
65 - 69	11	49	81.7	21		
70 - 74	3	60	95.2			
75 - 79	2	85	97.7	39	2	4.8
80 - 84		58	100			
85 - 89		43	100	31	11	26.2
90 - 94		35	100			
95 - 99		13	100	15	17	53.1
100 - 119		42	100	3	25	89.3
120 - 139		2			10	100
140 - 159		1			14	100
>= 160					10	100

Appendix 7.10. The percentage of mature L. niloticus in different length classes of fish in Lake Albert between 1989 and 1992. Males of >=20 cm and <100 cm were grouped in 5 cm classes and females in 10 cm classes. All fish of >=100 cm were grouped in 20 cm length classes (immat. = immature and mat. = mature).

Length	Males			Females		
class (cm)	No. immat.	No. mat.	% mat.	No. immat.	No. mat.	% mat.
20 - 24	11	1	8.3			
25 - 29	29	5	14.7	33		
30 - 34	48	3	5.9			
35 - 39	27	7	20.6	89		
40 - 44	23	10	30.3			
45 - 49	10	8	44.4	79	1	1.3
50 - 54	6	3	33.3			
55 - 59	4	15	78.9	68	2	2.9
60 - 64	6	15	71.4			
65 - 69	1	15	93.8	6	3	33.3
70 - 74	1	26	96.3			
75 - 79	1	23	95.8	16	8	33.3
80 - 84		8	100			
85 - 89		15	100	10	12	54.5
90 - 94		15	100			
95 - 99		6	100	6	17	73.9
100 - 119		8	100	8	14	63.3
120 - 139				1	9	90
140 - 159					8	100
>= 160					1	

Appendix 7.11. The size ranges within which 50% of male and female L. niloticus matured in Lakes Albert, Victoria, Nabugabo and Kyoga during different periods.

Block, Lake & Period:		Size range at 50% maturity (cm)	
		Males	Females
0:	Albert 1989 - 92	55 - 59	80 - 89
1:	Victoria 1964-67	30 - 34	40 - 49
2:	Victoria 1968-77	40 - 44	50 - 59
3:	Victoria 1982	45 - 49	90 - 99
4:	Victoria 1988-92	60 - 64	90 - 99
5:	Nabugabo 1991-93	50 - 54	-
6.	Kyoga 1967-68	-	-
7:	Kyoga 1978-80	50 - 54	80 - 89
8:	Kyoga 1988-90	50 - 54	-
9:	Kyoga 1991-93	55 - 59	90 - 99

Appendix 8.1. Changes in fish species diversity (H') and in the contribution of Nile perch (NP) and that of haplochromines cichlids (HP) to commercial catches in the Kenyan region of Lake Victoria.

Year	H'-Albert	H'-Victoria	HP	NP
1970		1.99	5357	28
1971	1.33	1.90	4762	46
1972	1.60	2.12	4644	38
1973	1.43	2.10	5569	146
1974	1.72	1.87	6013	89
1975	1.62	1.91	4620	51
1976	1.57	1.79	6368	94
1977	1.51	1.79	6225	203
1978	1.51	1.87	6621	1066
1979	1.55	2.05	6599	4286
1980	1.54	2.00	3636	4310
1981	1.78	1.35	916	22834
1982	1.81	1.64	764	37605
1983	1.91	1.05	612	52377
1984	1.94	1.17	41	41319
1985	1.94	1.13	6	500029
1986	1.77	1.06	3	56975
1987	1.86	0.96	183	68545
1988	1.80	1.09	1338	61210
1989	1.78	1.43	4751	56810
1990		1.19	1	71514

Appendix 8.2. Changes in prey selection and in life history parameters of the Nile perch in lakes Albert, Victoria, Nabugabo and Kyoga during different periods. (HP = Importance of haplochromines as prey in fish of >=20 cm and >100 cm; NP & LP = Mean number and mean length of prey ingested by fish of >=100 cm; CF = mean condition factor in fish of >=20 & <100 cm; GR = Annual growth rate for fish of 20 to 40 cm, MM = Size at first maturity of males and MF = Size at first maturity of females. Size at first maturity in this case was taken as the mid-value of the length class within which the size at first maturity occurred. SR = Sex ratios of mature fish. Sex ration is given as the number of females per 100 males.

Block, Lake & Period:	HP	NP	LP	CF	MM	MF	SR
0: Albert 1989-92	32.0	8.1	17.4	1.26	57	85	41
1: Victoria 1964-67				1.43	32	45	55
2: Victoria 1968-77	92.2	9.8	8.5	1.46	42	55	59
3: Victoria 1982				1.43	47	95	23
4: Victoria 1988-92	4.2	3.5	16.7	1.24	62	95	23
5. Nabugabo 1991-93	7.5			1.19	52		18
6. Kyoga 1967-68	3.0			1.06			26
7. Kyoga 1978-80	6.1	1.4	24.5	1.17	52	85	29
8. Kyoga 1988-90	2.4			1.20	52		6
9. Kyoga 1991-93	62.1	6.3	9.2	1.18	57	95	23