The biology and impacts of Oreochromis niloticus and Limnothrissa miodon introduced in Lake Kariba

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Introduction

Portia C. Chifamba
World-wide introduction of exotic fish species in waterbodies has had both beneficial and adverse ecological, social and economic outcomes of varying magnitude (Reynolds & Greboval 1988; Welcomme 1988, Balirwa 1992; Witte et al. 1995). Thus, information on impacts of introduced species and how well they have adapted to their new conditions, is essential when considering management options both to protect indigenous species and to enhance fisheries. In addition, information on the ecological impacts can enhance our understanding of ecological processes caused by introductions.

Differences in the modes of introduction might have some bearing on the type of impacts arising from the introduction. Fish introductions are either deliberate or planned, in order to fill a vacant niche or accidental, as a result of escapees invading an already occupied niche (De Silva & Sirisena 1987; Welcomme 1988; Balirwa 1992; van Zwieten et al. 2011). The deliberate introduction of a large predator, Nile perch (*Lates niloticus*), has well established negative ecological impacts, having caused the extinction of many haplochromine species from Lake Victoria. At the same time, Nile perch brings about large economic benefits from harvesting (Reynolds & Greboval 1988; Witte et al. 1995; Twongo 1995). Nile tilapia, *Oreochromis niloticus* (Linnaeus 1758), was also deliberately introduced into Lake Victoria. *Oreochromis niloticus* is today one of the three commercially important species caught in the lake but has caused the disappearance of some native tilapias (Goudswaard et al. 2002; Njiru et al. 2005). The introduction of *O. mossambicus* increased fish catches in reservoirs in Sri Lanka (De Silva & Sirisena 1987), just as the deliberate introduction of *Limnothrissa miodon* in Lake Kivu (de Iongh et al. 1995).

Lake Kariba provides a typical case study both for planned introductions of fish into supposedly open ecological niches as well as accidental, unplanned introductions into occupied niches. This was possible as the creation of Lake Kariba, a reservoir in the Zambezi River, created a completely new lacustrine ecosystem whose physical attributes such as oxygen concentration, water depth and distance from the lake margin differed profoundly from the lotic system to which the native riverine species were adapted (Jackson et al. 1988). This new, complex matrix not only presented economic opportunities for fisheries development and fish farming but also raised ecological challenges.

First, the newly created and therefore vacant pelagic niche was filled by a freshwater sardine, *Limnothrissa miodon* (Boulenger 1906). *Limnothrissa miodon* is native to Lake Tanganyika and was introduced to improve fish production (Bell-Cross & Bell-Cross 1971). Physical and environmental conditions in Lake Kariba were unlike those in Lake Tanganyika, and therefore changes in *L. miodon*’s biological characteristics were anticipated. For example, *L. miodon* in Lake Kariba was considered stunted (Marshall 1987a) until studies on growth rate using otoliths showed that the fish in Lake Kariba follows the same growth trajectory as in the
native Lake Tanganyika (Chifamba 1992). However, patterns appear to suggest that *L. miodon* may have inhibited the expansion of a small fish (*Brycinus lateralis*) native to the Upper Zambezi and affected the habits of the predatory tigerfish *Hydrocynus vittatus* (Woodward 1974). Since its introduction, the *L. miodon* population has been subjected to considerable fishing pressure which may have induced evolution of its life history parameters. Therefore, further research on *L. miodon* is essential to determine its adaptation to its new environment, its interaction with native fish species and factors affecting the biology of this fish.

Secondly, ponds on the Lake Kariba shore provided opportunities for the farming of *O. niloticus* which resulted in escapees entering the lake and invading the niche already occupied by the congeneric native *O. mortimeri* (Chifamba 1998, 2006). This negative interaction of the exotic and native species thus presented an opportunity to study factors that confer competitive advantage to the invader by comparing growth, diet and aggression in these two species. Research on the biology of *O. niloticus* and *L. miodon* in Lake Kariba would determine adaptations of these introduced species to their new environment.

