ABUNDANCE, GROWTH AND REPRODUCTIVE BIOLOGY OF *OREOCHROMIS NILOTICUS* (LINNEAUS, 1758) COMPARED WITH TILAPIINES INDIGENOUS TO THE MIDDLE ZAMBEZI

By

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A dissertation submitted to the University of Zambia in partial fulfilment of the Degree of Master of Science in Tropical Ecology and Biodiversity.

THE UNIVERSITY OF ZAMBIA

LUSAKA

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CERTIFICATE OF APPROVAL

This Dissertation by Masuzyo Steinslaus Nyirenda entitled: Abundance, Growth and Reproductive Biology of *Oreochromis niloticus* (Linnaeus, 1758) on Lake Kariba Compared with Tilapiines Indigenous to the Middle Zambezi, has been approved as fulfilling the partial requirements for the award of the Degree of Master of Science in Tropical Ecology and Biodiversity of the University of Zambia.

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ABSTRACT

The introduction of *Oreochromis niloticus* on Lake Kariba has been widely associated with the decline in preponderance of indigenous Tilapiines, especially *Oreochromis mortimeri*. Comperative aspects of abundances, growth and reproductive biology for *O. niloticus*, and three known indigeous Tilapiines: *Oreochromis andersonii*, *Oreochromis mortimeri*, and *Tilapia rendalli* were investigated.

The study was conducted at the riparian Sinazongwe District of Southern Zambia from August to September, 2014. Weight, length and reproductive stages of the different Tilapiine fish were determined. The morphometric and age data was used to determine growth parameters for the Tilapiines using Von Bertalanffy Growth Function (VBGF). Whole ovaries from sexually mature females (ripe and/ or ripe-running) were weighed and preserved in 5% formalin solution; fecundity was determined using gravimetric procedures. Analyses of Variance (ANOVA) were applied in comparing statistical significances in abundance, growth and reproductive parameters among the studied Tilapiines.

Detailed contribution by weight and number for each Tilapiine species at Sinazongwe indicated dominance of *O. niloticus* (IRI=8.62%) whereas *T. rendalli* accounted for 0.77%. *Oreochromis andersonii* and *O. mortimeri* made insignificant IRI contributions (<1%). Investigation into dependence of Tilapiine abundance on intrinsic growth rate, (K) indicated a positive linear relationship defined by a statistically insignificant regression equation: Abundance=92.49K-8.39 (R^2 =0.94; p>0.05). Specimens collected ranged in age from 2-6 years.

The intrinsic growth rate, K, was highest in *T. rendalli* (0.791yr^{-1}), followed by *O. mortimeri* (0.308yr^{-1}), *O. niloticus* (0.180yr^{-1}) and least in *O. andersonii* (0.147yr^{-1}). Growth performance indices (Φ') for the species differed marginally, being highest for *T. rendalli* (4.98) and *O. niloticus* (4.58), and moderately lower in *O. mortimeri* (4.57) and *O. andersonii* (4.36). There were significant differences (p<0.05) observed on the fecundities among the studied female Tilapiines. *Tilapia rendalli* had highest average number of oocytes, 5,135. Among the *Oreochromis* species, *O. niloticus* had an average 2,923 oocytes whereas *O. andersonii* had 1,650 oocytes. On the other hand, *O. mortimeri* had the lowest fecundity, 994 oocytes.

Oreochromis niloticus was the most abundant Tilapiine at Sinazongwe, and indeed an established species throughout Lake Kariba, on the Zambian shoreline. The studied characteristics among the Tilapiines indicated that *O. niloticus* was not superior in every aspect of its growth and reproductive biology.

DEDICATION

To my beloved

Mother,

Petronella Clara Malala Chaaba Nyirenda

&

Father,

Joseph Redson Nyirenda

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LIST OF SYMBOLS

b	Regression coefficient in length-weight relationship
e	Exponent
Φ'	Growth Performance Index
Kg	Kilogram
mm	Millimeter
k	Fulton's Condition Factor
K	Intrinsic Growth Rate
Log_{10}	Logarithm (Raised to base 10)
L_{∞}	Asymptotic Length or Length at Infinity
t_0	Age when Fish has zero length (t-zero)
TL_{50}	Total length at maturity
No	Number
p	Probability
%	Percent
yr^{-1}	Per year

ACRONYMS

ANOVA	Analysis of Variance
ASL	Above Sea Level
CAS	Catch Assessment Survey
CI	Confidence interval
df	Degrees of freedom
DoF	Department of Fisheries
ERA	Ecological Risk Assessment
GNS	Gillnet Survey
GSI	Gonadsomatic Index
IAS	Invasive Alien Species
IRI	Index of Relative importance
IUCN	International Union for the Conservation of Nature
LWR	Length-weight relationship
SADC	Southern African Development Community
SD	Standard Deviation
SE	Standard Error
SGW	Sampled Gonad Weight
SL	Standard Length
TGW	Total Gonad Weight
TL	Total Length
VBGF	Von Bertalanffy Growth Function

CHAPTER 1: INTRODUCTION

1.1 Background

The study and discussion on introduced species is divisive, with definitions often being floating targets of debate mainly due to lack of consensus among proponents (Colautti and MacIsaac, 2004). Whilst these debates rage, the more important effects of species introductions are either ignored or dealt with during phases when impacts may already be advanced and /or even irreversible. These impacts are generally classified as economic, environmental, social or health-related (Charles and Dukes, 2007; Almeida *et al*., 2013). Negative impacts arising from introduced species on ecosystem services have been rated of equal importance to climate change and over-exploitation in driving biodiversity loss (Global Biodiversity Outlook II, 2006). These negative impacts have further been categorised as either being species eliminators, modifiers of evolution, fisheries disruptors, and disease-causers *inter alia* (CBD, 2001). On the other hand, proponents in support of species introductions point to phenomena such as novel-facilitation (where a functionally different introduced species makes available a resource useable by the native species) as justification for continued introduction, and translocation of foreign species.

The economic benefits obtained from trade in introduced species are another aspect considered by promoters of introduced species (EEA 16, 2012). For instance, the 15-fold increase in global fish production from 87,555 tonnes to 1,311,372 tonnes between 1980 and 2002 has been largely attributed to tilapia aquaculture (De Silva *et al*, 2006). Another positive aspect of introduced species has been in their adopted use as control-agents for aquatic vegetation and unwanted aquatic fauna (e.g snails and mosquitos) (Petr, 2000; McIntosh *et al,* 2003). Research and past experiences, on the other hand, indicate that these affirmatives have variable successes (Childs, 2006). In Nicaragua for instance, introduced Nile tilapia escapees from aquaculture cages at Lake Apoyo resulted in establishment of breeding populations of Nile tilapia; the exotic fish species has further decimated *Chara* species, an important plant for native fish species (McCrary *et al*., 2001). Similarly, in the Philippines, millions of *Oreochromis niloticus* fry were stocked in lakes and reservoirs annually by Government agencies during the mid-1950s and have now been shown to dominate

catches in some open waters (Pullin *et al*., 1997). Fish-catch statistics on Lake Lanao (Philippines) indicate that native and endemic Cyprinids have become extinct partly due to Nile tilapia's dominance (Bleher, 1994).

Zambia has an estimated 15 million hectares of water in form of rivers, lakes and swamps, delineating 11 major fishery areas (Figure 1.1), that belong to either the Congo or the Zambezi basins (FAO, 2006). These fishery areas and their fish resources remain susceptible to the emerging threat of exotic introduced species. The portion of the Middle Zambezi at Lake Kariba for instance, has approximately forty (40) species of fish which are not excluded from the threats posed by species introductions. Once introduced species are established in an ecosystem they are known to have immense, insidious and usually irreversible impacts, and may be as damaging to the native species and ecosystems, on a global scale, as the loss and degradation of habitats (IUCN/SSG/ISSG, 2000). Unchecked and unabated, introduced species have been shown to further displace native species and/ or homogenise ecosystems, *inter alia*. These, and other actual or presumed phenomena, put both beneficiary human, and associated floral and faunal communities at risk.

The protection of biodiversity therefore depends on bolstering the science of invasion biology, and ensuring that its findings quickly lead to more effective policies to reduce harmful impacts (UCS, 2001). The starting point in this endeavour would be identifying the extant biodiversity, standing populations and their geographical distributions across Zambia. This approach may help to contextualise national strategies on [fish] biodiversity conservation and sustainable utilisation.

This study, conducted during 2014, aimed at providing objective observations of how abundance, growth and reproductive biology of Nile tilapia, *Oreochromis niloticus* (an introduced fish species) *compared* with indigenous Tilapiines of the Middle Zambezi (Lake Kariba). The indigenous Tilapiines in this investigation were: *Oreochromis andersonii*, *Oreochromis mortimerii* and *Tilapia rendalli.* Whilst this aim did not directly investigate the social, economic and environmental impacts of the introduced Nile tilapia, valuable inferences made from the observations have been included, and are intended to stir debate in management and utilization of capture fishery resources.

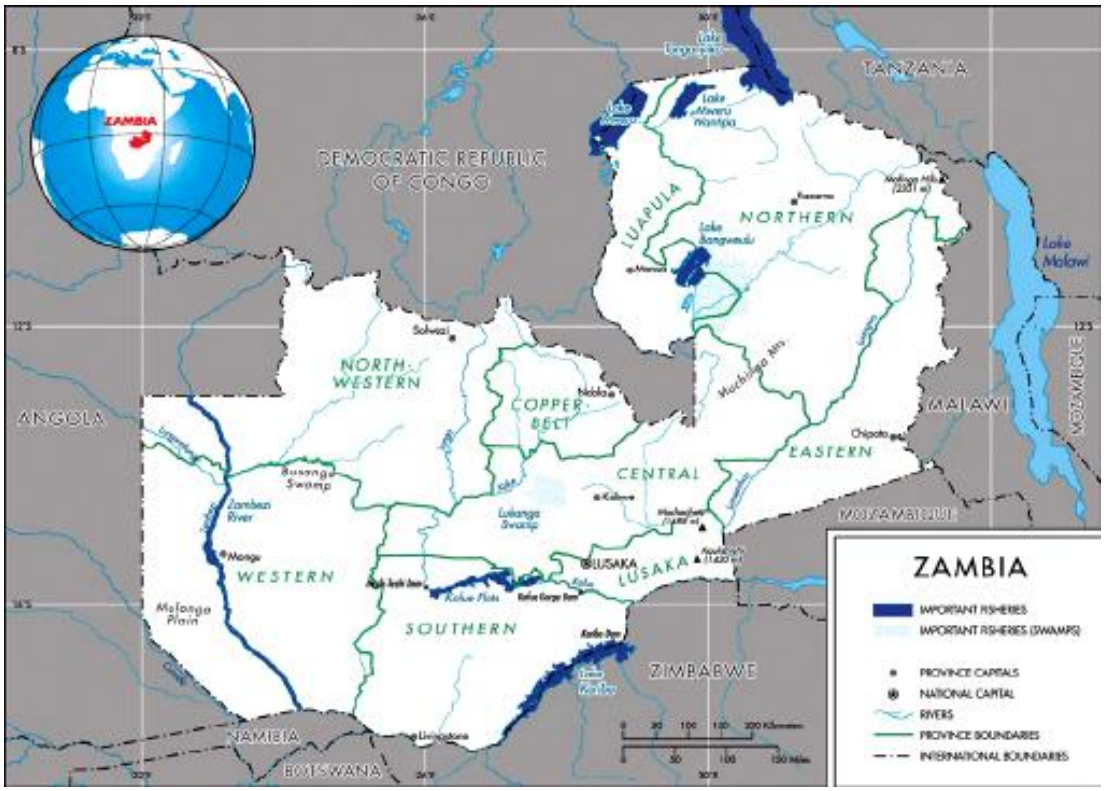

Figure 1.1 Major Fishery (Rivers, Floodplains, Lakes and Swamps) areas of Zambia (Source: Musumali *et al*., 2009)

1.3 The Middle Zambezi

1.3.1 Description

The Zambezi River is one of the longest rivers in Africa flowing over a distance of 2,650km from its source in the Kalene Hill of North-Western Zambia to its delta in the Indian Ocean in Central Mozambique. There are six (06) countries that are riparian on the Zambezi River along its length. From its source the river flows westwards into eastern Angola, and then south to re-enter Zambia at Caripande. Within western Zambia, the River then flows through a relatively flat stretch of country, called the Barotse Plains, before becoming the border between Zambia and Namibia along the Caprivi Strip. The Zambezi also becomes a border between Zambia and Botswana for a short distance and then changes its course from a southern to an easterly direction, as it becomes bounded by Zimbabwe and Zambia at Kazungula.

About 70km past Kazungula, the Zambezi River flows over Victoria Falls and then enters a stretch of dissected country where it forms gorges in the landscape. Notable gorges are Batoka, Devil's, Kariba and Mupata Gorges (Figure 1.2).

The Zambezi River is divided into three (03) sections: Upper, Middle and Lower Zambezi. The Upper Zambezi refers to the stretch of the River from its source to the Victoria Falls. The Middle Zambezi extends from the Victoria Falls to Cahora Bassa Dam, whereas Lower Zambezi covers the remainder of the River to the Indian Ocean. The current study was conducted at a section of the Middle Zambezi occupied by the man-made Lake Kariba.

1.3.2 Formation of Lake Kariba

The Kariba Dam was constructed from 1955–1960. Most of the civil works for the dam wall, the housing and town development were completed in 1959. The installation of the first generation units on the south bank was completed late in 1959 and the first electricity was generated in January 1960 (WCD, 2000). Zambia accounts for 45% of the water surface, with the remainder being in Zimbabwe.The normal operational level of the Lake is 488.5m (EIZ, 2015). The principal physical characteristics of the Lake at 485m above mean sea level are summarised in the Table 1.1

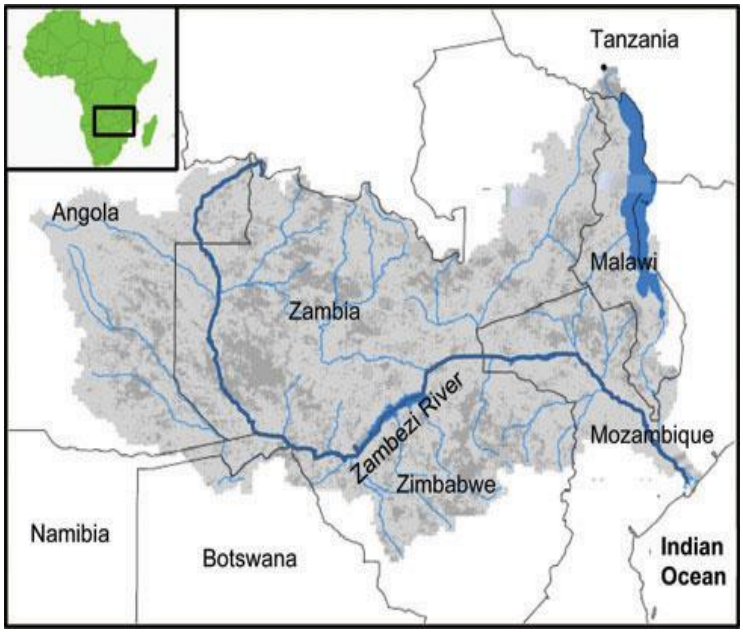

Figure 1.2 Zambezi River and Lake Kariba catchment (Source: wwf.panda.org)

1.3.3 Limnology of Lake Kariba

Lake Kariba has a relatively fast hydrological overturn with a mean water retention rate of about 3 years only. River flows and rainfall contribute about 50-70km^3 of water annually, of which about 80% is provided by the Zambezi River. The Zambezi water is clear and nutrient poor (Mitchell, 1973) compared with the Sanyati, the second largest River supplying about 8% of the water input (Marshall and Langerman, 1988). Lake Kariba is a warm monomictic lake having a mean surface temperature of 26ºC. Stratification begins around September and October each year and continues until July when mixing occurs (Begg, 1970). The thermocline ranges in depth from 15 to 20m when stratification begins and moves deeper as stratification intensifies to reach about 35m at the time of turnover. The oxygen concentration, in the hypolimnion, is high at the time of turnover reaching a maximum of about 6mg/l (Begg, 1970) and declines steadily as stratification sets in reaching a minimum of less than 2mg/l just before turnover.

Table 1.1 Characteristics of Lake Kariba at water level of 485m ASL

Catchment Area	409,600km^2
Surface Area	5,364 km^2
Maximum Length	320 km
Maximum Width	40 km
Mean Width	19.4 km
Maximum Depth	120 m
Mean Depth	29.2 m
Water Volume	156.6 km^3
Number of Natural Basins	5 (4 in Zambia)
Number of Islands in Zambia	103

(Source: Coche, 1971)

1.3.4 Lake Kariba Fishery

Apart from electricity, Lake Kariba provides excellent opportunities for the two landlocked riparian Countries to obtain fish (Karenge and Kolding, 1994). The Lake has two fish communities; an inshore (artisanal fishery), and an offshore (pelagic

fishery). Commercial gillnet fishing (the in-shore fishery) was started in 1962 and initially the catches were very high but soon declined, a pattern which has been repeated in other man-made lakes (Marshall, 1985). Prior to the creation of the reservoir, it was suggested that none of the indigenous Zambezi River fish species would be able to colonize the pelagic zone of Lake Kariba (Jackson, 1961). Therefore, it was recommended that a pelagic species from one of the great African lakes should be introduced. Consequently, the clupeid ("sardine") *Limnothrissa miodon*, locally known as *kapenta*, was introduced from Lake Tanganyika in 1967-68 (Bell-Cross and Bell-Cross, 1971). And by 1970, the species had colonised the entire Lake and had also established itself further downstream in the Cahora Bassa Reservoir.

Fish diversity is high in the Zambezi Basin. The fish species of the basin have been fairly well documented. There are about 165 freshwater species in the Zambezi basin (Moyo, 1998).

1.3.5 The Off-shore Fish Community

The off-shore fish community in Lake Kariba is very simple, as it is totally dominated by *L. miodon*. The Tigerfish, *Hydrocynus vittatus*, also occurs in this zone as a pelagic predator of *L. mioidon*. The introduction of *L. miodon* was a success and by July 1973, the offshore *L. miodon* fishery was borne on Lake Kariba. Exploitation of the *kapenta* has evolved into a million dollar business, with more than 30,000 metric tonnes landed annually (Anon., 1992; Marshall, 1992, 1993). Thus, with the introduction of the pelagic fishery, Lake Kariba has lived up to even the most optimistic pre-impoundment prediction, that the Lake might produce as much as 30,000 metric tonnes per year (Maar, quoted from Marshall, 1985).

1.3.6 The Inshore Fish Community

In addition to the introduction of *L. miodon*, it was recognized that the Middle Zambezi River had a limited number of riverine species. The cichlid species that are the backbone of the artisan fishery in Zambia were particularly lacking (Moyo, 1990). According to Karenge and Kolding (1994) a total of 64 fish species had been recorded on the Lake Kariba. On the other hand, pre-impoundment studies showed that the Middle Zambezi had only 28 species compared to 83 species in the Upper

Zambezi (Jackson, 1960; 1961). Later observations by Losse (1998) noted forty (40) species of fish indigenous to the Upper and Middle Zambezi River basin being present at Lake Kariba. Some of the species of interest encountered from these earlier studies included: *Oreochromis mortimeri, Oreochromis macrochir, Tilapia rendalli, Tilapia sparmanii, Oreochromis andersonii* as some of the Tilapiine representatives in Family Cichlidae. Cichlids are the mainstay of the Kariba inshore fishery. They are pre-adapted lacustrine fish and their biomass increased substantially soon after water impoundment of the Zambezi River at Kariba (Balon, 1974). Other families with representation on Lake Kariba include: *inter alia* Cyprinidae, Mormyridae, Clariidae, Mochokidae, Schilbeidae, Characidae, Distichodontidae (Bell-Cross and Minshull, 1988).

1.4 Statement of Problem

Lake Kariba, and in particular Sinazongwe District has been known as the '*Home of the Kariba bream'*, *Oreochromis mortimeri* (Figure 1.3). However, catch-trends indicate that *O. mortimeri* may have been usurped in dominance by the introduced Nile Tilapia, *Oreochromis niloticus*. It is further unknown how aspects of reproductive and growth biology for *O. niloticus* may be determining the general catch-trends of Tilapiines indigenous to Lake Kariba. Information regarding its spread and dominance on the Lake has been a matter of continued speculation because of the lack of objective and well researched observations. In addition, the biology of *Oreochromis niloticus* on a lacustrine system is an area that has not been well investigated in Zambia, particularly on the Lake Kariba. The ubiquitous catch records for *O. niloticus* is a problem; but the greater problem emanates primarily from the existing gaps in the knowledge of not only this species, but similarly of the Tilapiine species native to Lake Kariba, and how the former may be inadvertently influencing the abundance of the indigenous species. These knowledge gaps have in turn culminated in to poorly articulated management plans and policies, resulting in increased risk of biodiversity loss**.**

1.5 Objectives

1.5.1 General Objective

The overall objective of the study was to ascertain whether or not growth and reproductive biology of *Oreochromis niloticus* could explain the prevailing Tilapiine population dynamics (relative abundances) at Lake Kariba.

1.5.2 Specific Objectives

The present study's exact objectives were to:

a) Determine the most abundant Tilapiine species on Lake Kariba
b) Evaluate the growth parameters of Tilapiines on Lake Kariba
c) Compare the fecundities of female Tilapiines on Lake Kariba.

1.6 Hypotheses of the Study

a) *Oreochromis niloticus* is not the most abundant Tilapiine species on Lake Kariba
b) There are no differences between the growth aspects of *O. niloticus*, and those of indigenous Tilapiines on Lake Kariba
c) The fecundity of female *O. niloticus* is not higher than that of indigenous female Tilapiines on Lake Kariba.

1.7 Significance of the Study

The Middle Zambezi at Lake Kariba supports a fishery with an estimated total population of 27,067 fishers. Sinazongwe District alone accounts for approximately 39.6% of this demographic. Almost 1,401 locals have been directly employed, and unaccounted for numbers indirectly draw benefit from the trade in fish and ancillary products and services (Frame Survey Report, 2011). However, these livelihoods have come under threat from invasive alien species (IAS) of fish, specifically *O. niloticus.* Wise *et al*.,(2007) has, for instance, observed that in those systems that have become invaded by *O. niloticus*, the invasions have had a considerable impact on fish production, and whilst this study may not explicitly isolate the several other factors (including overfishing, disturbance of breeding grounds *etc*) which may lead to reduced fish production, it attempts to indicate the extent to which the presence of *O. niloticus* contributes to the observed population dynamics among Tilapiines on Lake

Kariba. The replacement of indigenous species with Nile Tilapia is known to change the quality of the fish caught - *O. niloticus* is often regarded as being of inferior quality to the species they replace and therefore command lower market prices (Wise *et al*., 2007). And in the wake of fish disease epidemics, knowledge of abundance and biological parameters would be valuable in predicting extents of possible economic and ecological damages/ losses; recent occurrences of Tilapia Lake Virus (TiLV) in the SADC region is a case in point. There is also an unexplored potential of using some of the positive observed Tilapiine attributes among indigenous species for restoring affected systems, (or establishing novel ones). The information generated from this study would therefore, be essential for rational utilization, risk assessment and management of fish stocks at Lake Kariba. The findings from the study are further expected to contribute to the scientific body of knowledge by addressing gaps in some biological details of the Tilapiines at Lake Kariba.