Both introduced fish species are important in the Lake Kariba fisheries, *L. miodon* as the main catch of the pelagic fishery and *O. niloticus* as one of the important species in the artisanal fishery. Hence, the objective of introducing *L. miodon* into Lake Kariba to improve fish production was realised. However, catches have declined since the beginning of the fishery, resulting in economic losses and a need to improve the management of the fishery. Informed management of the fish resource is needed to ensure sustainable fisheries. Such knowledge is currently needed for explaining changes in the productivity of the sardine industry that is thought to have crashed as a result of overexploitation or environmental changes.

The aim of this thesis is to establish the degree of suitability of the ecosystem created by the Lake Kariba dam to the introduced species *Oreochromis niloticus* and *Limnothrissa miodon*, to identify factors that may have caused *O. niloticus* to displace the native species *Oreochromis mortimeri*, and to investigate potential factors causing the decline of the *L. miodon* fishery.

**The environment**

*Lake Kariba physical characteristics*

Lake Kariba was formed on the middle Zambezi River at 485 m altitude in 1958 and was then the world’s largest reservoir (5820 km² at maximum storage) (Coche 1974). The reservoir became full in 1963 and the weight of water was so large that it increased
the seismic activity in the area. In 1963 alone, five tremors above 5.0 on the Richter scale were experienced (Tumbare & Sakala 2000). Lake Kariba has a length of 277 km, width of 32 km at its widest point, mean depth of 29 m, and a maximum depth of 120 m. The Zambezi River contributes most (77%) to the water volume in the lake, whilst other rivers contribute 16% and rainfall 7% (Balon & Coche 1974). The dam was constructed primarily for hydro-electricity generation. Hence, the bulk of the water is lost through hydro-electricity turbines and 14% by evaporation. Retention time of the water is about 3 - 4 years and the lake level experiences an annual change of 1 - 5 m, resulting from inflowing floods and drawdowns through turbines and spillage through the sluice gates (Karenge & Kolding 1995).

The lake is separated into five basins, marked by chains of islands and narrows (Figure 1.1). The uppermost two lake basins, Mlibizi and Binga, are riverine due to the influence of the Zambezi River. They are flushed out in May by the Zambezi River floods and thereby assume turnover characteristics earlier than the other three basins, which are truly lacustrine and have temperature-induced turnover. This river-lake environment gradient has a profound effect on the fish species composition (Begg 1974).
Rainfall and temperature
The Kariba area has one rainy season, with most rain falling in December and January. Annual rainfall is between 400 and 800 mm depending on location (Begg 1970). The amount of rainfall affects lake level and drawdown. Lake Kariba is monomictic and has a thermal stratification from September to early June. Mixing or turnover usually takes place in July each year. Stratification begins around September, with a thermocline at around 15 m depth, which gradually moves down to around 35 m at the time of turnover. Stratification prevents deep water in the hypolimnion from mixing with the epilimnion (Begg 1970).

Lake Kariba is a warm lake with a surface water temperature of 28 to 30 °C and a hypolimnion of about 22 °C when stratified. When mixed, the whole water column is 22 °C (Marshall 2012a). The mean maximum air temperature in Kariba has steadily risen from about 33.1 °C in 1968, to 35.5 °C in 1998 (Magadza 2010). As a result of the temperature increase, the depth of the thermocline decreased from 10 to 15 m in 1986 – 1987, to a consistent 5-m depth in 2007 – 2008 (Ndebele-Murisa et al. 2014).

A shallow thermocline likely means a reduction in the optimal habitat for phytoplankton and fish. Cochrane (1978) found a correlation between the catches of *L. miodon* and water volume above the thermocline, therefore the recent change of thermocline depth may have affected *L. miodon* abundance and catches negatively. Temperature and hydrological factors (rainfall, riverflow and lake level) are correlated with *L. miodon* catches through nutrients brought in by the rivers and the effect of temperature on phytoplankton and zooplankton on production (Chifamba 2000).

Phyto- and zooplankton productivity
During the stratification period, the hypolimnion becomes depleted of oxygen and the epilimnion of nutrients due to photosynthesis. Turnover increases the availability of nutrients in the epilimnion and the euphotic zone, increasing phytoplankton production (Ramberg, 1987; Masundire, 1989). Hence, turnover, rainfall and river mouths are associated with increased plankton production (Magadza, 1980; Ramberg, 1987; Masundire, 1992, 1994; Cronberg, 1997). Temperature therefore mediates nutrient cycling in the lake and is an important driver of productivity in the lake. Temperature also drives seasonal and annual variation in phytoplankton and zooplankton communities. Cyanobacteria (blue-green algae) dominated from December to May and diatoms from June to September, whilst 60% of the annual biomass consisted of cyanobacteria in 1982 – 1983 (Ramberg 1987). Chlorophyceae dominated during periods of relatively low temperature compared to Cyanophyceae.

Comparable results were found in a laboratory study by Sibanda (2003). The growth rates (% increase in number of cells per day) of Chlorophyceae in the laboratory declined at water temperatures above 25 °C, becoming negative above 28 °C. At the same time, the growth rate of Cyanophyceae increased almost exponentially up to 34 °C, resulting in a transition temperature from Chlorophyceae to Cyanophy-
ceae domination of about 28 °C (Magadza 2011). In Lake Kariba, that has warmed by a mean of 1.54 °C between 1965 and 1990, the mean epilimnion summer temperature reached this transition limit in 1987 (Magadza 2011).

The rise in water temperature in the lake has indeed caused a change in the phytoplankton towards a community dominated by cyanobacteria (Magadza 2011). Due to toxicity and morphology, cyanobacteria are poor food for zooplankton relative to small chlorophytes and flagellates (Wilson et al. 2006). This is reflected in the shift in the zooplankton from large- (Calanoida; Daphnidae) to small-bodied (Bosmina; Cyclopoidea) species, and a strong reduction in abundance, that accompanied the transition to cyanobacteria in the lake. Being a zooplankton feeder, *L. miodon* was expected to be negatively affected by these changes. Though a causal relation could not be established, it is remarkable that a decline in the catches of *L. miodon* started shortly after the mean epilimnion summer temperature exceeded 28 °C (Magadza 2011). This thesis evaluates changes in individual growth rate of *L. miodon* as a possible mechanism by which temperature can affect *L. miodon* production.

The shift in the phytoplankton composition is also of interest in relation to competition in the inshore planktivorous fish, the endemic *Oreochromis mortimeri* and introduced *O. niloticus*. The question is whether such a shift in the plankton community would then favour *O. niloticus*, which is known to feed and digest cyanobacteria (Moriarty 1973). Thus, to understand the recent changes in the fish populations in Lake Kariba, it is important to study the diet composition of both introduced (e.g. *O. niloticus*) and native species (e.g. the potentially competing indigenous planktivorous species, *O. mortimeri*).

**The Fish**

*Fish species composition changes*

At the future Kariba Dam site in the Zambezi River, which Jackson (1960) described as a sandbank river with little vegetation, *Hydrocynus vittatus*, *Distichodus* sp., *Barbus* sp. and *Labeo* sp. were dominant, while cichlids such as *O. mortimeri* and some small fish species were rare. The fishes were subjected to a seasonal period of flooding, when food and shelter were plenty, and a dry season when flow was low and remaining pools in the river small, thus providing little food and shelter (Jackson 1960). It could be anticipated that the transformation from a riverine to a lacustrine ecosystem would create new conditions that would alter fish distribution patterns. Initially, nutrients were high after impoundment from the decomposing submerged vegetation and leaching from the soil. The new lake was characterised by a high productivity of algae, the invasive water fern, *Salvinia molesta* and fish. Nutrients decreased with time as the lake matured. Macrophyte beds developed in the inshore area, increasing habitat diversity, shelter and food, supporting an increase in fish species such as *Tilapia sparrmanii*. 
Surveys done before the creation of Lake Kariba found between 28 and 31 species of fish in the Middle Zambezi River (Jackson 1961; Harding 1964; Bell-Cross 1965). In the late 1990s, when the reservoir was filled, 45 species were reported by Marshall (2006) and 50 by Songore & Kolding (2003). Species such as *Brycinus lateralis*, *Barbus poechii*, *Labeo lunatus*, *Oreochromis andersonii*, *Sargochromis giardi*, *Sargochromis carlottae*, *Serranochromis macrocephalus* and *Serranochromis robustus* which before the creation of the dam were restricted to the Upper Zambezi River, were captured in the lake (Balon 1974). However, of these, only *B. lateralis* and *S. macrocephalus* were caught in a lake-wide survey in 2006 (Zengeya & Marshall 2008).