Figure 1.3 A welcoming billboard to Sinazongwe District reads, ' *Home of Kariba Bream*'.

CHAPTER 2: LITERATURE REVIEW

2.1 Introduction

The Convention on Biodiversity (CBD, 2001) has recognised that biodiversity is under serious threat as a result of human activities. Introduction of alien species, with invasive potential, have been noted as being one of the main drivers of biodiversity loss, along with over-exploitation of natural resources by human populations, climate change and global warming, habitat conversion and urbanisation, and environmental degradation (Global Biodiversity Outlook, 2006). Fish species introduction can have positive and/ or negative impacts on the environment; impacts are mostly dependent on the biological attributes of the introduced or invading species. Beneficial impacts are normally associated with development of aquaculture and improvements in catch-rates. Even though introductions are justified for these reasons, biodiversity and ecosystem productivity in most cases diminish.

Southern African Development Community (SADC), to which Zambia is a member, has recognised threats on biodiversity arising from invasive species to greatly undermine regional ability to achieve economic and social development goals (SADC, 2006). Consequently, the region, with support from its development partners, has responded to some of the challenges through a number of initiatives. They include: developing a SADC Regional Indicative Strategic Development Plan; formulating regional instruments; signing and ratifying international conventions; establishing protected areas; implementing Community Based Natural Resource Management (CBNRM) projects; implementing Trans-boundary Natural Resources Management programmes; and carrying out biodiversity related projects and programmes (SADC, 2006).

2.2 Fish Species Composition of Lake Kariba

The distribution of various fish species in Lake Kariba is reflective of the limnological gradient of the Lake. The eastern region of the Lake is dominated by more potamodromous species (Cyprinidae and Distichodontidae) whilst the western region forms habitat for sedentary species such as Cichlids (Begg, 1974).

The following treatise makes reference to the Middle Zambezi as that portion of the (Zambezi) river occupied by Lake Kariba, and does not include the River's bounds beyond Namazambwe on the Western arm, and Kariba gorge on the eastern arm.

There have been several surveys and inventories conducted pre- and post-impoundment of the Middle Zambezi River. Jackson (1961b) conducted a gillnet survey on the pre-impounded Middle Zambezi River and observed 28 fish species. Post-impoundment surveys by Harding (1966) reported 33 species. Balon (1974a) on the other hand observed 39 fish species; the list of economically preferred species (as determined by Balon, 1974a) are summerised in Table 2.1.The inventory by Balon (1974a) indicated that *Brycinus lateralis* had an average occurrence of 58.78% followed by *Oreochromis mortimerii* (10%), *Cyphomyrus dischorynchus* (8%) and *Tilapia rendalli* (3.62%). By the 1980s, updated inventories indicated the presence of 43 fish species (Marshall, 1984), and 62 species towards the close of that decade (Bell-Cross and Minshull, 1988). More recent inventories have reported 50 different fish species in the Lake (Songore and Kolding, 2003). Certain of the species reported have only been encountered once and may be assumed to have been stray specimens that have not established viable populations in the Lake; these include *Barbus radiates, Hepsetus odoe, Labeo lunatus, Leptoglanis rotundiceps, Micropterus salmoides, Serranochromis angusticeps* and *Varicorhinus nasutus* (Kolding *et al*., 2004).

Table 2.1 Compilation of Lake Kariba Fish in economic order of size, abundance and frequency of occurrence

Order number	**Species**	**Frequency of occurence**	**Mean Percentage (%) of Total number**
1	*Oreochromis mortimeri*[1]	8	10.00
2	*Tilapia rendalli*	8	3.62
3	*Hydrocynus vittatus*	8	2.48
4	*Clarias gariepinus*	6	2.00
5	*Sargochromis codringtoni*	6	1.10
6	*Heterobranchus longifilis*	6	0.09
7	*Mormyrops deliciosus*	5	0.47
8	*Labeo cylindricus*[2]	5	0.18
9	*Mormyrus longirostris*	4	0.05
10	*Distichodus schenga*	3	0.28
11	*Labeo congoro*	3	0.02
12	*Tilapia andersonii*	2	0.85
13	*Sargochromis giardia*	2	0.16
14	*Haplochromis carlottae*	1	0.10
15	*Serranochromis robustus* [3]	1	0.04
16	*Serranochromis microcephalus*	1	0.04
17	*Distichodus mossambicus*	1	0.03

(Source: Balon, 1974a)

2.3 History of Fish Species Introductions in Zambia

Literature on early fish introduction into Zambia is very limited. However, an exhaustive review by Audenearde (1994) to describe early fish introductions is recapitulated in the following discussion.

The introduction of fish species in Zambian rivers and lakes dates back to the 1940s, a period when knowledge about fishes indigenous to Africa was scanty. These early

[1] Previously classified under Genus: *Tilapia*
[2] Previously classified under Species: *altivelis*
[3]Previously classified under Species: *jallas*

introductions of fish species into Zambia were done without any quarantine or precautionary measures, and fortunately they were failed introductions without any record of establishment. Between 1945 and 1950 several translocations of Tilapiines were performed with *Tilapia rendalli* and *Oreochromis macrochir* transported from the Luapula-Mweru systems into Lusaka (Chilanga). During the same period *Oreochromis mortimeri* was translocated from the Middle Zambezi into Lusaka (Chilanga). The decade that followed was characterised by greater translocations resulting from the perceived benefits of Tilapia species. After rigorous investigations into the niches and biololgical occupancy of Lake Kariba, it was found necessary to introduce *O. macrochir* during 1959-1962 from Chilanga but this species was not encountered during any of Balon's (1974a, 1974b) intensive sampling programme. However, experimental surveys in years that followed revealed small numbers of the species (averaging 10 specimens per year out of 5-10,000 samples). Even though Kenmuir (1984) had indicated *T. rendalli* and *Serranochromis robustus* as being introduced species, Jackson (1961b) argued that the former species was encountered in pre-impoundment surveys of the Middle Zambezi. The small clupeid *Limnothrissa miodon* introduced from Lake Tanganyika during 1967-1969 (Bell-Cross and Bell-Cross, 1971) and the Nile Tilapia are two true exotic species, completely foreign to the Zambezi River system; exact year of introduction for *O. niloticus* is unknown, but speculations place it during the mid to late 1990s. More recent experimental surveys on Lake Kariba have also revealed the presence of an exotic crayfish, *Cherax quadricarinatus*.

2.4 Description of Native Tilapiines on the Middle Zambezi

Tilapiines comprise a major branch of African Cichlid fishes. The group is represented by deep-bodied, vegetarian species. Some genera in this group are substrate spawners that guard their eggs or fry (*Tilapia*), whilst others are mouthbrooders demonstrating positive response to retrieving motions of the brooding female (*Oreochromis*) (Skelton, 2001). The descriptions that follow correspond with the indigenous Tilapiines of the Middle Zambezi (Lake Kariba), considered during this study (Figure 2.1).

2.4.1 *Oreochromis andersonii* (Castelnau, 1861)

Threespot Tilapia, *O. andersonii* is distributed in Cunene, Okavango, Upper Zambezi and Kafue Rivers, and has preference for slow-flowing or standing waters bodies. Adults of this species have blue-gray appearance with 3-4 mid-lateral spots. The species is generally hardy, tolerating fresh and brackish waters where it feeds on detritus, diatoms and zooplankton. The presence of the Threespot tilapia in Lake Kariba has been subject of debate. Balon (1974c), for instance suggested that the species survived the drop down from the Victoria Falls. Another school of thought assumes that the species may have been present in the Middle Zambezi, but was not captured during earlier sampling programmes. Jubb (1976a) has implicated the Victoria Falls power station as the likely route of accidental entry of the species into Lake Kariba. Audenaerd's (1994) reviews indicate that translocation of the Threespot tilapia within Zambia commenced in the late 1970s up to the early 1980s, well after the first records of the (species') encounter on Lake Kariba.

2.4.2 *Oreochromis mortimeri* (Trewavas, 1966)

The Kariba Tilapia, *O. mortimeri* is endemic to the Middle Zambezi River and the Luangwa tributary and has a preference for impounded and quiet waters of rivers (Skelton, 2001). The Kariba Tilapia has characteristic body form similar to that of *Oreochromis mossambicus* and their juveniles are indistinguishable. It has a diet of algae, especially diatoms, detritus, plant material, insects and zooplankton. The catch per unit effort (CpUE) for the species at Lake Kariba was fairly high during the period 1974-1978 averaging 18kg/100m of gillnet but declined to 5kg/100m of gillnet by 1985 (Moyo, 1986). Songore *et al.,* (1998) observed that the species made considerable contribution of approximately 50% by weight to the commercial fishery at Lake Kariba. The contribution of the species to annual catch has however, reduced to 17% by weight (Songore *et al*., 1998). Unreliable records of catch statistics are a hindrance to knowing the current status of the species on the Zambian side of the Lake.

2.4.3 *Tilapia rendalli* (Boulenger, 1896)

Redbreast Tilapia, *T. rendalli* has a typically deep body. Mature specimens appear olive green to brown with distinct vertical bars on the body, a bright red throat and chest. The redbreast tilapia has been recorded in the Cunene, Okavango, Zambezi system, Congo basin, Lakes Tanganyika and Malawi. The species feeds largely on aquatic vegetation and algae, aquatic invertebrates and even smaller fish. Redbreast tilapia is difficult to catch in gillnets because of its diurnal habits (Kenmuir, 1983). It attains total length of 400mm and weight of up to 2kg (Skelton, 2001). This species is a substrate spawner having high fecundity of approximately 5,000 to 6,000 eggs at each spawning (Coward and Bromage, 2000). On Lake Parakrama Sanudra in Sri Lanka, fecundity for *T. rendalli* was observed to range between 760 -6160 eggs (Chandrasoma and De Silva, 1981). Multiple spawning has been confirmed in this species, with temperatures above 21°C being most conducive (Coward and Bromage, 2000). *Tilapia rendalli* has been commercially important to the Lake Kariba fishery and contributes approximately 43% of the inshore catch on the Zambian side, and only 8% on the Zimbabwe side (Songore *et al*., 1998). The Zambian Department of Fisheries carried out augmentive introductions of *Tilapia rendalli* during 1959-1962 in an effort to boost the artisanal fishery production (Coche, 1971).

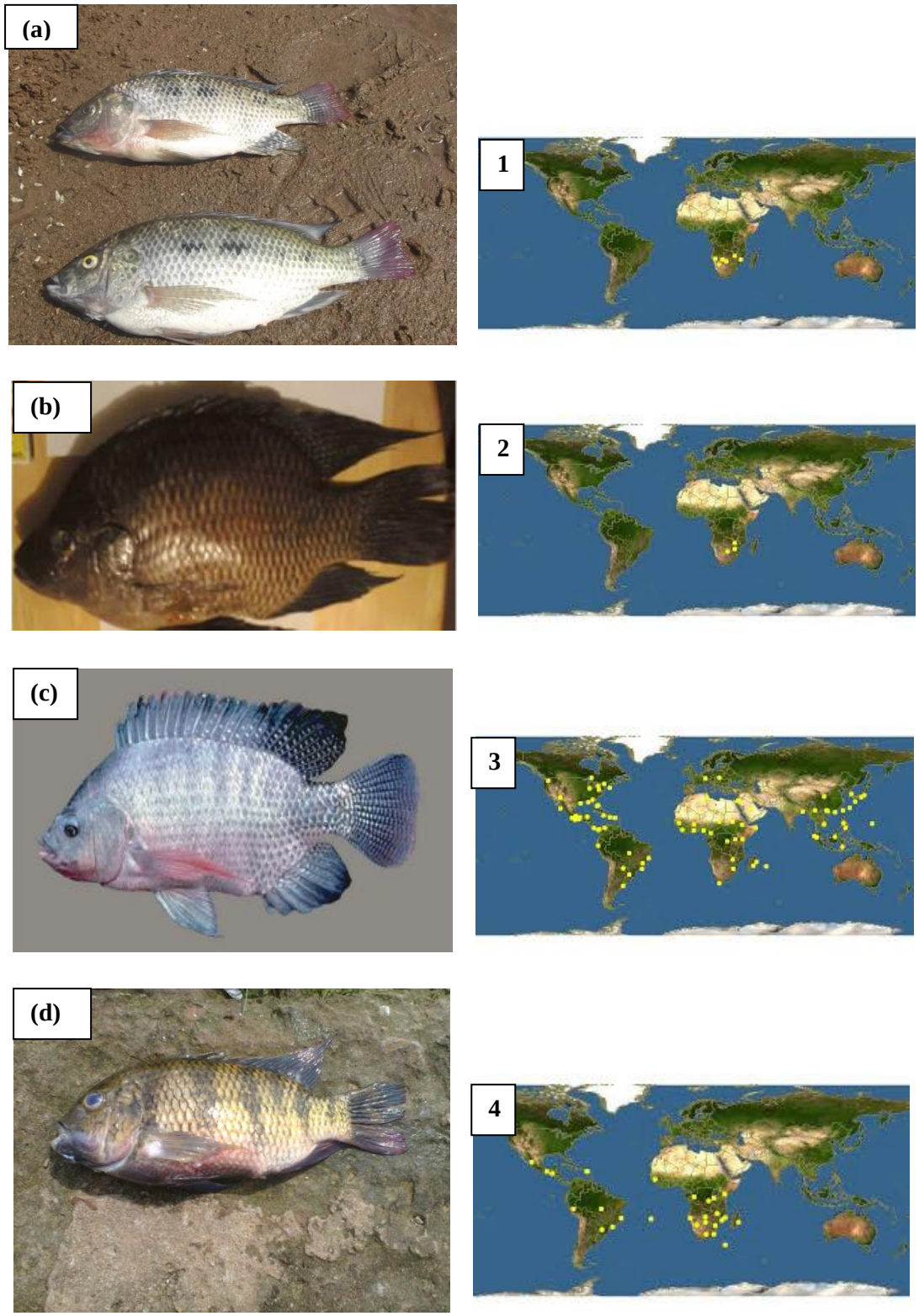

Figure 2.1 Global Distribution of Tilapiines: *Oreochromis andersonii* (a,1); *Oreochromis mortimeri* (b,2); *Oreochromis niloticus* (c,3); *Tilapia rendalli* (d,4). Distribution Map Source: www.discoverlife.org (2015).

2.5 Abundance and Distribution of Nile Tilapia in South-East Africa

Fish abundance and distribution is dependent on availability and quality of feed, and the substrate type in a particular habitat (Welcomme, 1985). The occurrence of Cichlids in inshore waters is a general indication that these environments provide adequate nutrition, shelter and breeding ground (Balogun, 2005). Lowe-McConnell (1991) later noted that cichlids (including Tilapiines) may have general preference for habitats characterised by warm water temperatures, being either shaded from or exposed to direct sunlight, in nutrient deficient or brackish estuaries.

In Lake Victoria, the introduction of *Oreochromis niloticus*, in the late 1950s resulted in the extinction of the highly-prized *Oreochromis esculentus*, and probably *Oreochromis variabilis* by the late 1980s. The introduction of Nile tilapia to Lake Victoria increased the overall fish catch from the Lake. However, despite increased catches, landed fish were of a lower quality (Wise *et al*., 2007). In this regard, at Lake Victoria, lower value Nile tilapia was able to withstand fishing pressure better than the higher valued *O. esculentus*, which it displaced from the Lake. At Lake Chicamba, on the Revue River system, in Mozambique the invasion by Nile tilapia added to the catch per unit effort of the gillnet fishery. The initial invasion into Lake Chicamba most likely came *via* the Zonue River from an irrigation reservoir located on the River along the Zimbabwe / Mozambique border (Weyl, 2008).

2.6 Fish Fecundity

Fish fecundity is considered as an indicator of the reproductive strength of any fish species (Bakhoum, 2002). Fecundity is the average number of eggs per brood, and the intensity of reproduction is determined by both the average number of eggs per brood and how often the eggs are laid by the female per unit time (Winberg, 1971). It has been demonstrated that fecundity is a function of several parameters and may vary from one system to another due to differences in food abundance and other environmental factors that affect the body size of fish (Moyle and Cech, 2000).

As a result of their mouth-brooding nature, *Oreochromis* species have been observed to produce only a few hundreds of offspring in a single spawn, but under favourable conditions they spawn frequently every 4 to 6 weeks (Pullin, 1991).
The mouthbrooding behaviour among *Oreochromis* species is only done by females of the species. *Tilapia* species are, on the other hand, termed as substrate-spawners and both parents guard the brood.

Water temperature and availability of feed influences the fecundity of fishes through their effect on body size; fecundity is closely related to body size of the egg-producing females (Winberg, 1971). Fabrice and Legendre (2000) have noted, for instance, that *O. niloticus* on Lake Ayame, Cote D'Ivoire has a relatively shorter and less intense breeding season compared to the other populations and a delayed maturity associated with a low fecundity and large eggs. A review of fecundity in *O. niloticus* in various habitats by several authors revealed alot of plasticity both within and among systems (Table 2.2). There was a certain dearth in fecundity data for indigenous species, with the bulk of observations being from experimental (captive) observations.

Table 2.2 Fecundity of *O. niloticus* observed at various locations by several Authors

Absolute Fecundity	**Mean Fecundity**	**Oocyte diameter (mm)**	**Author**
73-1,810	815	2.47±0.02	Komoloafe & Arawo (2007); Opa Reservoir, Nigeria
289-1,456		1.99-2.45	Kariman & Salama (2008); Abu-Zabal Lake, Egypt.
30-2,603			Peterson *et al* (2004); Coastal Mississippi
412-2,303	854		Nyakuni (2009); Albert Nile, Uganda
563-1,542	851±13.2		Kpelly (2010); Weija reservoir, Ghana
160-625			Duponchelle & Legendre (1995); Lake Ayame, Ivory Coast
178-717			Duponchelle & Legendre (1996); Lake Ayame, Ivory Coast
1,240-6,600		2.2±0.39	Chande A.L & Mhitu, H.A (1997); Lake Victoria
378-1,324		0.3-3.0	Bakhoum (2002); Lake Edku, Egypt
864-6,316	2,141		Lung'ayia (1994),Nyanza Gulf Lake Victoria Kenya

2.7 Size-At-First Sexual Maturity of Fish

The reproductive process in all animals commences once they attain sexual maturity at a particular size, which usually depends upon environmental and ecological factors, as well as the biological attributes of the animal. The size-at-maturity is

subject to variation between and within species. Therefore, all fishes of the same cohort or size need not attain maturity at some fixed age or length (Udupa, 1986). Fryer and Iles (1972) actually noted that Tilapiines have the capacity to direct the allocation of their resources to reproduction at the expense of growth, depending on prevailing environmental conditions. Lowe-McConnell (1982) further observed that same species of Tilapiines are able to exhibit wide variations in reproductive traits and habits between water bodies. There is further evidence indicating strong correlation between size and age-at-first sexual maturity with growth, maximum size and longevity (Froese and Binohlan, 2000). Size-at-first sexual maturity is therefore important in understanding life history theories because it addresses questions of a species' fitness (Stearns, 1992). Correct estimates of size-at-first maturity are also useful in stock management (Fontoura *et al*., 2009).

2.8 Fish Growth

Growth can be defined as the change in size (length, weight) over time. It can also be defined as the change in calories stored as somatic and reproductive tissues. The latter definition is useful for understanding the factors that affect growth because of conversion of the ingested food energy into metabolic or growth or excreted energy (Brett and Groves, 1979). Growth is expressed in relation to time, thus it is useful to determine the age of investigated Tilapiine species. Unlike most mammals, birds and insects, fish often continue to grow after they reach sexual maturity. This is termed as indeterminate growth; although growth may slow down as resources are re-allocated to reproductive demands, actual growth has been noted to continue well after maturation (Enberg *et al.,* 2008). The Von Bertalanffy Growth Function - (VBGF) is the most commonly used descriptive model in fisheries science. It is based on a simple mass balance equation similar to those underlying bioenergetic models (von Bertalanffy, 1938). Like all models, the VBGF is a simplification of reality and is useful in representing growth and/ or consumption.

Another important feature in describing growth of fish is the length-weight relationship (LWR). Length-weight relationship is capable of: giving information on condition and growth patterns of fish (Bagenal and Tesch, 1978); helping to estimate fish weight based on length, and *vice versa*, and; analyse growth patterns by the

allometric coefficient (*b*). The relationship between length and weight differs among species of fish according to their inherited body form, and within a species according to the condition of the individual fish (Schneider *et al*., 2000).

2.9 Impacts of Biological Invasions on Native Fish Biodiversity

The scope of species introductions and invasions is global and the cost is enormous in both ecological and economic terms (McNeely, 2001). Humans have been transporting species, both intentionally and unintentionally, around the world for hundreds of years (Van Driesche and Van Driesche, 2000). The numbers of introductions and resultant invasions are growing at an exponential rate in some regions. Increasing global domination by a few taxa threatens to create a relatively homogeneous world rather than one characterised by great biodiversity and local distinctiveness (Rejmanek, 2000). It is worth noting however, that only a small proportion of alien species become established, some of these spread, and a small subset produce major ecological, economic or social impacts as invasives (Brunel *et al*., 2010). Since the second half of the last century 1,354 introductions of 237 fish species into 140 countries have been documented worldwide (Welcomme, 1988). Africa accounted for 11% (147) of these introductions, represented in 50 fish species; 23 of these are from outside Africa, whilst the rest are intra-continental (Pitcher, 1995). Richardson *et al*., (2000) estimates that 50% of invasive species in general can be harmful, based on their actual impacts.

Introduction of non-native fish species to modify wild stocks is an important fisheries management intervention that essentially responds to three perceived needs: (1) establishment of new fisheries, (2) filling a vacant niche and, (3) augmentation of existing fisheries. Zambia had exotic species introductions as early as 1940 with an increase being observed in the 1970s and 1980s. Some of the early fish introductions carried out in the 1940s and 1950s included: *Cyprinus carpio* (Carp), *Lepomis macrochinus* (Bluegill), *Micropterus dolomieui* (small-mouthed Bass) and *Onchorynchus mykiss* (rainbow trout). All these apparently failed to successfully establish in Zambia. A second and third wave of introductions leading into the 1980s was conducted (Audenaerde, 1994). The first introduction of *O. niloticus* from

Sterling, England was documented for the Kafue River system in 1982 (Shwanck, 1995). Further introductions occurred near Lake Kariba (Van der Waal, 2007).
In both instances, the Nile tilapia escaped from dams which burst at their levees or simple escape from fish cages.

Peace Corp, in an effort to promote small-scale aquaculture, have also been implicated in aiding the spread of Nile tilapia in the Zambezi River system (Shipton *et al*, 2008). The introductions of *Limnothrissa miodon* by the Zambian Department of Fisheries on Lakes Kariba and Itezhi-tezhi present as some of the most successful interventions at establishing new fisheries in previously vacant pelagic niches on the two man-made Lakes; this has resulted in the emergence of a successful sardine fishery (Mbewe, 2000).

Invasive fish species have generally been implicated for reduction in native inland water species through predation, hybridization, parasitism, or competition and even alteration of community structure and ecosystem processes (Arthington, 1991). Despite the recognised trend for Tilapias to become feral wherever they have been cultured or introduced (Costa-Pierce, 2003), a systematic approach assessing and evaluating the potential environmental impacts has been absent (Canonicol *et al*, 2005) and as a result management decisions concerning Tilapia introduction have been highly based on extrapolation with divergent arguments from proponents of biodiversity conservation, on one hand and those of socio-economic, and politics on the other hand (Pullin *et al*, 1997). The trend in dealing with impacts of introduced species (with or without invasive potential) has revealed an 'externalisation' of the possible negative outcomes by those that facilitate the introduction (deliberate or inadvertently) because they might be expected to compensate those who may be negatively affected. And because of this lack of responsibility, future generations end up paying the costs (McNeely, 2001).

Documented impacts of Nile tilapia are varied but may be included in any of eight broad categories, namely; alteration of hydrologic regime; alteration of water chemistry regime; alteration of physical habitat; alteration of habitat connectivity; impacts on the biological community; impacts on specific populations; genetic impacts.

On Lake Victoria, *O. variabilis* and *O. esculentus* have been displaced by the Nile Tilapia (de Vos *et al*., 1990). Similar observations have been made about *O. mortimeri* on Lake Kariba (Chifamba, 1998). Gurevitch and Padilla (2004), on the other hand, present an argument that the importance of invasive species in causing declines and extinctions of species is unproven. They based their conclusions on IUCN Red List databases that have given an indication that only 6% of the taxa are threatened with extinction as a result of Invasive Alien Species (IAS) and less than 2% of 762 documented extinctions were a result of IAS. However, Clavero and Garcia-Berthou (2005) have disapproved the former assertions due to the limited scope of the statistics used to draw conclusions. The latter have instead pointed out that the system used by Gurevitch and Padilla (2004) was only applicable to 5.1% (39 out of 762) of the extinct species because of missing or incomplete detail in information about the causes of extinction. Indeed the evidence provided by Clavero and Garcia-Berthou (2004), and Gurevitch and Padilla's (2005) emphasise the need for holistic approaches in describing species' population dynamics. It is important therefore, that attempts at describing impacts from introduced species should galvanise all aspects important to an ecosystem. A complete description of species composition, interactions and understanding of their biology would be primary in such assessments, but this must further include aspects of the environment and how activities such as wetland agriculture, cage fish-culture and fishing practices influence fish catch-trends and biodiversity. The Global Invasive Species Programme (GISP) has, in this regard, recognised and placed emphasis on dealing with ecosystems as dynamic entities rather than advocating for attempts to 'freeze' any particular ecosystem in an imagined pristine state (McNeely *et al*., 2001).

The ecological impacts of invasive species on inland water ecosystems vary significantly depending on the invading species, the extent of the invasion, and the vulnerability of the ecosystem being invaded. Tilapia introductions have been blamed for eutrophication, a process through which enrichment with nutrients such as nitrogen and phosphorous leads to increased production of organic matter (Armantrout, 1998). Starling *et al*. (2002) have demonstrated a linkage between high Tilapia biomass in Lago Paranoa, a tropical reservoir in Brazil and increase in total

phosphorous (resulting from phosphorous release due to bioturbation and excretion), chlorophyll *a*, and cyanobacteria concentrations. These impacts may simultaneously influence more than one aspect of ecology, including individual level (life history, morphology, and behaviour), population dynamics (abundance, population growth, and recruitment), genetics (e.g hybridisation), communities (species richness, diversity, trophic status) and ecosystem processes (Hurlbert, 1972; Parker *et al*., 1999). The combined impacts of introduced species may, in the worst case scenario, promote biotic homogenisation in which an increase in genetic similarity, taxonomic and functional biota is observed (McKinney and Lockwood, 1999).

The few documented cases of positive environmental impacts arising from introduction of alien fish cite the use of herbivorous species to control aquatic vegetation (Petr, 2000; McIntosh *et al*., 2003). Other potential applications may be to control unwanted aquatic fauna (e.g snails, mosquitoes). Lake Nakuru was, for instance, transformed from an ecosystem of very low biodiversity (a large population of flamingos, two species of algae and a few invertebrate species) to one of greater diversity (including 30 species of fish-eating birds) after the introduction of *Tilapia grahami* to control mosquitoes in 1961 (Jacobs, 1975). However, research and past experience indicates that these ecological interventions have mixed success (Courtney and Maffe, 1989; Childs, 2006).

CHAPTER 3: MATERIALS AND METHODS

3.1 Description of Study Area

Lake Kariba lies in the Gwembe valley of Zambia's Southern Province at latitude 16º28´- 18º06´ South, and longitude 26º40´- 29º03´ East, with a main axis running in the SW-NE direction where it boarders with Zimbabwe. The Gwembe valley is a large rift valley 65 to 80 km wide on average and bordered on either side by escarpments 650m high. The extent of the valley has been described by Scudder (1962) as the area from the Gwaai River confluence with Zambezi River downstream of the Devil's Gorge to the Kafue River confluence with the Zambezi River 370 Km further downstream. Sinazongwe District in the Southern Province of Zambia is located at 17° 15' 0" S, 27° 28' 0" E. The District lies in the Gwembe valley and is riparian to Lake Kariba on the northern shore.

During the study period, the Lake had a retention level of 484.6 meters above sea level. The relatively low water levels during the period were attributed to low rainfall in the Upper Zambezi region, and over-generation at Kariba HEP complex (EIZ, 2015).

Three sampling stations (located at permanent Fishing Villages) were selected on Lake Kariba, Sinazongwe District; Simuzila, Sikalamba and Nzenga (Figures 3.1 and 3.2). Sampling was confined to estuaries and lagoons of the Lake. The sampled littoral subsystems at Sinazongwe belonged to either one of the following classes: rocky shore/ rocky bottom (Figure 3.2 (c)), unconsolidated shore/ unconsolidated bottom (Figure 3.2 (b), (d)), aquatic bed (Figure 3.2 (a)).

Nzenga (S17°15.863´; E027°26.226´; 483m ASL) and Simuzila (S17°17.968´; E027°26.849´; 484m ASL) sampling stations located on the South-Western portion of the Lake are drained by the Zongwe River. These sampled areas at Simuzila had a characteristic rocky-bed formation grading into pebbles landwards, and a sandy shoreline on either side of the jetting peninsula that forms the landmass.

Sikalamba river estuary (S17°12.513´; E027°32.142; 483m ASL) had characteristic unconsolidated bottom in the river channel whereas a stretch of sandy shore formed

the Lake-front. The estuary was lightly vegetated with emergent macrophytes, whereas patches of grass were present in the sandy shoreline.

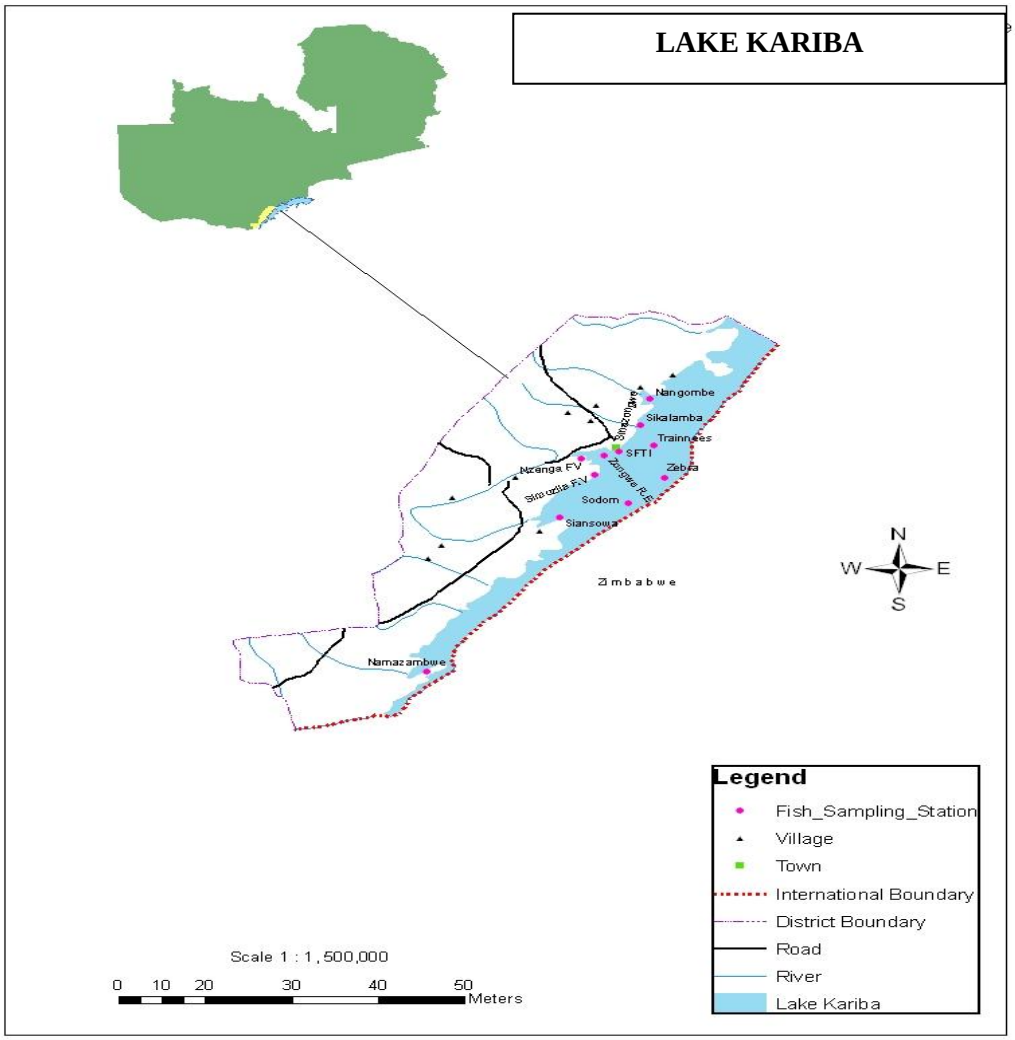

Figure 3.1 Sampling stations (Fishing Villages) of Sinazongwe District.

3.2 Sampling Design

Three stations selected on Lake Kariba, Sinazongwe District were sampled for the target fish species. The selection of sampling sites took into consideration wetland classification criteria for lacustrin systems (Cowardin, 1979). Four days were dedicated at each sampling station during each sampling month; one day was reserved for travel and setting up camp. Actual sampling was conducted in three consecutive nights at each site, from August to September, 2014. Sampling during this period coincided with previously observed periods of heightened breeding activity (Offem *et al*., 2007; Uchida, unpublished report).

A total of eighteen samples were collected. Abundance data were on the other hand, determined only from samples at the actual sampling sites; this approach ensured reliability. Accumulated specimens were supplemented with collections from local fishermen due to inadequate catches from the researcher's fleet of nets. Fishers at Sinazongwe tended to ply their fishing over wide and overlapping areas. Furthermore, some of their methods of fishing are 'active' and effective in capturing particular species. Therefore, using their landed catches for abundance studies would have introduced bias and skewness for particular species, hence specimens acquired from fishers were only included in analyses involving reproduction and growth, and this was based on the assumption that a single stock of each species was being investigated during the study.

For purposes of this study, the concept of a fish stock as defined by Sparre and Vanema (1998) was adopted; fish species in neighbouring fishing areas form one unit stock.

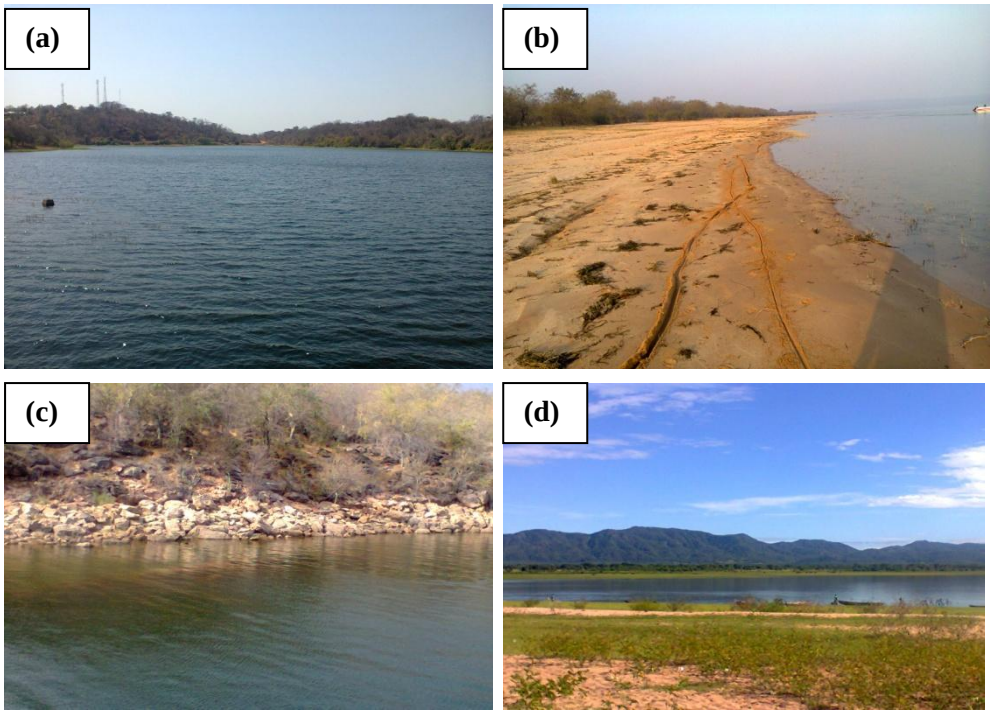

Figure 3.2 Estuarine environments on Lake Kariba sampled for Tilapiines:
(a) Zongwe River estuary, (b) Nchete Island, (c) Trainees Island (d) Sikalamba River estuary.

3.3 Sampling Procedure

Fish samples were collected from the selected sampling sites of Lake Kariba using a passive fleet of gillnets of the mesh sizes represented in Table 3.1 (following the Gillnet Survey Manual, Department of Fisheries, Zambia). The investigations targeted four Tilapiine species: *Oreochromis andersonii, Oreochromis mortimeri, Oreochromis niloticus* and *Tilapia rendalli*. The different mesh-sized gillnets were intended to capture specimens of different sizes, representing fish at different maturity stages and age-classes.

The gillnet panels were set on the Lake at 17:00hours and hauled at 07:00hours the following day. Trapped fish were removed from gillnets and stored on ice, awaiting identification and analyses. Each of the observed Tilapiines was identified to species level, weighed, measured, sexed and later on aged. This procedure was repeated for three nights at each of the designated sampling sites.

Table 3.1 Mesh sizes for gill-nets used in sampling for Tilapiines

Mesh size (mm)	25	37	50	63	76	89	102	114	127	140	152	165	178	190
Mesh size (Inches)	1	1.5	2	2.5	3	3.5	4	4.5	5	5.5	6	6.5	7	7.5

3.4 Data Collection

Data on the following variables were broadly presented under the general headings: Relative abundance, Growth and Reproduction. Proxy variables were inferred from these headings.

3.4.1 Relative Abundances

Following the sampling procedure described above, hauled catches from respective sites were identified to species level (Skelton, 2001), counted and weighed to the nearest gram (g). Non-target species were also subjected to enumeration and weighing for purposes of establishing their indices of relative importance (IRI).

An indication of Tilapiine abundance was also obtained from compilations and reviews of Catch Assessment Survey (CAS) data from the year 2011 to 2015. The analyses of CAS data further gave an indication of spread and establishment of *O.*

niloticus on the Lake. Catch Assessment Surveys are routinely conducted by DoF for purposes of determining the production (biomass) and average catches per unit of effort (CpUE) of all exploited fish species, expressed as Kg/boat. The compilations were performed for Stratum 1 and 2 (Sinazongwe District), Stratum 3 (Chipepo/ Gwembe District) and Stratum 4 (Siavonga District), (Figure 3.3). Species' indices of relative importance (%IRI) were compiled only for observations from the researcher's gill-netting surveys (GNS) at Sinazongwe District (Appendix B, Data Sheet 3).

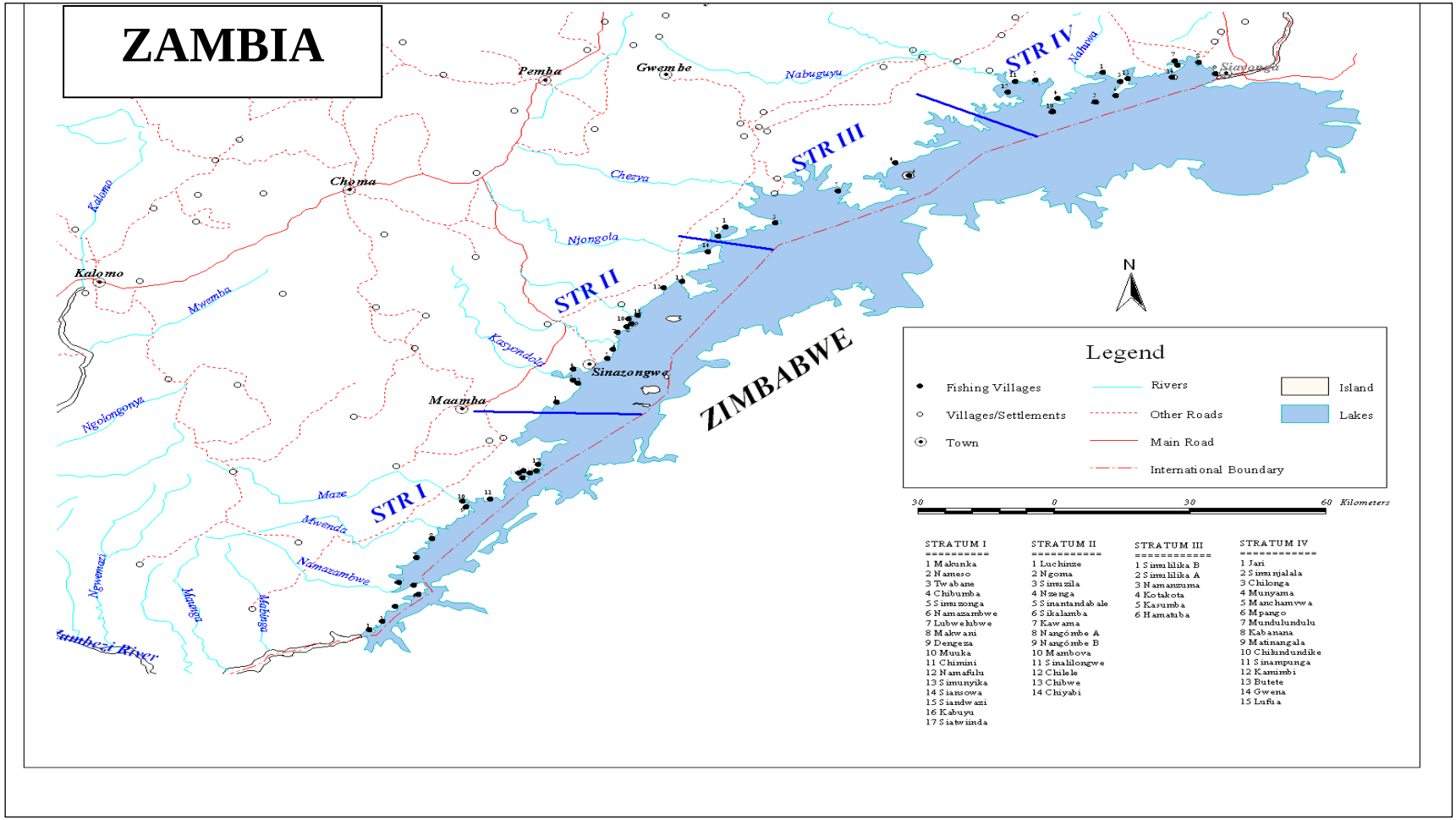

Figure 3.3 Stratification of Lake Kariba on the Zambian shore; four strata located at Sinazongwe, Gwembe and Siavonga District (Source: Department of Fisheries, 2011).

3.4.2 Growth

a) Weight frequencies

Body weight of individual target Tilapiine fish species obtained from the researcher's and fishermen's gillnets were cleaned and dried of moisture and other particles using blotting paper. The identified Tilapiine specimens were then placed on an electric balance and weighed to the nearest 0.1 g.

b) Length

The target species were individually placed on the measuring board (meter rule) and the total and standard lengths (TL and SL, respectively) determined (mm). The total length (TL) of the targeted fish was measured from the tip of the anterior part of the mouth to the fringe of caudal fin. The SL was measured from the anterior part of the mouth to the caudal peduncle (Figure 3.4).

c) Age Determination from Scales

Five scales (from above the lateral line) were removed from each identified target Tilapiine specimen using forceps. The extracted scales were placed on a clean microscope slide. A second microscope slide was glued over the scales using clear adhesive tape. This was done to prevent scales from curling up as they dried up. The slides were then labelled by species, total length (TL), sex, date sampling site and then stored dry in readiness for annuli reading. (Appendix A, Data Sheet l)

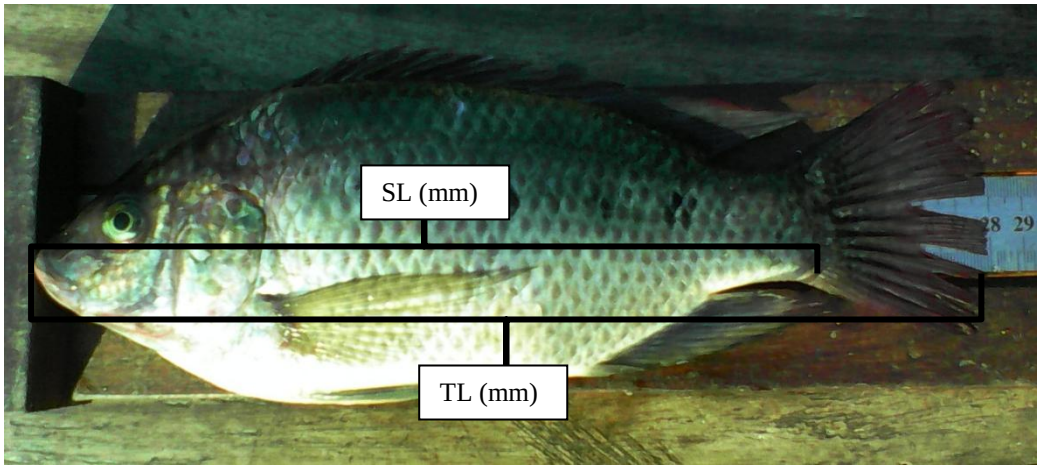

Figure 3.4 Determination of total length (TL) and standard length (SL) using measuring-board.