Fish species in the new water body revealed preference for diverse conditions. Many riverine species, especially tilapias, prefer still-water pools and marshes in a river (Jackson 1966). These fishes found the lake’s stable and stagnant environment favourable and thrived particularly in the most lacustrine Sengwa, Bumi and Sanyati basins (Figure 1.1) (Begg 1974). In these basins, the cichlid fishes, mainly *Oreochromis mortimeri*, *Sargochromis condronitoni* and *Tilapia rendalli*, made up between 64.1 and 96.2% of the catch in 1968 to 1970. In an unpublished report from 1959, only 0.75% of the fish caught were *O. mortimeri*, while in 1962, as the lake filled, the contribution had increased to 35% of the catch (Kenmuir 1984; Jackson et al. 1988). For these species, the lake environment mimicked the period of plenty in a flooded river when food and shelter were plenty resulting in high survival and reproduction, and consequently high catches. The genera that prefer flowing water and were abundant in the river before impoundment, *Hydrocynus*, *Distichodus*, *Barbus* and *Labeo*, became dominant only in the more riverine uppermost two lake basins and in the estuaries of inflowing streams (Jackson 1960; Begg 1974). The rheophilic species, in the estuaries of inflowing streams (Jackson 1960; Begg 1974). The rheophilic species, in the estuaries of inflowing streams (Jackson 1960; Begg 1974). The rheophilic species, *Chiloglanis neumanii*, *Opsaridium zambezense* (and possibly also *Leptoglanis rotundiceps*) are now confined to the tributaries of the two uppermost basins (Balon 1974). All the former river fishes are restricted to the inshore shallow (< 15 m depth) area, except *Clarias gariepinus*, *Mormyrus longirostris* and *Syndontis zambezensi* that can live in water down to 30 m depth when the water is well oxygenated (Jackson 1960; Coke 1968; Sanyanga et al. 1995).

The inshore fish species are the basis of a gill-net artisanal fishery that started in 1958 and 1962 in Zambia and Zimbabwe, respectively. Between 1964 and 1972, three species dominated the inshore catches: the predator *H. vittatus* and two cichlids, *Oreochromis mortimeri* and *Serranochromis condronitoni* (Karenge & Kolding 1995). The Shannon diversity index for the Lakeside fish increased between 1972 and 1990 as a result of natural introduction from the upper Zambezi and tributaries, as well as fish introductions (Karenge & Kolding 1995). To monitor the inshore fish population, the Lake Kariba Fisheries Research Institute (LKFRI) in Zimbabwe established in the 1960s a Lakeside Experimental Sampling Programme where gill-
Introduction net nets are set routinely at a site named Lakeside, situated on the shores of Kariba town. Data from this programme were used in my research.

Introduction of fish species
Although at least five species are known to have been introduced into Lake Kariba, only the clupeid *L. miodon* and the tilapiine cichlid *O. niloticus* have been successfully established and are now widespread throughout the lake. *Oreochromis macrochir* is found only sporadically; on average about 10 specimens per year were caught out of 5 – 10 000 total number sampled in Zimbabwe at Lakeside between 1974 and 2001 and only three specimens in 1985, 1992 and 1996 in the Zambian Experimental Gillnet Survey (Kolding *et al.* 2003; Marshall 2006). The introduced *Micropterus salmoides* was caught only once and has probably not established a viable population. Two of the introduced species, *Tilapia rendalli* and *Serranochromis robustus*, may have invaded the lake naturally and the former might have been in the system pre-impoundment (Kolding *et al.* 2003).