3.4.3 Reproductive Biology

a) Fecundity

The Tilapiine fish specimens were dissected using a mounted scalpel by making a longitudinal slit from the cloaca to the region below the pelvic fins; respective sexes were then determined on the basis of morphological appearance (by macroscopic examination) of the gonads. Classifications of the fish gonad maturity stages followed Nikolsky (1963), *see* Table 3.2. Stages of maturity of gonads were determined by macroscopic observations in both females and males. Ripe and/ or ripe-running gonads from only female specimens were weighed (g) and fixed in 5% formalin, and stored in labelled vials for fecundity and oocyte size analysis. Both ovi-sacs were stored. The choice of formalin as a preservative was because of the advantages that it has over mercurial Gilson's fluid: lower shrinkages rates varying between 0 and 7% (Hiemstra, 1962, Hislop and Bell, 1987); relative ease of handling (Hunter *et al*., 1985); ability to preserve hydrated oocytes over long periods of time, as well as having short fixation period. The main constraint in the use of formalin was the solidifying of the ovarian tissues; a process that makes enumeration tedious.

Table 3.2 Gonad maturity stages, codes and descriptions in female Tilapiine fish (Nikolsky, 1963)

Maturity state of Gonads	**Code**	**Description**
Immature	I (I)	Young individuals not yet engaged in sexual activity; gonads are small and may present with difficulty in distinguishing the sexes
Inactive	Q(II)	Sexual products still undeveloped; gonads still small sized; Oocytes not distinct
Active	A (III)	Oocytes distinguishable; gonads rapidly attain greater weight and size; testes assume a pale rose colour from transparent appearance
Ripe	R (IV)	Sexual products ripe; gonads have attained maximum weight
Ripe-running	K (V)	Oocytes and milt released easily from genital aperture by application of gentle pressure over the belly
Spent	S (VI)	Sexual products have been discharged: genitalia appears inflamed, flaccid with residual oocytes, and sperm

To prevent entire ovaries from becoming solid masses, ovarian tissue was slit longitudinally before storage. The storage vials containing the ovaries were vigorously shaken in the preservative during the subsequent days to ensure maximum release and separation of oocytes from the ovarian tissue.

b) Oocyte size

The diameters of oocytes collected from respective Tilapiine fish species were determined using an Axiom® BM-100 compound microscope set at x150 magnification with transmitted light, on an objective micrometer (100x0.01=1mm). The sampling procedure assumed that the number of oocytes measured provides acceptably precise estimates of oocyte diameters (Lau and DeMartini, 1994). A gonadsomatic index (GSI) ≥ 0.15 was set as criterion for sampling females during oocyte size-determination. A total of 10 oocytes were sampled from ovaries of at least 10 females of each species that satisfied the GSI condition (Appendix C, Data Sheet 3).

c) Condition Factor (k)

Condition factor of fish is an expression of relative fatness. Condition indices provide a useful assessment of the plumpness and physiological well-being of fishes. The target species hauled in from the researcher's gillnets and those from fishermen gear were individually weighed, W, (g) on an electronic balance and related to their respective TL (mm).

d) Size at Maturity

Target fish species were analysed for sexual maturity using Nikolsky (1963) taking note of specimens that were in the active, ripe, ripe-running or spent stages. These observations were associated with respective TL for respective species. The Classical method used to estimate size-at-first-maturity was based on fitting a logistic function and calculating the size class where randomly chosen individuals had 50% chance of being mature (Somerton, 1980).

3.5 Data Analysis

The data were variously analysed using the following Statistical Software packages: Pasgear Ver. II, SPSS Ver. 16, Statistix Ver. 9 and MS-Excel 2007- (Data Analysis ToolPak). Significance in observations was judged at α=0.05.

3.5.1 Relative Abundance

This analysis gave total catch composition with respect to numbers, weights (kg), as well as frequency of occurrence (*i.e.* whether the species was present or not, irrespective of the abundance). Each of these values was also expressed as percentage of total catch.

A measure of relative abundance or commonness of each species (*i*) in the catch composition was therefore expressed as Index of Relative Importance (% IRI) (Kolding, 1989) as:

$$\%IRI = \frac{(\%W_i + \%N_i).\%F_i}{\sum_{j=1}^{S}(\%W_j + \%N_j).\%F_j} \text{X } 100$$

Where $\%W_i$ and $\%N_i$ is the percentage weight and percentage number of each species of total catch, respectively and $\%F_i$ is the percentage frequency of occurrence of each species (Pinkas *et al*. 1971; Caddy and Sharp, 1986).

3.5.2 Growth

a) Growth Rates

These were determined by measuring the morphometric parameters, that is: standard length (SL) and total length (TL). Graphical representations were made by plotting TL (mm), against age (years) to indicate growth rates *per* target species from which asymptotic length (L_∞), and growth coefficient (K) were derived as determined by the Von Bertalanffy Growth function (VBGF) (von Bertalanffy, 1938; Sparre and Venema, 1998).

Analyses were performed using the Ford (1933) and Walford (1946), (combined as the Ford-Walford methods) to estimate the asymptotic length (L_∞) and growth coefficient (K). The VBGF written in the form below was used:

$$L_{t+1} = L_\infty (1- e^{-K}) + e^{-K}L_t$$

Where: L_t and L_{t+1} are fish lengths at age t and t+1 respectively. From this equation, L_∞ was estimated by linear regression between L_t and L_{t+1} as:

$L_\infty = a / 1-b$ and $K = -\log_e b$

Since K and L_∞ are constants, **a** and **b** were also treated as constants at constant time, ***t***.

b) Age

Determination of age was performed by back-calculations based on the linear regression model (Lee, 1920) which assumed that fish TL is directly proportional to scale radius and number of cumulated annuli (Dahl, 1909). Scales from the specimens were read using a dissecting microscope. Scale radii at time of annulus formation (S_i) followed:

First annulus (age one): $S_1=S_a$

Second annuli (age two): $S_2=S_a+S_b$

n^{th} annuli (age *n*): $Sn=S_a+S_b+...S_n$

c) Length-Weight Relationship

Length-weight relationships are a cornerstone of fisheries research and management (Anderson and Neumann, 1996) because they find wide application in assessing body condition and estimating biomass (Froese, 2006). The relationship between length and weight was described by the power function:

$$W= aL^b$$

Where W is total weight (g) and L is the total length (mm). The parameters *a* and *b* were estimated by linear regression of logarithmic transformed length-weight data:

$$\text{Log}_{10}(W) = \text{Log}_{10}(a) + b.\ \text{Log}_{10}(L),$$

Where $\text{Log}_{10}(a)$ is the y-axis intercept and b is the slope.

d) Condition Factor

The traditional approach to the assessment of condition involved the use of Fulton-type condition factors, *k*, calculated as:

$$k = \left(\frac{W}{TL^3}\right).100{,}000$$

Where W (g) is total weight and TL (cm) is total length. Analyses of Variance (ANOVA) were used to test significance of observed averages ($\bar{x} \pm$ SE)

e) Growth Performance Index

Growth performance (Φ') was estimated using the empirical equation (Pauly and Munro, 1984) for each of the target species as follows:

$$\Phi' = \log_{10}(K) + 2\log_{10}(L_\infty)$$

Where: K and L_∞ are the Von Bertalanffy's Growth parameters. The observations made were analysed by ANOVA to determine any significant differences among growth performance indices for the target Tilapiine species.

3.5.3 Reproductive Biology

Reproductive biology was determined from fecundity, oocytes sizes, length at maturity and Gonad-Somatic index (GSI). Determination of GSI, however, was primarily for purpose of establishing the criterion for sampling of oocytes to be included in measurements of [oocyte] size and weight.

a) Fecundity

Fecundity was estimated as the number of oocytes belonging to the size class of the greatest dimension (i.e all specimens in immediate pre-spawning (IV) stage). This was the basis of comparing variability in the fecundity of the respective species during the study period. Enumeration of oocytes followed the gravimetric method (Gaikwad *et al*., 2009; Hunter and Goldberg, 1980); the sampled gonad weight (SGW) of enumerated oocytes (x_1) were extrapolated to total gonad weight (TGW) in order to approximate the absolute fecundity (x_2) for each selected female target Tilapiine species:

$$x_2 = \frac{TGW(mg).x_1}{SGW(mg)}$$

Ten sampling replications were carried on each ovary *per* target female Tilapiine specimen (at stage IV) of sexual maturity. One-way ANOVA was used in ascertaining statistical significance in the observed average fecundities ($\bar{x} \pm 95\%$ CI).

Figure 3.5 Weighing whole ovaries on digital scale

b) Oocyte size

Observed oocyte length (*l*) and width (*w*) (mm) were subjected to ANOVA, testing for any significant statistical differences among oocytes from each species.

Due to the non-spherical shape of the oocytes observed in all species, an effective diameter (d_e) was calculated as:

$$d_e = w^2 . \sqrt[3]{l}.$$

Where *w*= oocyte width (mm), *l*= oocyte length (mm).

The effective diameter is essentially the diameter an oocyte would have if its contents were re-shaped into a perfect sphere (Coleman and Galvani, 1998).

c) Gonad-Somatic Index

Gonad somatic indices were calculated for each female of the Tilapiine species, as follows:

$$GSI = \frac{TGW(g)}{TBW(g)} \text{X100}$$

Where TGW is the total gonad weight and TBW is the total body weight (Figure 3.5).

d) Size at Maturity

Length data was resolved into 10 mm intervals, determined by the smallest observed size of sexually active males and females, for all the target Tilapiine species. The cumulative frequencies were calculated as percentages and plotted against TL (mid-points from ascertained length classes).The size at maturity (L_{50}) was extrapolated from the logistic model of the form:

$$P_{50} = P_{max} / (a+e^{-(b-c.TL)})$$

P_{max} = is the asymptote (assumed to be 1,) a = constant (steepness parameter), b= Total Length corresponding to 50% of $P_{max,}$ c= steepness parameter, TL= i^{th} Total Length class considered. Models were plotted using MS-Excel, comparing maturity of each species by sex.

CHAPTER 4: RESULTS

4.1 Abundance and Distribution

4.1.1 Abundance

Review of average production figures from Catch Assessment Survey (CAS) data for the years 2011 to 2015 indicated that *Oreochromis niloticus* had the largest average contribution at 80.54% (5, 478.27 metric tonnes) of the species production at Lake Kariba.*Tilapia* species accounted for 13.15% (1,202.83 metric tonnes) of production during the period. The production figures showed significant differences ($p< 0.05$) with regard to categorised species and also in production years (2011-2015), *see* Table 4.1 and Table 4.2.

Table 4.1 Percentage Production for Tilapiines at the four strata of Lake Kariba (2011-2015)

	Percentage Production (%)			
	Tilapia spp.	***Orechromis spp***	***O.niloticus***	**Other Cichlids**
2011	6.89	1.54	89.19	2.38
2012	13.66	6.04	79.48	0.82
2013	22.63	7.83	64.77	4.78
2014	18.94	5.38	74.79	0.90
2015	3.65	1.47	94.48	0.41

The general observation from the review of CAS data (2011-2015) was the preponderance of *O. niloticus* over other Cichlids (including *Oreochromis*, *Tilapia* and *Sargochromis* species), from 2011 to 2015 (Figure 4.1).

Table 4.2 ANOVA: Comparison of production for Tilapiines at Lake Kariba (Stratum I, II, III and IV) for the period 2011-2015

Source of Variation	***SS***	***df***	***MS***	***F***	***P-value***	***F crit***
Production yrs	34929753.06	4	8732438	3.400175	0.044416	3.259167
Species	91635662.08	3	30545221	11.89348	0.00066	3.490295
Error	30818780.26	12	2568232			
Total	157384195.4	19				

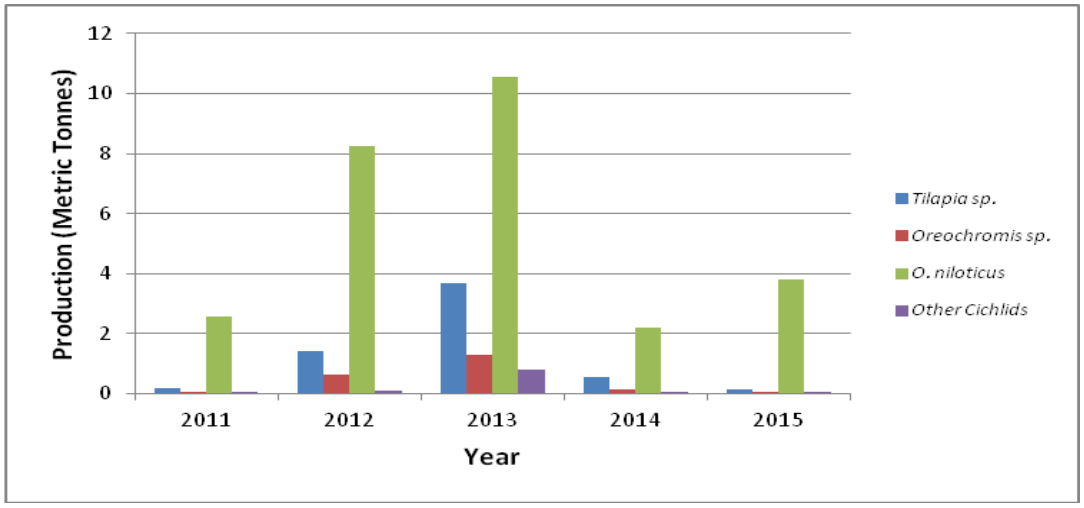

Figure 4.1 Average Annual Tilapiine productions from Lake Kariba (2011-2015).

Abundance attributed to *O. niloticus* seemingly distorted the regression of abundance on Intrinsic growth rate (K) for the Tilapiines. In order to verify the observation, outlier analyses were performed on the data, where outlier was described as:

$$x > Q_3 + 1.5(IQR) \text{ or } x < Q_1 - 1.5(IQR).$$

x= observed variable; Q_1 = first quartile; Q_3= third quartile; IQR= inter-quartile range.

Abundance values greater than 334.25 and those less than -181.75 were determined as outliers, and thus excluded from the analyses as shown in Figure 4.2.

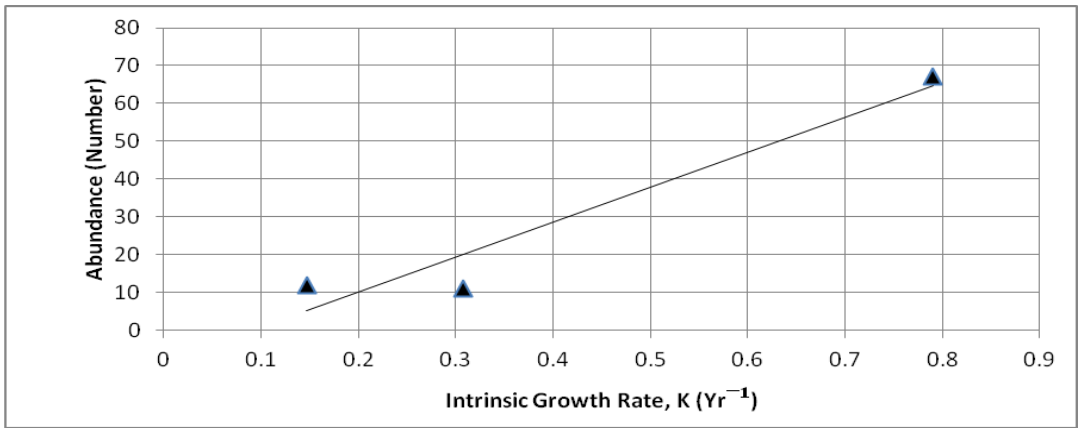

Figure 4.2 Relationship between intrinsic growth rate, K and abundance of Tilapiines at Lake Kariba. A positive relationship defined by: Abundance=92.49K-8.39; R^2=0.94.

Even though there was strongly positive correlation observed between Tilapiine abundance and intrinsic growth rate (K), (R^2 =0.94), there was no statistical significance in the observations (p>0.05), (Abundance = 92.49K-8.39; p=0.164).

Detailed contribution by number and weight of Tilapiines, and other species encountered during the study at Lake Kariba, Sinazongwe have been presented as Indices of Relative Importance (%IRI) in Figure 4.4. It was observed that the contribution in terms of weight (Kg) and numbers (N), *Oreochromis niloticus* was third in significance only to *Synodontis zambezensis*, and slightly higher than *Hydrocynus vittatus* in numbers. *Tilapia rendalli* had the second largest contribution among the Tilapiines in terms of weight and numbers (%IRI =0.77), followed by *O. mortimeri* with %IRI= 0.08 whereas *O. andersonii* had the least, %IRI=0.02.

Figure 4.3 Fish catch comprising exclusively of *Oreochromis niloticus* from seine netting at Sikalamba river estuary, Lake Kariba in Sinazongwe.

In terms of frequency of occurrence, *O. niloticus* was encountered at 45.6%, whereas *T. rendalli* accounted for 25.0 %. Occurrences of *O. mortimeri* and *O. andersonii* were 11.8% and 5.9% respectively (*see* Appendix D). During the study, encountering fish-landings comprising solely of *O. niloticus* was common (Figure 4.3); the catch indicated *here* was obtained from beach-seining activity at Sikalamba river estuary (Figure 4.7).

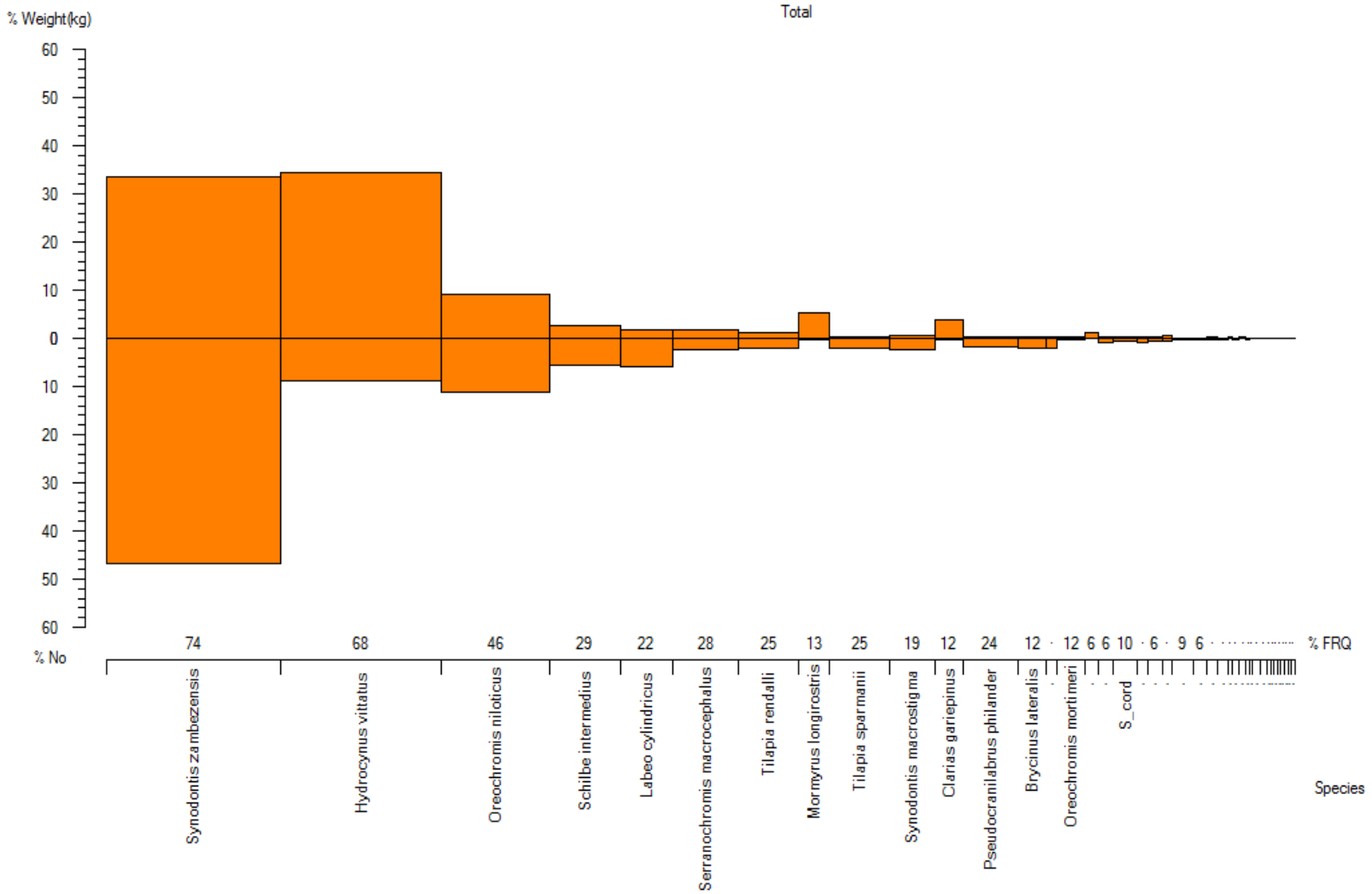

Figure 4.4 Indices of relative importance for Tilapiines, and other species encountered at Lake Kariba, Sinazongwe

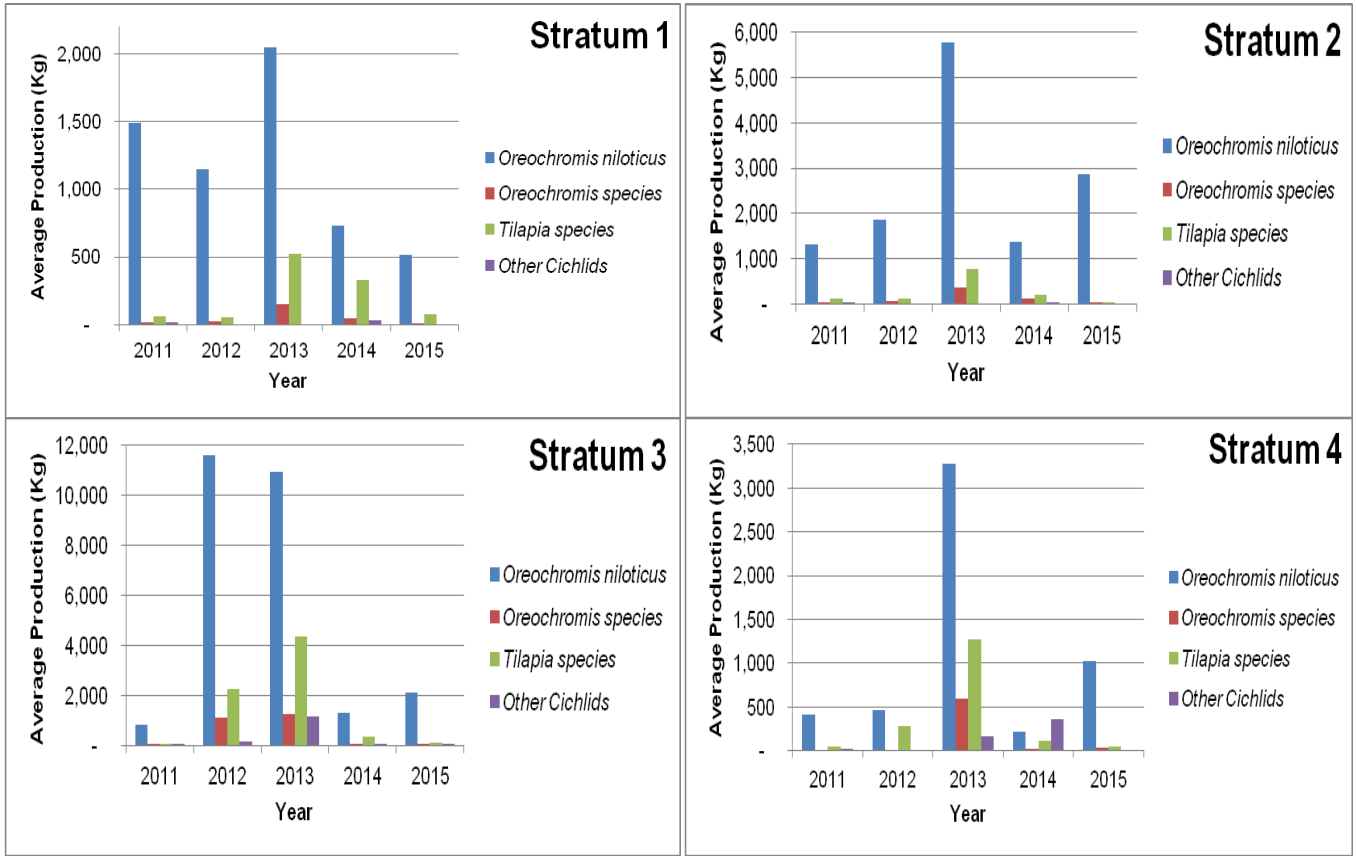

Figure 4.5 Relative Abundances of Tilapiines in Stratum 1, 2 (Sinazongwe District), 3 (Chipepo/Gwembe District) and 4 (Siavonga District) of Lake Kariba from year 2011-2015.

4.1.2 Distribution

Compilation of annual Tilapiine production, collated from CAS data of 2011 to 2015 at each of the four (04) strata of Lake Kariba was done, and it was observed that *O. niloticus* had presence and preponderance in every stratum (Figure 4.5). Comperative analyses of the average species catches within the four strata indicated that there were no significant differences among the locations (p>0.05) [ANOVA: $F_{(3,12)}$; p= 0.40].

4.2 Growth

4.2.1 Length-Weight Relationship

The length-weight relationships observed in the four target Tilapiine species showed minor variations around the isometric reference point of b=3, and also among the Tilapiine species. The greatest growth exponent was observed in *O. andersonii* (b=3.33; R^2 =0.788). *T. rendalli* had growth exponent of 3.24 (R^2 =0.914). *O. niloticus* and *O. mortimeri* had b-values of 3.03 (R^2 =0.874) and 2.92 (R^2 =0.911), respectively (Figure 4.6).

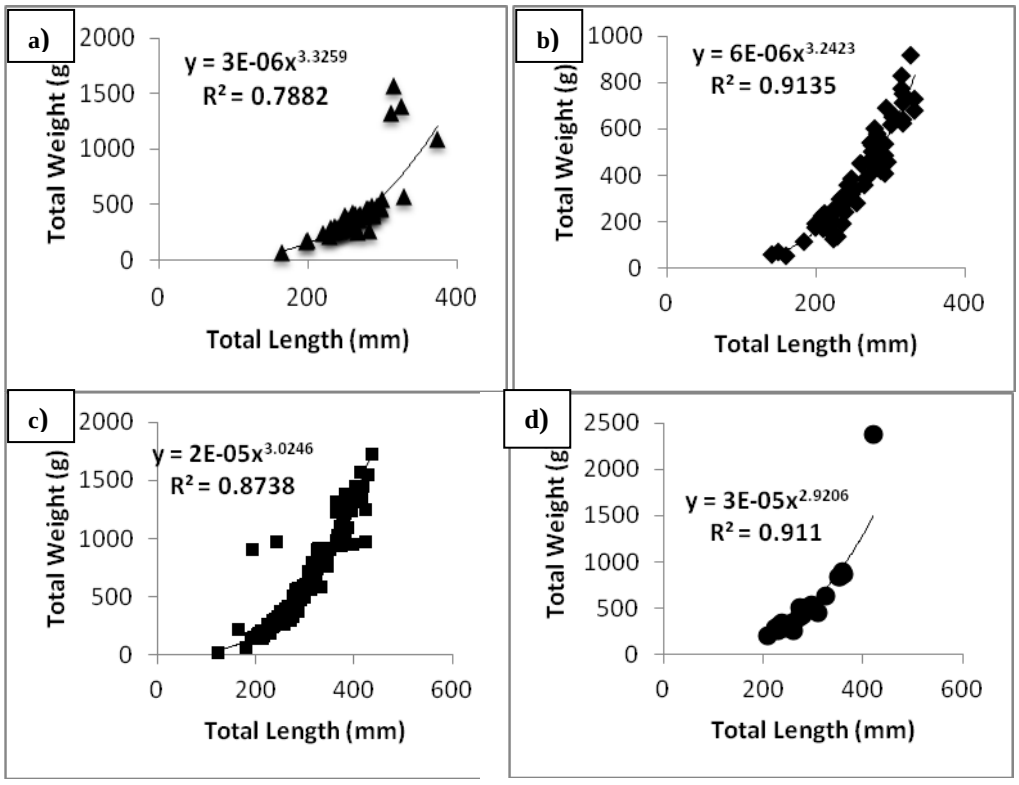

Figure 4.6 Length-Weight relationships for *T. rendalli* (a), *O. niloticus* (b), *O. andersonii* (c) and *O.mortimeri* (d).

Figure 4.7 Fishermen seine netting at Sikalamba river estuary

The Von Bertalanffy Growth Function (VBGF) curves summarised in Figure 4.8 indicate that *T. rendalli* had the fastest growth rate with a growth coefficient (K) of 0.7905. Among the *Oreochromis* species, *O. mortimeri* grew faster (K= 0.3077), than *O. niloticus* (K= 0.1798), and *O. andersonii* (K= 0.1468).

It was observed, however, that the greatest attainable length (L_∞) occurred in *O. niloticus* (458.0 mm). *Oreochromis andersonii* had L_∞ = 393.68 mm whereas *T.rendalli* had L_∞= 350.52mm. Lowest maximum attainable length among the studied Tilapiine species was seen in *O. mortimeri* (L_∞ = 347.37mm). Table 4.3 summarises the VBGF parameters, including growth performance indices (Φ') whilst Table 4.4 presents mathematical growth models for the studied species.

Table 4.3 Von Bertalanffy Growth Function parameters for Tilapiines at Lake Kariba, Sinazongwe

Species	**t_0**	**K (yr^{-1})**	**L_∞ (mm)**	***Φ′***
Oreochromis andersonii	-3.1366	0.1468	393.68	4.36
Oreochromis mortimeri	-0.5611	0.3077	347.37	4.57
Oreochromis niloticus	-3.0023	0.1798	458.0	4.58
Tilapia rendalli	-1.0470	0.7905	350.52	4.98

t_0 =Theoretical age of fish at length zero ; K(yr^{-1})= Intrinsic Growth Rate per year;
L_∞(mm)= Asymptotic Length in milimeters; *Φ′*= Growth Performance Index

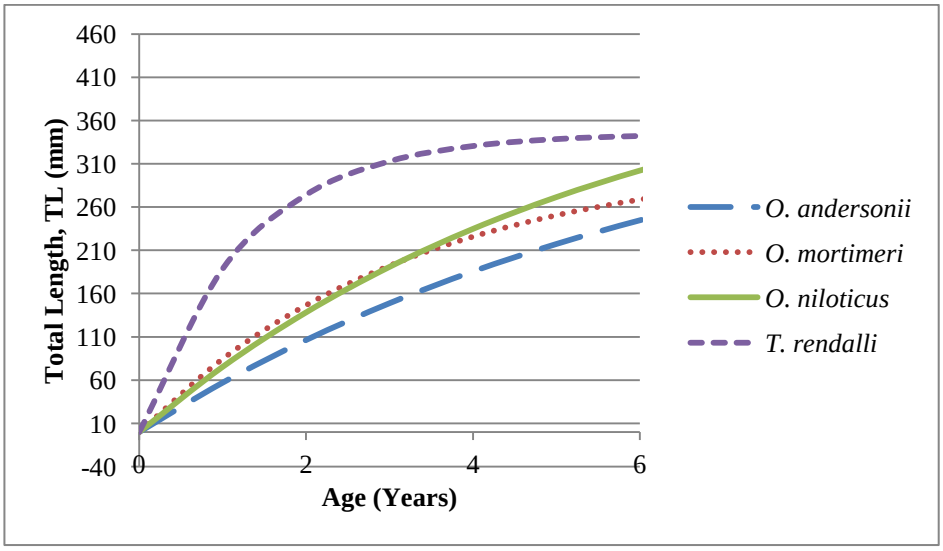

Figure 4.8 Growth curves for target Tilapiines at Lake Kariba, Sinazongwe.

Table 4.4 Summary of Von Bertalanffy Growth Functions for Tilapiines at Lake Kariba, Sinazongwe

Species	**Von Bertalanffy Growth Function**	***R^2***
O. andersonii	$L_t=393.68(1-e^{(-0.147(t+3.137))})$	0.31
O. mortimeri	$L_t=347.37(1-e^{(-0.308(t+0.561))})$	0.62
O. niloticus	$L_t=458.00(1-e^{(-0.180(t+3.002))})$	0.80
T. rendalli	$L_t=350.52(1-e^{(-0.791(t+1.047))})$	0.85

The average TL (±SE) was greatest in *O. niloticus*, followed by *O. andersonii*, *T. rendalli* and least in *O. mortimeri* (Figure 4.9).

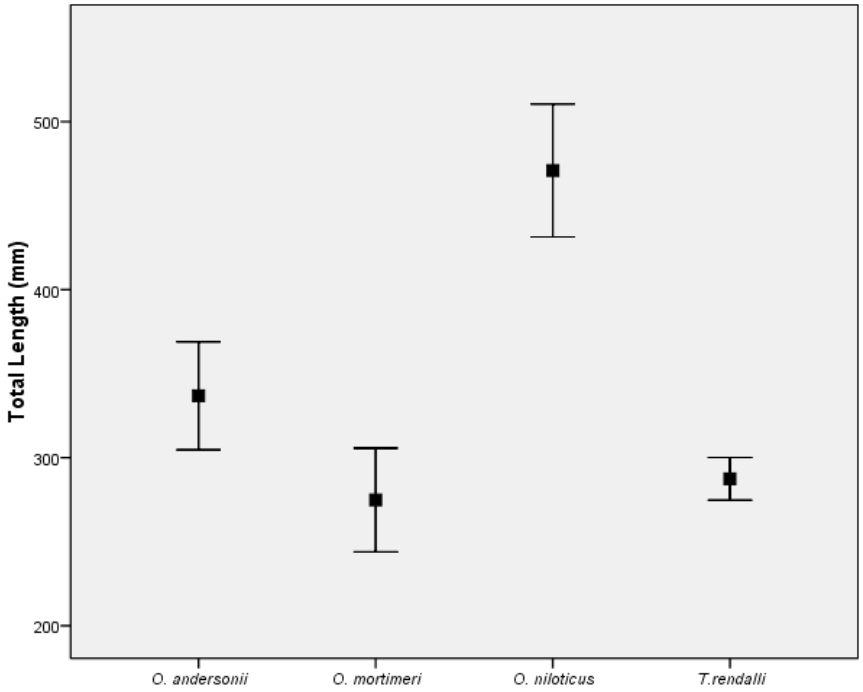

Figure 4.9 Total Lengths for the Tilapiine species at Lake Kariba, Sinazongwe.

4.2.2 Age

Tilapiine fish sampled ranged in age from two years to six years. The oldest fish (≈6 years) were encountered among *O. niloticus*, *T. rendalli* and *O. mortimeri*. The youngest and oldest samples for *O. andersonii* species were two and five years old, respectively.

4.2.3 Growth Performance

The growth performance indices (Φ') for the species summarised in Table 4.3 show the highest being *T. rendalli* (4.98) followed by *O. niloticus* (4.58). The Growth performance in *O.mortimeri* and *O. andersonii* were 4.57 and 4.36 respectively.

4.2.4 Condition factor

There were no significant differences in the mean condition factors observed (p>0.05) among the females of the Tilapiine species [ANOVA: $F_{(3,268)}$= 0.06; p=0.980], (Table 4.5). The highest condition factor was observed in *O. andersonii* (2.191±0.182). The lowest condition factor was noted in *O. mortimeri* (2.108±0.166). *Oreochromis niloticus* and *T. rendalli* had moderate condition factor values of 2.167±0.065 and 2.138±0.097, respectively.

Table 4.5 ANOVA: Condition Factor (k) observed among studied Tilapiines at Lake Kariba, Sinazongwe

Source of Variation	*SS*	*df*	*MS*	*F*	*P-value*	*F crit*
Between Species	0.120977	3	0.040326	0.0608304	0.980322	2.638285585
Within Species	177.6625	268	0.66292			
Total	177.7835	271				

4.3 Reproduction

The maturity stages for female Tilapiines, shown in Figure 4.10, revealed similarities in the proportions that were ripe and ripe running. However, more sexually immature females were observed among *O. andersonii* than in other species.

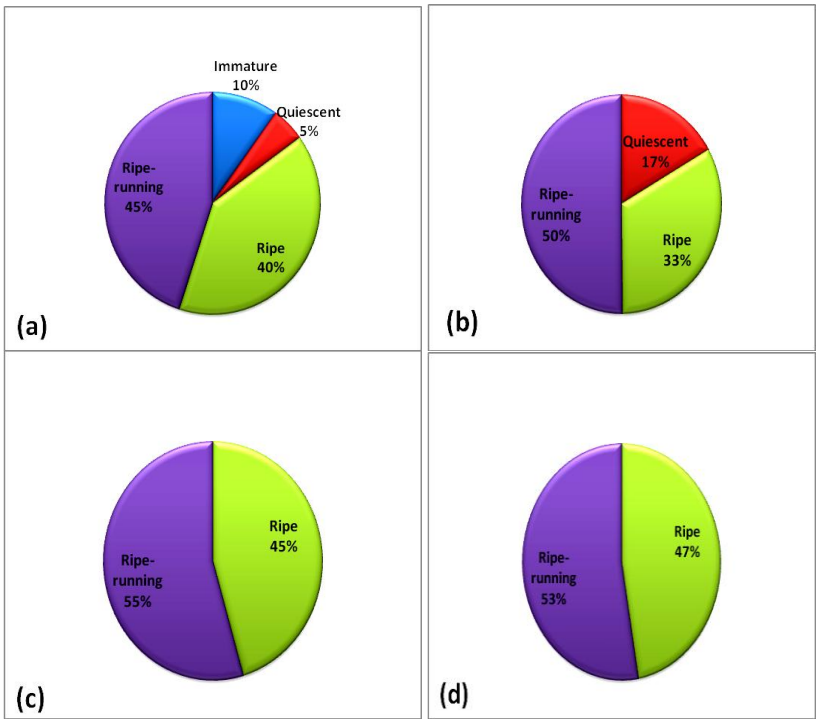

Figure 4.10 Observed sexual maturity stages in studied Tilapiines: (a) *O. andersonii*, (b) *O. mortimeri*, (c) *O. niloticus* and (d) *T.rendalli*.

4.3.1 Fecundity

There were wide variations observed in the number of oocytes borne by the sexually active/ ripe females. *Oreochromis andersonii* had an average of 1,650 oocytes, ranging from 934-3,062 oocytes. An average of 2,923 oocytes was observed in

Oreochromis niloticus, ranging between 1,306-3,455 oocytes. The highest fecundity was noticed in *Tilapia rendalli* averaging 5,135 oocytes (3,828-6,941 oocytes). The lowest average fecundity was observed in *O. mortimeri*, 994 oocytes ranging in number from 807-1,205 oocytes (Figure 4.11).

Statistical analyses revealed significant differences in the average fecundities of the various Tilapiines ($p<0.05$), [ANOVA: $F_{(3,20)}=22.81$; $p=0.000$], (Table 4.6). Application of *post hoc* Bonferroni All-Pairwise Comparison Test indicated that average fecundity for *T. rendalli* (5,135 ±1,222.9 oocytes) and *O. niloticus* (2,922 ±787 oocytes), *O. mortimerii* (993 ±200.14 oocytes) were markedly different and dissimilar from each other, whereas average fecundities for *O. andersonii* were intermediate (1,322 ±467.17 oocytes).

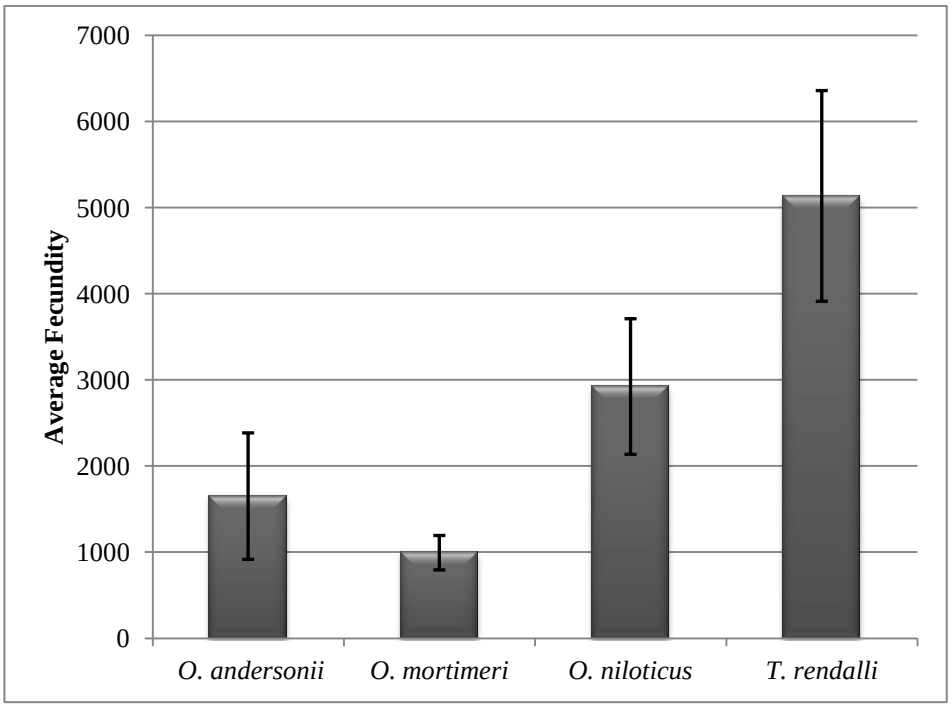

Figure 4.11 Average fecundities (±95% CI) for studied Tilapiines at Lake Kariba, Sinazongwe.

Table 4.6 ANOVA: Comparisons of fecundity among studied Tilapiines from Lake Kariba, Sinazongwe

Source of Variation	*SS*	*df*	*MS*	*F*	*P-value*	*F crit*
Between Species	51780600.31	3	17260200.1	22.81	1.15E-06	3.098391
Within Species	15131193.52	20	756559.6762			
Total	66911793.83	23				

4.3.2 Mean Oocyte weight

The observations from the gravimetric determination of fecundity allowed for further approximation of the average weight of individual oocytes *per* target Tilapiine species. The highest oocyte weight was observed in *O. mortimerii* (17.08mg) with an average of 9.16mg. Oocytes from *O. niloticus* had a lower average weight of 6.83mg, whilst the lowest was observed in *T. rendalli* (1.67mg). Statistical analyses revealed significant differences (p<0.05), [ANOVA: $F_{(3,249)} = 48.02$; p=0.000], in the average weight of oocytes among the Tilapiines studied, *see* Table 4.7, Table 4.8 and Figure 4.12. Three homogeneous averages were discerned from *post hoc* Bonferroni All-Pairwise comparison test; *O. mortimerii* (9.16 ±5.08mg) and *T.rendalli* (1.67 ±0.35mg) were different from each other whilst *O. andersonii* and *O. niloticus* showed homogeneity (6.46 ±3.84mg).

Table 4.7 Average oocyte weight (± SE) among Tilapiines at Lake Kariba, Sinazongwe.