*Limnothrissa miodon* (sardine), a zooplanktivorous pelagic freshwater clupeid, was deliberately introduced into Lake Kariba from Lake Tanganyika from 1967 to 1968 in order to fill a vacant pelagic niche and increase fish production (Bell-Cross & Bell-Cross 1971). About 30% of the lake is shallower than 17 m and only the shallow area less than 20 m is used by most of the indigenous Zambezi River fishes, because they are not adapted to a pelagic environment (Begg 1970; Coke 1968). By 1969, there was evidence that the sardine had become established (Kenmuir 1971). The introduction is considered a success because *L. miodon* has the largest single fish stock in Lake Kariba. Annual commercial catches landed reached a maximum of about 31 000 tonnes in 1990, and a minimum of 15 000 t in 2003 (Kinadjian 2012). From the beginning of the fishery, the Lake Kariba Fisheries Research Institute in Zimbabwe and the Department of Fisheries in Zambia collected data on the catches and fishing effort. Data collected by the two institutions and from other research, show that catches of sardines vary seasonally and annually (Marshall 1988b, 2012a). Each year catches usually reflect two peaks that differ in magnitude. A small peak occurs during April – May and a larger peak during August – September.

The exotic Nile tilapia (*Oreochromis niloticus*) was first caught in gillnets set routinely at Lakeside in 1993 (Chifamba 1998). Up to August 1994, *O. niloticus* were only caught close to the fish farms where they may have escaped. Even then, the abundance of *O. niloticus* was low, constituting a mere 0.4% of the catch by mass and 0.17 % by numbers. Judging from the range of fish size caught (3 – 30 cm and 1 – 1 069 g) and the presence of both sexes in the sample, these fish were by then already established in the lake.

The farming of *O. niloticus* on the shores of Lake Kariba is responsible for the introduction of this species into the lake. *Oreochromis niloticus* was selected for farming in Kariba because it is widely used in aquaculture all over the world. This
is due to its superior growth rate and adaptation to aquaculture condition, compared to other cichlids (Philippart & Ruwet 1982; Blow & Leonard 2007). Prior to this fish introduction, there was no assessment of its suitability and of the probable impacts.

Impact of fish introductions

*Oreochromis niloticus*

Since the introduction of *O. niloticus* resulted from escapees from fish farms, it was not carefully monitored (Chifamba 1998). However, with the introduction of *O. niloticus*, the once abundant *O. mortimeri*, an endemic to the Zambezi system, declined and disappeared in many parts of Lake Kariba (Chifamba 2006; Zengeya & Marshall 2008). Several factors may have contributed to this species displacement, and a key aim of this thesis is to evaluate the major potential causes.

Competition is a potential driver of local species displacement (MacArthur & Levins 1967). Because *O. mortimeri* and *O. niloticus* show similarities in their diets and reproduction strategies (Chifamba 1998; Mhlanga 2000; Marshall 2011), competition between these species can be expected. Both species feed on algae and organic detritus, plant material, insects and zooplankton, varying with availability (Lowe-McConnell 1958; Moriarty 1973). In both species, the male constructs a large nest in an arena, which it defends (Jubb 1974; Marshall 2011. Therefore, competition for food, nesting and nursery space may have stimulated antagonistic behaviour. Aggression is one mechanism that *O. niloticus* may have used to displace native *O. mortimeri* in Lake Kariba.

Life history trade-offs are reported to be strong determinants of competitive abilities, under both stable and changing ecological conditions (Lancaster *et al.* 2017). A higher growth rate or an ultimate large size of *O. niloticus* could be another mechanism to displace *O. mortimeri*. Many studies have shown that large fish tend to have a larger number of eggs (Schemske 1974, Baglin & Hill 1977, Schenck & Whiteside 1977, Bagenal 1978; Wanink & Witte 2000; Barneche *et al.* 2018). High growth rates contribute to fitness when large size has benefits such as higher fecundity and reduced mortality. Fast growth would therefore result in a larger number of eggs at an earlier fish age. In addition, fast growth may also reduce the time an animal spends at a vulnerable size because smaller animals tend to be more vulnerable to predation (Sutherland 1996). Hence, a comparison of growth rate and maximum size of the introduced *O. niloticus* and the native *O. mortimeri* will give an indication of potential relative competitiveness of these species.
In this thesis I evaluate the potential for competition between *Oreochromis mortimeri* and *Oreochromis niloticus*, by comparing their reproductive effort, aggression levels, growth rates and diet. To compare their diet, I analysed the stomach contents of the two species and estimated the Schoener similarity index (Schoener 1970) and the Pianka overlap coefficient (Pianka 1973) to assess the level of potential competition between the two species. Fish of known size and weight were aged by counting annual increments on scales, opercula and otoliths, and the results used to estimate the growth parameters. The mean length of each age group in the fish sample was estimated and, together with the growth parameters, used to determine which species grows faster and thus can confer size advantage in a contest.