	O. andersonii	*O.mortimeri*	*O. niloticus*	*T. rendalli*
Average Weight (±S.E)	6.09±0.41	9.16±0.67	6.83±0.38	1.67±0.38
Max. Weight (mg)	12.44	17.08	16.67	3.78
Min. Weight (mg)	0.01	1.00	0.05	1.04

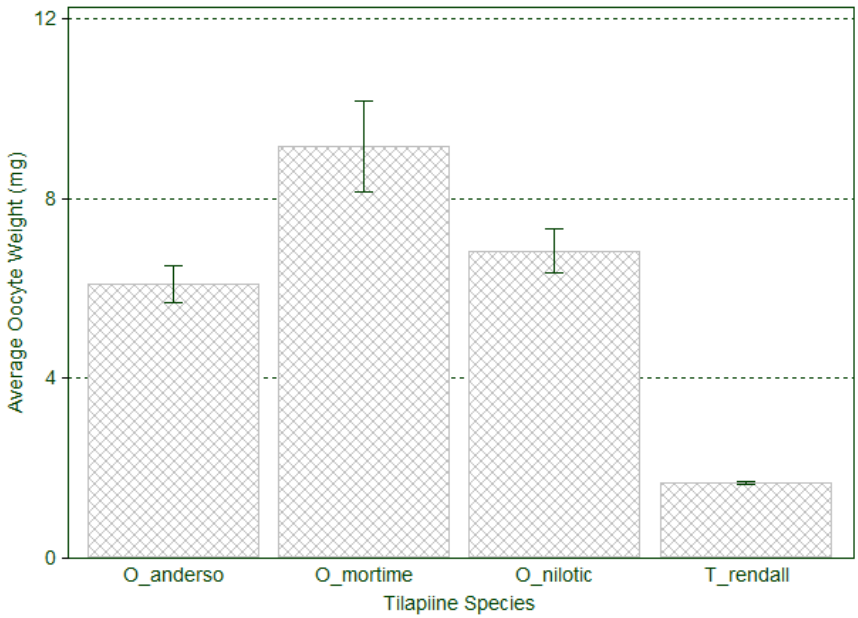

Figure 4.12 Average oocyte weights (±SE) for Tilapines at Lake Kariba, Sinazongwe

Key :O_anderso= *O. andersonii*, O_mortime= *O. mortimeri*, O_nilotic= *O. niloticus*, T_rendall= *T. rendalli*

Table 4.8 ANOVA: Comparison of oocyte weight among Tilapiines at Lake Kariba, Sinazongwe

Source of Variation	***SS***	***df***	***MS***	***F***	***P-value***	***F crit***
Between Species	1650.156	3	550.0522	48.02818	0.00000	2.640854
Within Species	2851.722	249	11.4527			
Total	4501.878	252				

4.3.3 Gonadsomatic Indice (GSI)

The GSI was calculated for all the Tilapiines during the sampling period. There were no significant differences observed in the average GSI for the studied Tilapiine species ($p>0.05$), [$F_{(3,111)} = 2.47$; $p=0.065$], (Table 4.9).

The calculation of mean GSI during this study was cardinal in determining the range of ovaries and oocytes for inclusion in measurements of oocyte length and width. It was decided, therefore, that only oocytes from specimens with GSI ≥ 0.212 (±0.062) be included in analyses. The observed variations in GSI are reflected in Figure 4.13.

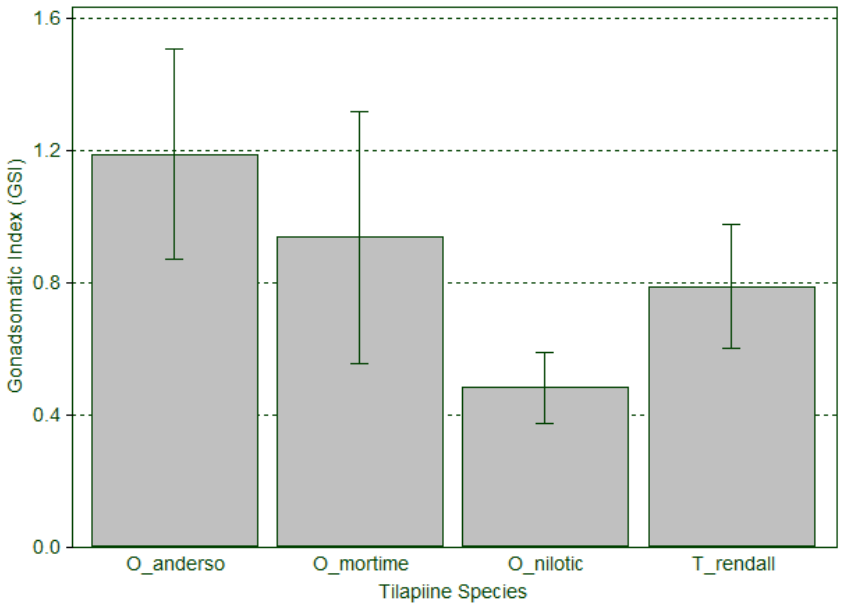

Figure 4.13 Average gonad-somatic indices (GSI) (±SE) for Tilapiines at Lake Kariba, Sinazongwe (Key: O_anderso= *O. andersonii*, O_mortime= *O. mortimeri*, O_nilotic= *O. niloticus*, T_rendall= *T. rendalli*)

Table 4.9 ANOVA: Comparison of GSI among Tilapiines at Lake Kariba, Sinazongwe.

Source of Variation	***SS***	***df***	***MS***	***F***	***P-value***	***F crit***
Between Species	7.04135	3	2.347117	2.467851	0.065815	2.686384
Within Species	105.5696	111	0.951077			
Total	112.6109	114				

4.3.4 Average Oocyte Sizes

The Oocytes from the studied Tilapiines were observed to be more ovoid than spherical. Considerable variation in length and width of oocytes was noticed within species. Oocytes from *O. niloticus* were longer (2.85mm) than those from its congenerics; oocytes from *O. mortimeri* averaged 2.52mm, and 2.46mm in *O. andersonii* (Figure 4.14). *Tilapia rendalli's* oocytes measured 1.74mm on average. The variation in the average oocyte lengths was noted to be statistically significant (p<0.05) among the four Tilapiines species [ANOVA: $F_{(3,196)}$ =9.23; p=0.000].

Post hoc comparisons using the Bonferroni All-Pairwise comparison test indicated that mean oocyte lengths among *Oreochromis* species (2.61 ±0.44mm) were significantly different from that observed in *T. rendall* (1.74 ±2.02mm).

Oocyte widths from *Oreochromis niloticus* and *Oreochromis mortimeri* were the highest observed 2.27 and 1.94 mm, respectively. *Oreochromis andersonii* oocytes measured 1.85 mm whilst *T. rendalli* had the least wide oocytes (1.68 mm). There was high variability in the width of oocytes from *T. rendalli*, compared with those of *Oreochromis* species (Figure 4.15). The average oocyte widths showed significant difference (p<0.05), [ANOVA: $F_{(3,196)} = 29.94$; p=0.000]. *Post hoc* comparisons using the Bonferroni All-pairwise comparisons test indicated that the mean oocyte width from *O. niloticus* (2.27 ±0.38mm) was significantly different from *T. rendalli* (1.68 ±0.22mm), *O. mortimeri* (1.94 ±0.16mm), and *O. andersonii* (1.85 ±0.43mm).

Oocytes from the *Oreochromis* species depicted stronger prolate-spheroid shape than those of *T. rendalli* which tended to be less prolate. Effective diameters were observed to be similarly greatest for *O. niloticus* (7.567±0.387mm), and least for *T. rendalli* (1.531±0.056mm) as indicated in Table 4.10, with statistics summarised in Table 4.11 and Table 4.12

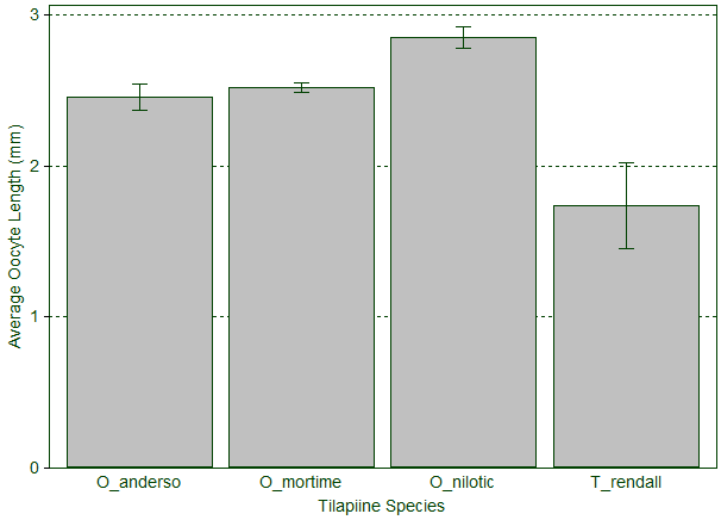

Figure 4.14 Average oocyte lengths (±SE) among Tilapiines at Lake Kariba, Sinazongwe.

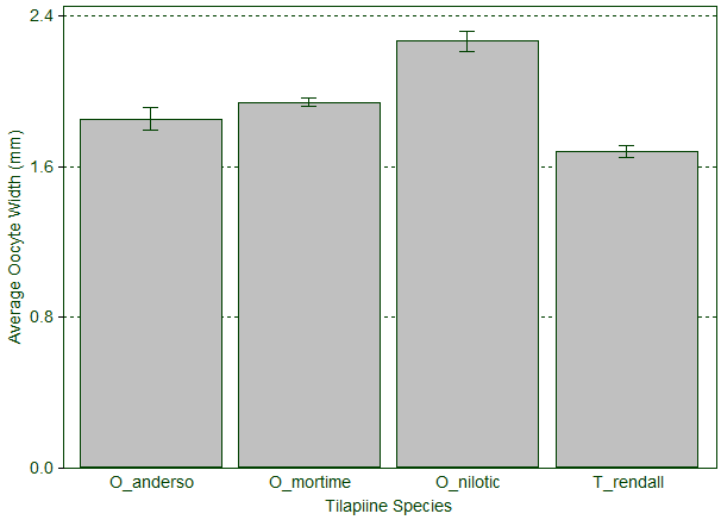

Figure 4.15 Average oocyte width (±SE) among Tilapiines at Lake Kariba, Sinazongwe. (Key :O_anderso= *O. andersonii*, O_mortime= *O. mortimeri*, O_nilotic= *O. niloticus*, T_rendall= *T. rendalli*)

Table 4.10 Average oocyte size (±SE) for Tilapiines at Lake Kariba, Sinazongwe.

	O. andersonii	*O. mortimeri*	*O. niloticus*	*T. rendalli*
Average Oocyte Length (mm)	2.458±0.009	2.518±0.003	2.850±0.720	1.736±0.003
Average Oocyte Width (mm)	1.852±0.006	1.940±0.002	2.266±0.005	1.682±0.029
Average Effective Diameter (mm)	4.994±0.327	5.163±0.130	7.567±0.387	1.531±0.056

Table 4.11 ANOVA: Comparison of Oocyte length among Tilapiines at Lake Kariba, Sinazongwe.

Source of Variation	***SS***	***df***	***MS***	***F***	***P-value***	***F crit***
Between Species	33.01615	3	11.00538	9.229394	9.7E-06	2.650677
Within Species	233.7158	196	1.192428			
Total	266.732	199				

Table 4.12 ANOVA: Comparison of oocyte width among Tilapiines at Lake Kariba, Sinazongwe.

Source of Variation	*SS*	*df*	*MS*	*F*	*P-value*	*F crit*
Between Species	9.0242	3	3.008067	29.9419	5.57E-16	2.650677
Within Species	19.6908	196	0.100463			
Total	28.715	199				

The regression analyses for average oocyte weight ($\bar{O}_{w)}$ on average effective diameter (d_e) for all Tilapiines indicated a positive Pearson correlation with no statistical significance (Figure 4.16):

$\bar{O}_w$.= 0.952.$\overline{d}_e$ +1.356; r=0.75; p>0.05, df= 1,6.

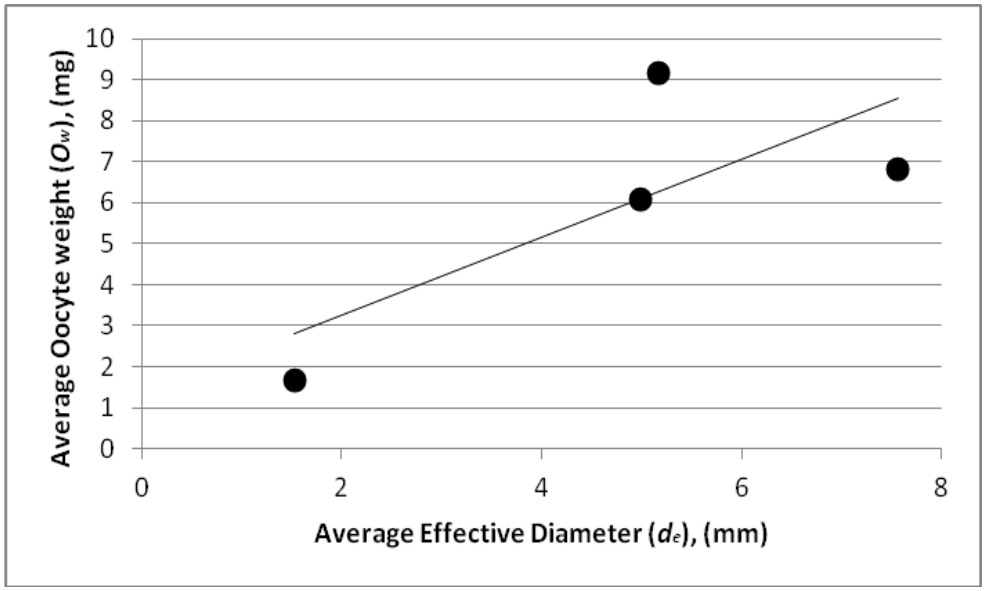

Figure 4.16: Regression of average oocyte weight on average effective diameters of Tilapiines at Lake Kariba, Sinazongwe.

4.3.5 Length-at-Maturity

The smallest sexually active female was observed in *O. mortimeri* (208mm TL) followed by that of *T. rendalli* (211mm TL). *Oreochromis niloticus* females showed an onset of sexual activity at 230mm TL whereas *O. andersonii* were first sexually active at 221mm TL. On the other hand, males of the species were observed to

generally attain sexual activity at greater TL, with the exception of *T. rendalli* (see Table 4.13).

Actual sexual maturity among female Tilapiines showed that *O. niloticus* matured at L_{50}=240.91mm TL whilst *O. andersonii* matured at a greater length L_{50}=242.17mm TL (Table 4.14). There was a remarkably close overlap observed in L_{50} among the indigenous female Tilapiines; 50% of all females from each species attained sexual maturity between 240.97-242.17mm TL. The maturity ogives for *O. andersonii*, *O. mortimeri* and *T. rendalli* in Figure 4.17 reflect the overlap, indicating similarity in the average L_{50} (242.17mm) for the (03) three species. On the other hand, the maturity ogive for female *O. niloticus* was distinct and L_{50} averaged 240.90mm.

Conversely, male *T. rendalli* matured earlier than any of the other (male) Tilapiines; *O. niloticus* L_{50} =240.90mm TL, *O. mortimeri* L_{50}=241.38mm TL, *O. andersonii* L_{50}=243.90mm TL. (*see* Figure 4.18 and Table 4.8).

Table 4.13 Smallest observed sizes (mm) exhibiting sexual activity among studied Tilapiines.

Species	**Total Length (mm) at Sexual Activity**	
	Female	**Male**
O. andersonii	221	236
O. mortimeri	208	225
O. niloticus	230	234
T. rendalli	211	209

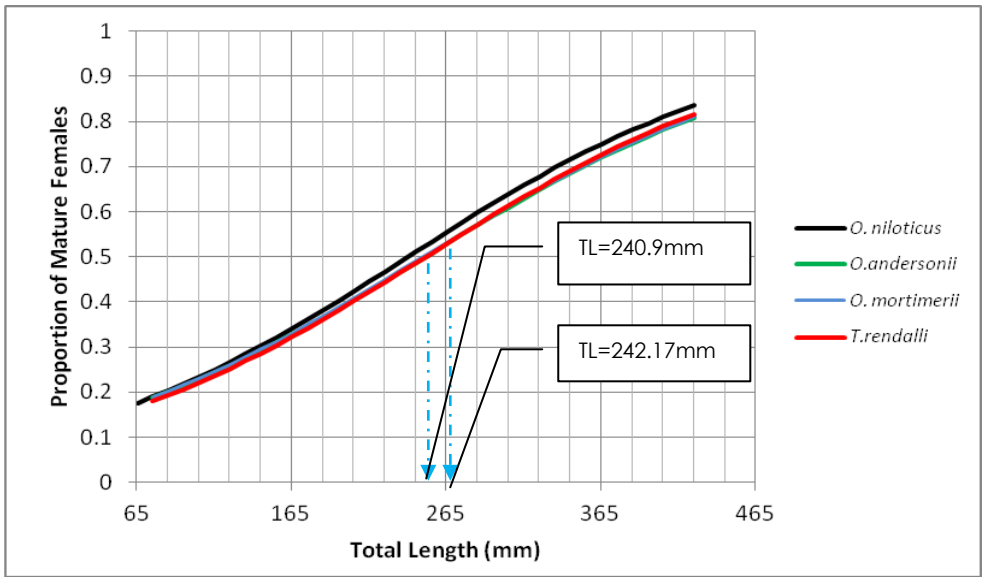

Figure 4.17: Length-at-first maturity for females of studied Tilapiine species.

Table 4.14 Length, and age-at-first maturity for female Tilapiines at Lake Kariba, Sinazongwe.

Species	**Best-fit Logistic Model**	**L_{50} (mm)**	**Corresponding Age at sexual maturity (yr)**
O. andersonii	$P = 1/(1 + e^{-(2.01-8.3X10^{-3}\ TL)})$	242.17	3.00
O. mortimeri	$P = 1/(1 + e^{-(2.00-8.3X10^{-3}TL)})$	240.97	2.73
O. niloticus	$P = 1/(1 + e^{-(2.12-8.8X10^{-3}TL)})$	240.91	1.23
T. rendalli	$P = 1/(1 + e^{-(2.08-8.6X10^{-3}TL)})$	241.86	3.01

Generally, males of the study species attained sexual maturity, L_{50}, at lower lengths averaging 239.31mm TL than females which matured at an average of 241mm TL. However, individual variation within sexes was present. The differences in L_{50} for males and for female of the same study species were marginal. An exception was observed in male *T. rendalli* which matured at lower length (231.04mm TL) than

males of the other species, as well as in comparison with females of the same (*T.rendalli*) species (by ≈10mm).

It was important however to ascribe corresponding ages to the extrapolated L_{50}. Using the sex-independent Age-Length Keys (Appendix F), age-at-sexual maturity were ascertained and ascribed for females and males respectively (Table 4.14 and Table 4.15). It was observed that larger, and/or smaller fish (in length) did not precisely infer older, and/or younger attained ages (in years). For instance, *O. niloticus* female at 240.91mm TL was much younger than similarly sized female *O. mortimeri*. On average, female Tilapiines were observed to generally mature at slightly older age than males. However, as was observed with L_{50}, individual age-variations within sexes was present. *Oreochromis niloticus* females reached sexual maturity within the first year, whereas *O. mortimeri* and *T. rendalli* females matured within year-two. *Oreochromis andersonii* females were the oldest at first sexual maturity (≈3.00 years).

Male *O.niloticus* was observed to similarly mature earlier (≈1.23 years) than males of the other Tilapiines. The sexual maturity ages for *O. andersonii* females and males showed close correspondence, and also happened to be the greatest observed among the Tilapiines (Tables 4.14 and 4.15).

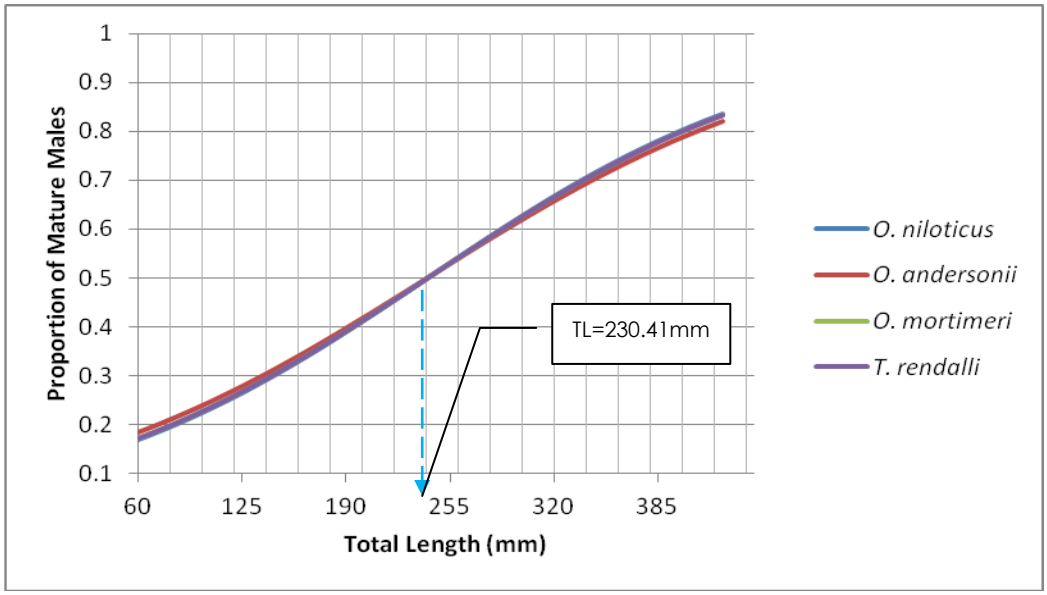

Figure 4.18 Length-at-first maturity for males of studied Tilapiine species.

Table 4.15 Length, and age-at-first maturity for male Tilapiines at Lake Kariba, Sinazongwe.

Species	**Best-fit Logistic Model**	**L_{50} (mm)**	**Corresponding Age at sexual maturity (yr)**
O. andersonii	$P = 1/(1 + e^{-(2.00-8.2X10^{-3}TL)})$	243.90	3.01
O. mortimeri	$P = 1/(1 + e^{-(2.10-8.7X10^{-3}TL)})$	241.38	2.74
O. niloticus	$P = 1/(1 + e^{-(2.12-8.8X10^{-3}TL)})$	240.90	1.23
T. rendalli	$P = 1/(1 + e^{-(2.01-8.7X10^{-3}TL)})$	231.04	2.61

CHAPTER 5: DISCUSSION

5.1 Abundance and Distribution

The general sentiment shared by fishers on Lake Kariba is that *O. niloticus* (*munyima*) has displaced indigenous Tilapiine fishes which were commonly encountered during past years. Findings from the current study indicated a lower occurrence of *O. mortimeri* with IRI = 0.1% (of all species encountered during the investigation). In 1962, *O. mortimeri* had comprised 35% of commercial catches in the Sinazongwe area (Fisheries Research Bulletin, Zambia, 1965). Balon (1973), during fish population studies in the coves of Lake Kariba, observed higher occurrences of *O. mortimeri* and *T. rendalli* at 10.0% and 3.6% respectively. *Oreochromis andersonii* was encountered at a rate of 0.9% (Van Der Lingen, 1973). By 1974, *O. mortimeri* represented 38.0% of landed catches. An extreme scarcity of juveniles from 1964 gave indication that the species was not being recruited as previously observed. Studies by Songore *et al* (1998, Unpublished) on the Zimbabwe side of the Lake encountered *O. mortimeri* at 42%.

The fluctuating abundances for *O. mortimeri* seem to indicate the species' struggle to find ecological equilibrium. Observations by Karenge (1992) indicate that *O. mortimeri* was already in stiff competition with *Serranochromis codringtonii* (as early as 1979), and the latter was even assumed to have been replacing the former in prominence at Lakeside Station, Lake Kariba, Zimbabwe. Therefore, Chifamba's (1998) hypothesis that *O. niloticus'* emergence in the mid-1990s was entirely responsible for the decline in the Kariba Tilapia falls short of mention that *O. mortimeri's* dominance was never guaranteed; *Oreochromis mortimeri* seems to have long been struggling to adapt to disturbances resulting from conversion of a riverine system into a lacustrine system. In fact, Donnelly (1971) was of the view that the reduced recruitment of *O. mortimeri* after the filling phase (1960) was a result of reducing areas of shallow water (breeding, nesting and nursery areas); effectively this meant reduction in suitable habitat for hatchlings, and an increased exposure/ susceptibility to predation from *Hydrocynus vittatus* and *Clarias gariepinus*. This notion is also shared by Weyl and Hecht (1998) whose observations on populations of *T. rendalli* and *O. mossambicus* in Lake Chicamba showed that failure of annual

drawdown and flooding phase resulted in low recruitment. What seems likely from current observations is that: extremely high and/ or extremely low water levels in Lake Kariba have not favoured breeding and recruitment of *O. mortimeri*.

Arising from the preceeding observations, two fundamental questions may be worth asking: how has the flow-regime from the major tributaries and catchment of Lake Kariba morphed over the past decades, and secondly what has been the pattern of draw-downs on the Lake? In dealing with the latter question, it can be observed from Zambia-Zimbabwe Joint Annual Report of Lake Kariba (Figure 5.1) that the pattern of drawdowns from year 1962-2000 was characterised by significant fluctuations.

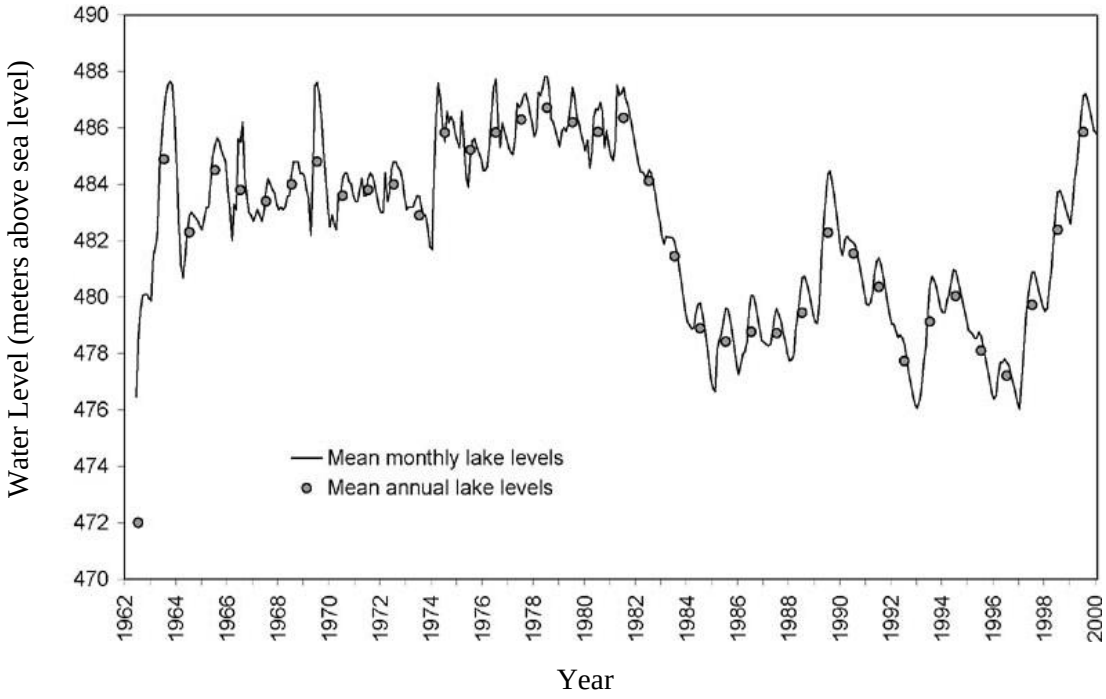

Figure 5.1 Mean annual Lake Level (m.a.s.l) in Lake Kariba (1962-2000). (Source: Zambia-Zimbabwe Joint Annual Reports).

The greatest reduction in water level before 2014-2015 drawdowns occurred between the years 1984-1999. The period was further characterised by high atmospheric temperatures, low rainfall and reduced river flows into the Lake (Ndebele-Murisa, 2011). It is plausible that during that period in the mid-1990s a greater proportion of the Lake remained more pelagic than littoral, resulting in reduced shallow areas for Tilapiine breeding and nesting. McLachlan (1970) provides further perspective by

elaborating on the importance of nutrient cycling; he notes that release of nutrients from the inundated shoreline (where animals had been trampling, grazing, defecating and urinating) is probably very significant for breeding Tilapiines during the flooding phase. That being the case, it is possible that the relatively low water levels during 1984-1990 and 1992-1998 further deprived indigenous Tilapiines of nutrients in the littoral zones of the Lake, hence depressing the population of recruits.

The reduced water volumes in the Lake may have also meant increased ease of encounter between Tilapiine fish and fishers' gears; Bernacsek's (1984) schematic summary of effects of water fluctuations seem to apply perfectly to the Lake Kariba scenario. The fishing pressure could have consequently driven down the indigenous breeding stock. Njiru *et al* (2002; 2006), have for instance attributed predominance of *O. niloticus* on Lake Victoria (Kenya) to overfishing of endemic Tilapiines. This may also be a plausible explanation for Lake Kariba where present IRI for *O. niloticus* was higher (8.6%). The fishing effort for Lake Kariba has seen an increase from 2,804 fishers in 2006 to 4,653 fishers in 2011 (Frame Survey Report for Lake Kariba, 2011); the number of gillnets also increased from 17,102 in 2006 to 27,492 in 2011 (with 97.1% of gillnets being in active use). These fisher demographics are normally conservative and under-reported due to low license compliance on the open-access Lake, but are a clear reflection of pressure piling on the artisanal fishery. The increase in fishing effort may have had the likely delayed-effect of subduing numbers for the most potent (indigenous Tilapiine) competitors to the exotic *O. niloticus*.

Marshall (1985) on the other hand, described a general pattern typical of man-made lakes where production is initially high, but soon after begins to decline. This trend was observed true by Marshall (1985) for Lake Kariba commercial gillnet fishery during his study on the population dynamics, production and potential yield of *L. miodon*. This view is shared by Moss (1988) whose conclusion was that lakes do not maintain their fertility unless an external loading of nutrients occurs continually. Based on the foregoing deductions, it is clear that the initial abundances of *O. mortimeri* were supported by the post-impoundment abundance in nutrients.

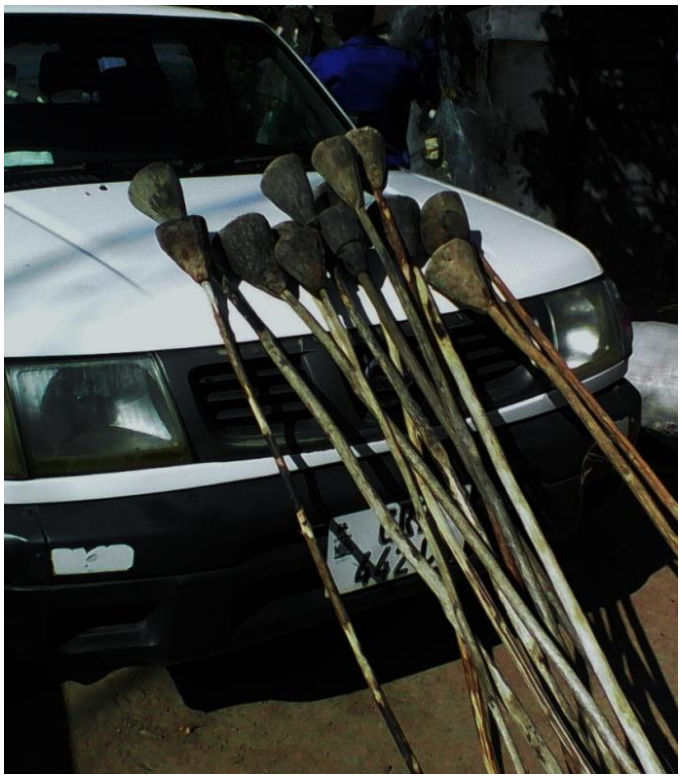

Figure 5.2 Knob-sticks used during the fish-driving practise, *kutumpula*.

Tilapia rendalli, on the other hand, has always been encountered in lower-than-actual numbers from experimental gillnets. Observations by Kenmuir (1978) indicated that spear-fishing and angling yielded greater catches, especially in areas of extensive submerged aquatic-macrophyte beds and also in areas with submerged trees where they fed off periphyton (Kenmuir, 1978). As a result of the difficulty in setting nets in such vegetated environments, fish-driving methods (*kutumpula*) using knob-sticks (*shown in* Figure 5.2) have been improvised and are preferred techniques employed for catching, especially *T. rendalli*. The underwater disturbance that results from these methods has further been suspected to scare fish into more serene *refugia* (rocky beds and submerged forests). The current study's observations on abundances of the evasive *T. rendalli* may not therefore, reflect its true abundances on Lake Kariba, Sinazongwe.

It can thus be postulated that the abundance of Tilapiines is determined by factors additional to the intrinisic growth rate, K (which explained 94% of observed variation). As intrinsic growth rate is directly related to environmental factors such as

temperature, it is justifiable to conclude that variations in environmental conditions and anthropogenic factors influence abundance of Tilapiines on Lake Kariba.

Duncan *et al* (2001), in observing aves concluded that preponderance and successful establishment of exotic species was supported by re-introductions at various locations. Whilst their study weas biased towards birds, it fits perfect logic that introductions over a geographical area having variable conditions improves the odds of atleast some of the populations surviving and successfully being established. The existence of aquaculture facilities on the Lake at Siansowa and Siavonga may also strongly support the notion of Duncan *et al* (2001) and the observed abundances of *O. niloticus* during the study.

The seemingly harmonious coexistence of *O. niloticus* and *T. rendalli* (which were the most abundant Tilapiines) may lend credence to postulations based on resource partitioning; *T. rendalli* is a proven herbivore, phytoplanktivore whereas *O. niloticus* not only has a broad phytoplankton preference but will consume planktonic detritus and epiphytic algae (Moriarty and Moriarty, 1973). This view (of coexistence) is shared by Jembe *et al* (2006) in studies on the distribution and associations of Tilapiines in the Lake Victoria catchment (Kenya). Furthermore, studies by Zaganini *et al* (2012) on the Barra Bonita reservoir where *T. rendalli* and *O. niloticus* were introduced have confirmed coexistence of the two species. The same study by Zaganini *et al* (2012) concluded that this demonstrable coexistence of the sympatric species could be attributed to morphological differences and wide plasticity in feeding preferences. It was additionally noted that ontogenic variability exists for different size classes of these two fish species. These differences are likely true for *T. rendalli* and *O. niloticus* on Lake Kariba, having both shown positive allometric growth.

In conclusion, the combination of hydrological instability, increased fishing pressure, shifting ecological equilbria may partly explain the decline in indigenous Tilapiine populations; *O. niloticus* seems better adapted at absorbing these ecological and anthropogenic shocks.

5.2 Growth

5.2.1 Length-Weight Relationship

The estimation of growth using the LWR indicated that *O. andersonii*, *O. niloticus* and *T. rendalli* became more rotund as length increased. *Oreochromis mortimeri* on the other hand, had slightly lower (near-isometric) allometric growth (b=2.92). Findings by Olurin and Aderibigbe (2006) from studies of *O. niloticus* in ponds at Ijebu-Ode, Ogun State, Nigeria were quite similar with those of the current study.

The negative allometric growth in *O. mortimeri* could be indicative of wide size variation among the collected samples of the species. The implications of this negative allometry are that: either larger fish were longer than they were rotund, or smaller sized specimens were more rotund and in better nutritional condition during the sampling period. Field observations from the current study seem to support the former view; the limitation of few samples of the species being encountered during the study makes it difficult to confidently settle for the notion, however.

The assumptions made by Sparre and Vanema (1998), that species in neighbouring fishing areas form one unit stock may not be absolutely true; this is most unlikely for fishery areas that have been subjected to unmonitored, and unregulated introductions or translocations of fish species such as Lake Kariba. Therefore, growth models premised on the assumption that growth and mortality parameters are constant throughout a distribution area may therfore fail to fully explain trends in systems exposed to species introductions and translocations.

5.2.2 Intrinsic Growth Rate, K, Asymptotic Length, L_{∞} and Growth Performance Φ'

Observations from the current study on *O. niloticus* indicated higher asymptotic length (458mm) compared with Gomez-Marquez *et al* (2007) findings in Lake Coatetelco, Mexico which revealed asymptotic length of 178.8mm with TL ranging between 90-165mm (females) and 89-148mm (males); intrinsic growth (K) was comparatively lower in the present study.The disparity in attained sizes could be explained by differences in the relative sizes of Lakes Kariba and Coatetelco, the latter being only a fraction in size (120 Ha) and depth (1.5m) compared to the

former. The size of a system and its catchement area has a large bearing on the nutrient availability (Antti, 2015 *et al*). Studies conducted by Chikopela *et al.*, (2011) at Kafue River in Zambia indicated that *O. niloticus* had an intrinsic growth rate of $0.836yr^{-1}$, and attained maximum length of 477mm, greater than in the current study. This could primarily be indicative of differences in the productivity of the two systems; river-floodplain systems have been noted to be more productive than lake systems (Junk *et al.*, 1989).

Kolding *et al* (1992) provided brief baseline data of Tilapiines on Lake Kariba (Table 5.1); the compilation was however short of *O. andersonii* which they did not encounter during their study, and of course *O. niloticus* which may have not yet been introduced/ encountered on the Lake. Comparison of present study's growth parameters observations on *O. mortimeri* with Kolding *et al*., (1992) indicated an increase in K and Φ' from 0.256 to 0.308 yr^{-1}, and 2.878 to 4.50, respectively. The asymptotic length, however, declined from 480.0 to 318.84mm during the same period. The increase in K and Φ' could be an evolutionary attempt by the species to keep pace with increasing fishing pressure and variability in the environment. The higher K ensures that the species grows faster, matures earlier and exploits a broader range of resources, compared with the stock observed by Kolding *et al*., (1992). Pauly (1979) aptly referred to K as a stress-factor indicator for how population characteristics and environmental parameters (such as high temperature, low density of feed, disease and status in some peeking order) may affect the growth performance of a fish species. Additionally, Pauly (1984) indicated strong correlation between K and length-at-maturity; meaning higher K values induce early sexual maturation of fish. The observed depensation in asymptotic length also suggests that *O. mortimeri* has been affected by over-exploitation and/ or adaption-failure. Data on growth for indigeous Tilapiines of Lake Kariba were very scanty. The restricted distribution range (endemism) of *O. mortimeri* to the Middle Zambezi, compounded with limited published studies on the species made it difficult to perform valuable comparisons.

Tilapia rendalli showed higher values of K and Φ', 0.791yr^{-1} and 4.97, respectively compared with Kolding *et al* (1992). The asymptotic length for the species was however lower (298mm) than Kolding *et al* (1992).

Table 5.1 Compilation of growth parameters for Tilapiines native to the Zambezi basin.

Species	**L_{max} (mm)**	**L_∞ (mm)**	**K (yr^{-1})**	**t_0 (year)**	**Φ'**	**b**	**Author**
O. mortimeri	480^{TL}	543(±25.8)	0.256(±0.026)	-0.351(±0.055)	2.878	2.98	Kolding *et al*, (1992); Lake Kariba
	330^{TL}	347.37	0.308	-0.5611	4.57	2.92	Present study
T. rendalli	380^{SL}	485(±12.0)	0.145(±0.005)	-0.419(±0.014)	2.533	2.89	Kolding *et al* (1992); Lake Kariba
	258^{SL}	327	0.267	-	4.46	-	Peel (2012); Kavango River
	215^{SL}	217	0.966	-	4.66	-	Peel (2012); Lake Liambezi
	216^{SL}	257	0.337	-	4.35	-	Peel (2012); Kwando River
	255^{SL}	268	0.584	-	4.62		Peel (2012); Zambezi River
	184^{SL}	188	0.636	-0.905	4.35	-	Weyl and Hecht (1998); Lake Chicamba, Mozambique
	-	470	0.78		3.24	-	Mosepele & Kolding (2003); Okavango Delta
	333^{TL}	350.52	0.791	-1.047	4.98	3.24	Present study
O. andersonii	303^{SL}	493.0	0.163	-	4.60	-	Peel (2012); Kavango River
	312^{SL}	822.3	0.005	-	5.53	-	Peel (2012); Lake Liambezi
	236^{SL}	284.0	0.329	-	4.42	-	Peel (2012); Kwando River
	332^{SL}	814.5	0.006	-	5.60	-	Peel (2012); Zambezi River
	-	530.0	1.00	-	3.45	3.42	Mosepele & Kolding (2003); Okavango Delta
	374^{TL}	393.68	0.147	-3.137	4.36	3.33	Present study

TL-Total Length; SL-Standard Length; L_{max} -Maximum observed Length; L_∞ -Asymptotic Length; K- Intrinsic Growth Rate; t_0 - Age when fish has zero length; b- regression coefficient in LWR

The preceeding explanations for these variations in *O. mortimeri* may similarly hold true for *T. rendalli*, with the greatest driver probably being resource scarcity.

Populations of *O. andersonii* and *T. rendalli* in the Upper Zambezi, Okavango, Kwando and Liambezi systems (all part of the greater Zambezi basin) were compared with those at Lake Kariba (Table 5.1); it is worth noting that Tilapiines native to Lake Kariba evolved under riverine conditions prior to inundation (Fryer and Iles, 1972; Greenwood, 1974), descending from the same Zambezian stocks. *Oreochromis andersonii* from the present study compared favourably with Kavango and Kwando River stocks in terms of growth performance (Peel, 2012). *Tilapia rendalli* on the other hand had greater growth performance on Okavango Delta (Mosepele and Kolding, (2003); Kwando River, Lake Liambezi, Kavango River (Peel, 2012) and Lake Chicamba (Weyl and Hecht (1998)). The observed variations in asymptotic lengths, K and Φ' reflects the plasticity among Tilapiines, and is driven by differences in the environments as well as in fishing practices.

5.3 Reproduction

Cichlids are typically considered as equilibrium strategists; exhibiting parental care and producing fewer but larger offspring with often associated sedentary local populations (FishBase, 2015). The degree with which these traits and strategies are manifested differs within and among cichlid species, and the case of the Tilapiines in the present study exemplifies that fact as evidenced by the wide variations in fecundity, oocyte size, oocyte weight, size and age/length-at-maturity.

5.3.1 Fecundity

The number of oocytes (absolute fecundity) for *O. niloticus* on Lake Kariba at Sinazongwe was higher than was observed at Opa Reservoir where fecundity ranged from 73-1,810 oocytes (Komolafe and Arawomo, 2002), and in Lake Naivasha, 300-2,800 oocytes (Babiker and Ibrahim, 1979). The present study's fecundity figures were equally higher than those observed by Duponchelle and Legendre (2000) on Lake Ayame where absolute fecundity ranged between 160 to 717 oocytes in *O. niloticus*; the rather low fecundity observed at Lake Ayame was attributed to abiotic factors (pollution) (Duponchelle and Legendre, 2000). It may be difficult to

confidently attribute the higher fecundity observed on Lake Kariba to lack of pollution, bearing in mind that the Lake has come under increasing anthropogenic influence. Effluent from farming and irrigation schemes, cage-aquaculture, crocodile-farms, oil and carbon discharge from mechanised *Kapenta* fishing rigs are some of the processes that may be impacting on the reproductive biology of Tilapiines. There have not been any studies relating aspects of fish biology with changes in water chemistry.

5.3.2 Oocyte Size

The oocyte sizes for *O. niloticus* from the current study were greater than those observed by Garcia-Abiado *et al.,* (1996), (1.3±0.5mm) in a Phillipines strain of Nile tilapia cultured under pond conditions. However, the present study's *O. niloticus* oocyte sizes compared favourably with those in Duponchelle *et al*., (2000) at Ayame, Lokpoho and Sambakaha Reservoirs where diameters of 2.5±0.15mm, 2.5±0.26mm and 2.4±0.18mm were observed respectively. Studies by Orlando *et al.,* (2017) were able to show that oocyte diamteres were positively correlated to diets with variable amounts of digestable energy, and ranged between 2.05-2.21mm.

Tilapia rendalli was observed to have had the smallest oocytes 1.682±0.003mm (length) /1.736±0.029mm (width) with an average fecundity of 5,135 oocytes on Lake Kariba. The average size and fecundity among all the mouth-brooding Tilapiines was 2.609 ±0.244mm (length) /2.019±0.005mm (width) and 1,856 oocytes respectively.

Oocytes are one of the most quantifiable aspects of an organism's life-history (Coleman and Galvani, 1998). Francis and Barlow (1993) have further shown that oocyte size is a key determinant in the sex of cichlids: larger oocytes mostly result in male whilst smaller oocytes often become female hatchlings. Based on those observations, it would be expected that, among the *Oreochromis* species, *O. andersonii* would have more females, than *O. mortimeri*, than *O.niloticus*. However, the benefits that might have accrued from having more females diminish due to lower fecundity, lower intrinisic growth rate and lower growth performance. Because predation and competition are most intense in nursery and breeding grounds, the hatchlings from smaller oocytes have lower chances of surviving to maturity. The

current study did not, however, attempt to observe sex ratios among the studied Tilapiines.

Due to the fact that increased fishing pressure dampens maximum attained sizes in fish exhibiting allometric growth, proportional decrease in buccal volumes results in reduced brood sizes. For mouthbrooders, there is an added challenge: the larger the oocytes, the fewer that can be contained in the buccal cavity (*quality over quantity*). This is an important trade-off which seems to ensure survival of a species, at the expense of mere numbers. In explaining the Tilapiine abundances, it can be further postulated that maternal *O. niloticus* may spend relatively shorter time offering parental care because their offspring grow faster, thus allowing for the females to resume their breeding cycle. The observations by Orlando *et al*., (2017) also suggest that *O. niloticus* (with the greatest observed oocyte sizes) could have a diet with greater amounts of digestable energy compared with the indigenous congenerics.

There was general consistency between the current study and that of Peters (1959) which showed that a given Tilapiine species will either have small oocytes in larger numbers, or larger oocytes in fewer numbers.