In order to assess the relative aggression of the two species, pairwise contests were setup in an aquarium. The number of aggressive acts such as ‘biting’ and ‘ramming’ were used to score aggression. Aggression indicates which of the two species is likely to be outcompeted in the event of a contest arising during competition for a resource such as food and a breeding site.

Reproductive effort was estimated using the monthly proportion of fish in the samples of both species, that were ready to release gametes (eggs or milt). Having a higher reproductive effort may help a species to outcompete the other by increasing its own population rapidly. The monthly proportions of breeding fish were correlated to rainfall and temperature, both known to trigger reproduction (Clark *et al.* 2005; Taranger *et al.* 2010; Quintana *et al.* 2004), to find out if the influence of those abiotic on the two species is different.

*Limnothrissa miodon*

*Limnothrissa miodon* was deliberately introduced into Lake Kariba to utilize the plankton production in the newly formed pelagic area. This may have prevented population expansion of the native zooplanktivore *Brycinus lateralis* (Woodward 1974). Early catches of *L. miodon* from the open water contained 20.5% *B. lateralis*, showing the capability of the latter species to expand from the Upper Zambezi River and fill the vacant pelagic niche in the lake. Therefore, the expansion of *B. lateralis* into the pelagic area may have been prohibited by competition from *L. miodon* (Marshall 1991).

The introduction of *L. miodon* also affected the habits of the native tigerfish (*Hydrocynus vittatus*). This predator soon added *L. miodon* to its diet and began to inhabit open water in pursuit of its new prey, where it occurred in the developing sardine fishery (Cochrane 1976; Marshall 1987b, 1991). From April 1969 to March 1970, only 1.5% of the stomach content of *H. vittatus* consisted of *L. miodon*, whereas from April 1970 to March 1971 the amount rose to 41.4% and remained high thereafter.
(Kenmuir 1973; Mhlanga 2003). *Hydrocynus vittatus* was an important bycatch species from the beginning of the *L. miodon* fishery. Between 1973 and 1975 the catches of *H. vittatus* increased with increasing catches of *L. miodon* (Cochrane 1976). A decline in catch per unit effort (CPUE) of less than one year old *H. vittatus* between 1974 and 1986 correlated with a decrease in CPUE of *L. miodon* (Marshall 1987b). Already before its introduction into Lake Kariba it was known that, in Lake Tanganyika, *L. miodon* is not an obligate pelagic species but that it inhabits the inshore area for a substantial part of its life (Poll 1953; Matthes 1968). In the inshore area *L. miodon* competes with small cichlids, *Brycinus* sp. and *Barilius* sp.

In this thesis, I investigate the causes of the decline in the pelagic catches by analysing the relationships between *Limnothrissa miodon* catches, fishing effort, and several key environmental variables: air temperature and the hydrological factors, rainfall, river flow, and lake level.

**Fishing on Lake Kariba**

Although power generation is the most important economic function of Lake Kariba, it is also the largest source of fish in the country. Two fisheries evolved, one based on the introduced *L. miodon*, operating in deep/pelagic water, and an inshore fishery. During 1994, the major economic activities on and around Lake Kariba, combined for Zambia and Zimbabwe, generated revenue of about 124 million USD, of which 54% was from power generation and 37.9% from the fisheries (Tumbare 2000).

The pelagic fishery is semi industrial and of greater value than the artisanal inshore fishery, contributing 33.9% against 4.0% of the overall revenue and landing 28 423 and 2 473 metric tonnes of fish, respectively. Dried sardines are an important source of protein, particularly in the rural areas, because of the long shelf life of the dried fish. However, while the sardine catches rose with fishing effort at the beginning of the fishery, they have steadily declined since 1990 (Magadza 2011).

In this thesis, the impact of the sardine fishery on the inshore fish species, through the capture of juveniles, will be explored by analysing the bycatch. I also assess the relationship between *Limnothrissa miodon* and *Hydrocynus vittatus*, to elucidate the response of *H. vittatus* to changes in the population of *L. miodon*. 
Introduction

Objectives of the thesis

PART I – BIODIVERSITY AND IMPACTS OF OREOCHROMIS NILOTICUS

In the first part of the thesis, I evaluate the contribution of the increase in Oreochromis niloticus to the decline of its native congener Oreochromis mortimeri, a species endemic to the Middle Zambezi River.

First, to determine the suitability of the new environment for O. niloticus, I estimate its growth parameters and compare them to those of the same species in other water bodies. This is because environmental suitability can be judged by the individual growth rate and the maximum size the fish attains in that environment, as compared to other environments. Such information can be used for the estimation of fishable biomass.

Furthermore, I look at possible interactions that could have contributed to the displacement of O. mortimeri, by comparing the growth rates, the degree of diet overlap, and aggression levels in O. niloticus and O. mortimeri. Fast growth may confer competitive advantage to the introduced O. niloticus if this translates to more surviving offspring. A large diet overlap can result in a strong competition for food resources (Hanson & Leggett 1985). Higher aggression levels offer advantage in the form of access to better nesting and brooding sites (Philippart & Ruwet 1982; Seppänen et al. 2009).

PART II – BIODIVERSITY AND IMPACTS OF LIMNOTHRISSA MIODON

In the second part of the thesis, I evaluate the declining catches of the freshwater sardine Limnothrissa miodon, by investigating growth rate and age at first maturity as potential causes of the decline. Other potential causes are overfishing and environmental changes. These are assessed by correlating the catches with fishing effort, air temperature, rainfall, river flow, and lake level.

Information on growth rate and age at maturity should reveal whether the fishery catches too small, immature fish. Limnothrissa miodon in Lake Kariba is considered stunted, and the bulk of the catches consists of small fish (< 6 cm total length) compared to those in the fisheries on Lakes Tanganyika and Kivu (Marshall 1987a).

In an exploited fish population, environmental and fishing effort simultaneously affect the fished population. I use multiple regression analysis to determine the relative contribution of environmental factors and fishing effort to the declining catches. I also estimate the Maximum Sustainable Yield from two fisheries models. That provides a guideline for the level of fishing effort, to be used together with considerations such as environmental variation and the biology of the target species, in order to achieve a sustainable fishery on Limnothrissa miodon in Lake Kariba.
Outline of the chapters

PART I – BIOLOGY AND IMPACTS OF Oreochromis niloticus

- **Chapter 2** describes the displacement of the indigenous tilapia *Oreochromis mortimeri* by the introduced *Oreochromis niloticus*, and it explores the possible role of interspecific differences in reproductive potential. Monthly variation in the gonadal activity of the two species is presented in relation to rainfall and temperature.
- In **Chapter 3**, growth rates of *O. niloticus* and *O. mortimeri* are determined and compared. Ages are estimated from reading scales, opercula and otoliths. Ages from these body parts as well as ages from three time periods are compared.
- **Chapter 4** shows the results of stomach content analyses performed on *O. niloticus* and *O. mortimeri*. Diet overlap was estimated to inform on the degree of competition between the two species.
- **Chapter 5** deals with the comparison of aggression levels and dominance of *O. niloticus* and *O. mortimeri*, observed in paired contests in an aquarium. The working assumption is that a high aggression level will infer competitive advantage.

PART II – BIOLOGY AND IMPACTS OF Limnothrissa miodon

- In **Chapter 6**, catch trends of *Limnothrissa miodon* are evaluated to determine to what extent they can be explained by fishing effort and temperature and how they relate to the catches of their predator, *Hydrocynus vittatus*. The occurrence of large sized sardines in the inshore waters is discussed in terms of feeding and breeding. Impact of the sardine fishery on other fish species is explored by analysing incidental catches.
- Growth of *L. miodon* and spatial differences therein are evaluated in **Chapter 7**. Fish were aged using daily increments in otoliths. Deposition rate of the increments was validated using electron microscopy. Implications of age and size at first maturity for fishery management are discussed.

SYNTHESIS

- **Chapter 8** gives an integrated discussion of the results from all the previous chapters. Here the achieved answers to the research questions are evaluated.

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Oreochromis niloticus (left; from Boulenger 1907) and Limnothrissa miodon (from Poll 1952).
PART I

BIOLOGY AND IMPACTS OF *Oreochromis niloticus*