5.3.3 Oocyte weight

The findings from the current study compared favourably with observations made at Lake Ayame where Duponchelle and Legendre (1995, 1996) observed oocyte weights of 7.7 ±0.44mg and 7.9 ±0.9mg in a study investigating life history traits of a diminished *O. niloticus* population. Kefi *et al.,* (2009) similarly found *O. niloticus* oocyte weights of 7.26mg under controlled pond conditions.

Oocytes weights for *Oreochromis andersonii* were the least weighty among the mouthbrooding Tilapiines. Oocytes weights of *O. andersonii* from the current study (6.09±0.41mg) were as similarly heavy as those in Kefi *et al*., (2009) study, (7.106mg).

Oocytes from *O. mortimeri* were heavier than those of any of the other Tilapiines in the current study, and this could be a demonstration of the specie's committement to ensuring its survival. However, the observed oocyte weights could not be confidently attributed to nutritive matter (protein, lipids or carbohydrates), as opposed to water.

There has not been much published on oocyte weights for the studied Tilapiines species anywhere in their native nor expanded range. The major constraint being the strong endemism observed on the species' distribution.

In conclusion, the combination of higher fecundity and greater effective diameter of oocytes in *O. niloticus*, compared with moderate and lower observations in *O. mortimeri* and *O. andersonii* respectively, may explain the trend in abundance among the congenerics, but not *T. rendalli*. Production of more oocytes of larger size by *O. niloticus* could have translated into more fingerlings of greater size and having an inherent advantage in avoiding predators, and further being able to exploit a wider range of habitat resources.

5.3.4 Length and Age-at-maturity

Age and size-at-maturity have been shown to be affected by at least three (03) factors: demographic structure, resource availability, and size selective predation (Belk, 1995).

The observed age-at-maturity for female (and male) *O. niloticus* in Lake Kariba (1.23 years) was higher than that observed among females of the same species at Lake Ayame (10 months). Differences were also observed in the lengths-at-maturity, 240.91mm on Lake Kariba against 116-135mm in Lake Ayame. Ojuok (1999) also found that female *O. niloticus* matured earlier than males, 280-300mm against 320-340mm respectively, in the Nyanza Gulf of Lake Victoria. Studies by Shalloof and Salama (2008) indicated that *O.niloticus* males and females both matured within the first year at lengths of 115mm and 105mm respectively, both maturing much earlier than the Lake Kariba stock. Female *O. niloticus* on Lake Ayame were also noted to mature at lower length of 116 ±0.13mm and 13 ±0.72mm during 1995 and 1996 respectively (Duponchelle, 2000). Bwanika (2007) noted that male and female *O. niloticus* on Lakes Nabugabo and Wamala attained maturity at similar age ~1.5-2 years at lengths of approximately 200-250mm TL; these findings compare favourably with those of the current study. Baijot (1994) in studies on a man-made lake observed that female *O. niloticus* attained maturity at 110mm TL, aged between 1-2years. Trewavas (1983) reviewed several observations of size-at- maturity for *O. niloticus* noting 280mm TL in Lakes George and Albert, 390mm TL in Lake

Turkana, and 250mm TL in Lake Edward. Meanwhile, Babiker and Ibrahim's (1979), maturation observations in the Nile (Khartoum) were 114mm (males) and 143mm (females). Length at maturity in Emiliano Zapata Dam, Mexico observed by Pena-Mendoza *et al* (2005) were 152 and 151mm for males and females respectively. Generally, the population of Nile Tilapia from Lake Kariba, Sinazongwe attained sexual maturity at lower sizes than in populations from the East African Lakes. However, size-at-maturity in Tilapiines has been noted to be a very plastic trait; Duponchelle and Legendre (2000) for instance noted a variation of 20mm within two consecutive years of studying *O. niloticus* on Lake Ayame.

Females of *Tilapia rendalli* matured at a greater length and age than males of the species. The length-at-maturity for *T. rendalli* females and males from the current study was higher than that observed by Weyl and Hetch (1998), 218mm and 223mm respectively on Lake Chicamba. Kolding *et al* (1992) observed *T. rendalli* maturity on the Southern shore of Lake Kariba and found that females matured at 168mm whilst males matured at 184mm (lengths standardised to SL). The differences observed from the different locations could be linked to difference in lake size (De Silva, 1986) and environmental conditions. James and Bruton (1992) noted for instance, that sexual maturity in stable environments occurs at a later age than in unstable systems. Early maturity, on the other hand, has been noted in systems with unpredictable conditions of draughts, drawdowns and food-resource shortages (James and Bruton, 1992). Comparing the current study's findings on sexual maturity for *T. rendalli* with Kolding *et al.,* (1992) is difficult because the latter did not assign age-data to the length-at-maturity observations. Correlating average L_{50} and average intrinisic growth rate (K) did in fact reveal inverse relationship (except for slight distortions from *O. mortimeri* and *O. niloticus*); higher K values correlated strongly with early onset of maturatity among the studied Tilapiines. This observation supports the notion by Pauley (1979) that the variable K is an indicator of stress; and in this instance the high stress levels steer the Tilapiines at Lake Kariba, Sinazongwe to mature early. Among the three factors (demographic structure, resource availability, and size selective predation) described by Belk (1995), it is likely that resource shortages arising from unstable environmental conditions and, size-dependent predation may be factors strongly explaining the

observed pattern in the maturity lengths (and ages) of Tilapiines at Lake Kariba, Sinazongwe; predation in this context refers to the explicit acts of fishing by humans, and normal (non-human) predation.

Fouda *et al* (1993) and Phillips (1994) concluded that, in many fish species, males mature earlier than females. However, the observations made after comparing maturity stages in species from the present study were inconsistent with that generalisation, except for *T. rendalli* where it held true. This shift from the norm could be a reflection of changes in the social structure among the congeneric *Oreochromis* species, as well as changes in accessing and partitioning of resources (Reznick, 1993). It is therefore, possible that the territorial and known aggressive nature of *O. niloticus* (Lowe-McConnell, 2000) initiated fitness-promoting evolutionary responses among the other congenerics - resulting in males attaining maturity earlier.

5.4 Synthesis

There is great temptation to make running conclusions that *O. niloticus* has tendency to out-compete congenerics in ecosystems where it has been introduced. However, such a line of suggestion presents as a weak formulaic escape of all possible causes for collapse of Tilapiine populations in systems invaded by Nile Tilapia. Such claims have been forwarded by Vicente and Fonseca-Alves (2013) who however, are quick to point out that local extinction of native species are as much a consequence of exotic species as they are of environmental and anthropogenic inputs. The loss of 300 species of haplochromine cichlids from Lake Victoria has, for instance, been blamed not only on the invasion by *Lates niloticus*, but also limnological changes to the Lake (increase in algal biomass, anoxia, eutrophication and new (destructive) fishing methods). Similar changes have occurred at Lake Kariba; cage-culture facilities and effluent releases from agriculture and crocodile farms around Siansowa and Siavonga may have played a role in altering the limnology of the ecosystem, thereby making it less suitable for especially the indigenous Tilapiines. The location of most of these cage-culture facilities are in sheltered lagoons and well watered bays which are preferred breeding areas for Tilapiines.

Although there have not been any studies correlating, for instance resource availability, resource partitioning and utilisation among congeneric Tilapiines on Lake Kariba, it may be true that competition exists for resources that are common but in limited quantity. In fact, Twongo (1995) verifies that competition for food is important among Tilapiines. Potts *et al*., (1994) further confirms that territories are critical for male reproduction because female *O. niloticus* will almost exclusively mate with dominant, territorial males; the mating ritual among male *O. niloticus* strongly resembles lekking behaviour in higher animals (Fessehaye, 2006). Lekking behaviour occurs when sexually mature males defend clustered territories into which sexually mature females visit for the sole purpose of courtship and mating (Bradbury and Gibson, 1983). Studies have actually shown that *O. niloticus* is strongly territorial and aggressive in habit (Coward and Bromage, 2000; www.mexfish.com/mexico /nile-tilapia/). The implication of larger oocytes and larger male emergents (as postulated by Francis and Barlow, 1993) therefore means that *O. niloticus* males systematically take up more territory on Lake Kariba. The combination of a larger size-at-hatching and greater intrinsic growth rate (K) would further mean greater access to resources (both in quality and quantity), resulting in even greater growth and presence compared with congeneric age-mates. The type and size of food items consumed by fish is known to change with age and size owing to mouth-size and gut-volumes (Outa *et al*., 2014), hence advantaging the larger and faster growing hatchlings of *O. niltoicus and T. rendalli.*

The key observation from the study was that *O. niloticus* was only superior in some aspects of its biology (growth performance, fecundity, effective diameter and L_{50}) compared with the indigenous congenerics. On the other hand, comparison between *O. niloticus* and all other indigenous Tilapiines (to include *T. rendalli*) revealed that Nile Tilapia had a demonstrable advantage only in aspects of effective (oocyte) diameter; all other aspects of its biology were intermediate.

The table 5.2 provides a brief comparison of studied characteristics in *O. niloticus* with indigenous Tilapiines at Lake Kariba, Sinazongwe.

Table 5.2 Comparisons of relative abundances, growth and reproductive aspects in the biology of *Oreochromis niloticus* and Tilapiines indigenous to Lake Kariba; (+) indicates strength in a particular attribute; (*) in grading length-at-maturity, greater advantage was ascribed to smallest observed length at maturity (*for* combined sexes).

VARIABLES	**TILAPIINESPECIES**			
	O. niloticus	*O. andersonii*	*O. mortimeri*	*T. rendalli*
Relative Abundance	**++++**	+	++	+++
Intrinsic growth rate (K)	++	+	+++	**++++**
Growth performance index(Φ')	+++	+	++	**++++**
Fecundity	+++	++	+	**++++**
Average Oocyte weight	+++	++	**++++**	+
Effective diameter of Oocytes (d_e)	**++++**	++	+++	+
Length-at-maturity (L_{50})*	+++	+	++	**++++**
Rank	1st	4th	3rd	2nd

CHAPTER 6: CONCLUSIONS AND RECOMMENDATIONS

6.1 Conclusion

The observed presence of breeding populations, and various size and age-classes of *O. niloticus* at Sinazongwe confirms that the species is established in that sector of Lake Kariba, and constitutes the most abundant Tilapiine species. The low incidence of *O. mortimeri* further confirms that the species is no longer as commonly reported during the 1960s and 1970s; the reference to Sinazongwe as '*Home of Kariba Bream*' is therefore no longer supported by empirical observations. The impending, if not already ensuing, bottleneck-effect resulting from a combination of human and nature-driven events (species translocations, introductions, over-exploitation, droughts, and floods) will certainly pose a challenge for any efforts of restoring the indigenous Tilapiine biodiversity of Lake Kariba. However, without the necessary interventions to curb the extinction of *O. mortimeri* and *O. andersonii* the future populations of Tilapiines at Lake Kariba will most certainly comprise *O. niloticus* and *T. rendalli*. This co-dominance and coexistence may be supported by inherent differences in feed and habitat preferences, further allowing for the two species to thrive without much interspecific inhibition or competition. Therefore, the first hypothesis of this study stating that: "*Oreochromis niloticus* is not the most abundant Tilapiine species on Lake Kariba", was not supported.

It was determined that a relationship existed between intrinsic growth rate (K) and Tilapiine abundances; the statistical insignificance in the observation may have resulted from the assumption that Tilapiine species populations across the study area were respective unit stocks. The study further revealed that *O. niloticus* did not have a significantly superior intrinsic growth rate (K) *per se*, but instead strong compensatory effects from higher asymptotic lengths placed it second in growth performance (lower than *T. rendalli*). Differences were observed in growth aspects of the studied Tilapiines with *O. niloticus* having the greatest asymptotic length and growth performance among the mouthbrooding *Oreochromis* species; *O. mortimeri* on the other hand, exhibited greatest intrinisic growth rate among its congenerics. *Tilapia rendalli* had a uniquely greater intrinisic growth rate and growth performance- the highest observed among all the studied Tilapiines.

As a result, the second hypothesis stating that: 'there were no differences between the growth aspects of *O. niloticus*, and those of indigenous Tilapiines', was rejected.

Furthermore, the relatively higher fecundity in *O. niloticus* (with oocytes of greater effective diameters) could have improved probability of survival for its hatchlings compared with those of congenerics. On the other hand, *T. rendalli* had the highest observed fecundity among the studied Tilapiines. The sexual maturation of *O. niloticus* (males and females) at the same relative ages further improved chances of successful breeding encounters, unlike in cases where males delayed in reaching sexual maturity. The observed early maturity in male *T. rendalli* may greatly assist with the species' continued survival. These observations resulted in rejection of the third hypothesis which stated that: 'the fecundity of female *O. niloticus* is not higher than that of indigenous female Tilapiines on Lake Kariba'.

6.2 Recommendations

One of the challenges encountered during the study was the critical lack of publications on the growth and reproductive biology of, especially, *O. andersonii* and *O. mortimeri* in environments similar to that of Lake Kariba; most of the literature on the species had a focus on captive (aquaculture) conditions. It was therefore difficult to make any meaningful comparisons among the studied species. Furthermore, the low presence of *O. andersonii* and *O. mortimeri* at Lake Kariba, Sinazongwe limited the scope of fully appreciating aspects of growth and reproductive biology due to the few samples analysed.

The method of aging Tilapiines using scales was wrought with difficulty; yearly annuli were in some instances indistinguishable from daily/ monthly annuli. There is need for investment in equipment and expertise in aging fish using more reliable techniques such as reading saggital otolith bones.

Resulting from the un-coordinated and sometimes undocumented introductions of unknown strains of Tilapiines on the Lake, it will be important that future studies treat the fish populations on the Lake as meta-populations, using meta-population analyses as opposed to treating them as unit stocks.

In an effort to confidently evaluate fish species biodiversity, it is further important that Department of Fisheries surveys such as CAS begin to desegregate questionnaires that lump-up species under broad categories. Therefore, instead of capturing data as *Oreochromis* species, improvements could specify particular species (especially for those indigenous species that are rare, endangered or merely endemic). Such improvements would improve the relevance of data collected for particular species, and will be a key step in attaching value to, especially, local fish biodiversity.

In order to secure the genetics of *O. mortimeri*, the study recommends that the distribution range of the species be artificially expanded through translocations and introductions on systems that have not been invaded by *O. niloticus*. This is based on the *quasi*-option value from the undiscovered (life-history, genetic, evolutionary) benefits of the Kariba bream.

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APPENDICES

APPENDIX A: DATA SHEET 01

DATE.....

LOCATION .....

GPS.....

SPECIES.....

Total weight (g)	**Sex**	**Gonad state**	**Weight of gonads (g)**	**Body length (mm)**	
				TL	**SL**

Scales *(stick in space below)*

APPENDIX B: DATA SHEET 02

DATE.....

LOCATION.....

GPS COORDINATES.....

S/No	Species	Weight , *W* (g)	Number ,*N*.

NOTES

APPENDIX C: DATA SHEET 03

SPECIES :		**REPLICATIONS**									
SAMPLE		01	02	03	04	05	06	07	08	09	10
TOTAL GONAD WEIGHT (mg)	SAMPLE WEIGHT (mg)										
TOTAL LENGTH (mm)	NUMBER OF OOCYTES COUNTED										

SPECIES :		**REPLICATIONS**									
SAMPLE		01	02	03	04	05	06	07	08	09	10
TOTAL GONAD WEIGHT (mg)	SAMPLE WEIGHT (mg)										
TOTAL LENGTH (mm)	NUMBER OF OOCYTES COUNTED										

APPENDIX D: Complete Catch Composition for Fish Species at Sinazongwe.

Species	No	% No	Weight (kg)	% Weight	FRQ	% FRQ	IRI	% IRI
Synodontis zambezensis	1497	46.79587	72.948	33.56555	50	73.5	5,906.564	54.90393
Hydrocynus vittatus	285	8.909034	74.94	34.48212	46	67.6	2,933.242	27.26568
Oreochromis niloticus	362	11.31604	19.579	9.008881	31	45.6	926.8162	8.615135
Schilbe intermedius	178	5.564239	5.866	2.699121	20	29.4	242.9428	2.258252
Labeo cylindricus	186	5.814317	4.161	1.9146	16	23.6	182.4024	1.695505
Serranochromis macrocephalus	71	2.219444	3.714	1.708922	19	27.9	109.6014	1.01879
Tilapia rendalli	67	2.094405	2.663	1.225326	17	25	82.99325	0.771456
Mormyrus longirostris	13	0.406377	11.509	5.295633	9	13.2	75.26654	0.699633
Tilapia sparmanii	64	2.000625	0.834	0.383748	17	25	59.60934	0.554093
Synodontis macrostigma	74	2.313223	1.254	0.577003	13	19.1	55.20331	0.513137
Clarias gariepinus	14	0.437637	8.127	3.739475	8	11.8	49.28991	0.45817
Pseudocranilabrus philander	57	1.781807	0.441	0.202917	16	23.5	46.64101	0.433547
Brycinus lateralis	65	2.031885	0.388	0.17853	8	11.8	26.0829	0.242451
Barbus paludinosus	62	1.938106	0.567	0.260894	3	4.4	9.675597	0.089939
Oreochromis mortimeri	11	0.343857	0.863	0.397092	8	11.8	8.743203	0.081272
Mormyrus anguilloides	20	0.625195	4.134	1.902176	7	10.3	26.03193	0.241977
Cymphomyrus dischorynchus	34	1.062832	0.981	0.451387	4	5.9	8.933895	0.083044
Serranochromis cordringtonii	16	0.500156	0.399	0.183592	9	13.2	9.025475	0.083895
Petrocephalus catastoma	30	0.937793	0.564	0.259513	3	4.4	5.268147	0.04897
Sargochromis mortimeri	23	0.718975	0.377	0.173469	4	5.9	5.265417	0.048944
Limnothrissa miodon	12	0.375117	0.067	0.030829	6	8.8	3.572324	0.033206
Oreochromis andersonii	12	0.375117	0.003	0.00138	4	5.9	2.221336	0.020648
Labeo molybdinus	9	0.281338	0.325	0.149542	3	4.4	1.895872	0.017623
Brycinus imberi	5	0.156299	0.17	0.078222	3	4.4	1.031892	0.009592
Distichodus schenga	1	0.03126	0.9	0.414117	1	1.5	0.668065	0.00621
Labeo altivelis	2	0.06252	0.341	0.156904	2	2.9	0.636329	0.005915
Babrbus fasciolatus	10	0.312598	0.092	0.042332	2	3	1.064789	0.009898
Heterobranchus longifilis	3	0.093779	0.273	0.125615	1	1.5	0.329092	0.003059
Synodontis nebulosus	2	0.06252	0.1	0.046013	2	2.9	0.314744	0.002926
Oreochromis macrochir	2	0.06252	0.08	0.03681	2	2.9	0.288057	0.002678
Labeo congoro	1	0.03126	0.306	0.1408	1	1.5	0.258089	0.002399
Serranochromis angusticeps	3	0.093779	0.069	0.031749	1	1.5	0.188292	0.00175
Marcusenius macrolepidotus	2	0.06252	0.124	0.057056	1	1.5	0.179363	0.001667
Sargochromis giardi	1	0.03126	0.165	0.075921	1	1.5	0.160772	0.001494
Mormyrus lacerda	3	0.093779	0.006	0.002761	1	1.5	0.14481	0.001346
Cherax quadricarinatus	2	0.06252	0	0	1	1.5	0.093779	0.000872
Total	**3,199**	**100**	**217.33**	**100**	**-**	**-**	**10,758**	**100**

APPENDIX E: Compilation of Field Observations for Studied Tilapiines

SPECIES	TOTAL LENGTH (mm)	STANDARD LENGTH (mm)	TOTAL WEIGHT (g)	SEX	GONAD STATE	GONAD WEIGHT (g)
O. andersonii	250	194	316	female	i	0.1
O. andersonii	245	193	305	female	i	0.1
O. andersonii	243	183	258	male	r	1
O. andersonii	165	112	71	-		
O. andersonii	297	242	471	-		
O. andersonii	251	179	305	-		
O. andersonii	244	174	270	-		
O. andersonii	249	194	281	-		
O. andersonii	315	241	1570	female	r	1.1
O. andersonii	311	243	1320	male	a	1
O. andersonii	249	194	321.6	male	s	0.1
O. andersonii	325	252	1390	male	a	1
O. andersonii	283	220	446.9	male	q	
O. andersonii	283	175	266.4	male	a	
O. andersonii	260	194	419.4	male	a	
O. andersonii	264	202	413.3	female	q	
O. andersonii	264	206	381.1	male	r	
O. andersonii	255	191	311.8	male	q	
O. andersonii	259	193	332.9	female	r	
O. andersonii	279	213	457	male	r	
O. andersonii	252	194	369.3	male	a	
O. andersonii	268	251	403.4	male	a	
O. andersonii	236	176	267.8	male	a	
O. andersonii	253	193	356.9	male	r	
O. andersonii	249	184	294.7	female	r	3.6
O. andersonii	198	151	170.7	male	i	
O. andersonii	228	168	213.2	female	a	
O. andersonii	240	186	289.1	female	a	
O. andersonii	374	296	1090	female	r	
O. andersonii	299	227	550	female	r	13

SPECIES	TOTAL LENGTH (mm)	STANDARD LENGTH (mm)	TOTAL WEIGHT (g)	SEX	GONAD STATE	GONAD WEIGHT (g)
O. andersonii	294	229	480	male		
O. andersonii	288	227	410	female	r	17.6
O. andersonii	263	201	400	-		
O. andersonii	280	214	440	-		
O. andersonii	292	224	490	-		
O. andersonii	276	223	390	-		
O. andersonii	281	219	460	-		
O. andersonii	287	222	436	female	r	5
O. andersonii	297	224	458	female	r	10
O. andersonii	200	158	175	male	i	
O. andersonii	253	194	326	female	a	1
O. andersonii	264	204	396	female	a	6
O. andersonii	249	191	342	female	a	1
O. andersonii	221	177	241	female	a	1
O. andersonii	271	212	412	male	r	
O. andersonii	286	223	489	male	r	
O. andersonii	249	190	330	female	a	3
O. andersonii	249	209	402	male	r	
O. andersonii	236	182	296	female	r	8
O. andersonii	231	177	284	female	a	1
O. andersonii	288	227	397	nn		
O. andersonii	232	177	247	nn		
O. andersonii	235	146	263	nn		
O. andersonii	329	259	572	nn		
O. andersonii	267	209	246	nn		
O. andersonii	264	205	318	nn		
O. andersonii	256	198	332	nn		
O. andersonii	269	209	359	nn		

SPECIES	TOTAL LENGTH (mm)	STANDARD LENGTH (mm)	TOTAL WEIGHT (g)	SEX	GONAD STATE	GONAD WEIGHT (g)
O. mortimeri	361	283	863	nn	nn	-
O. mortimeri	358	271	900	nn	nn	-
O. mortimeri	232	181	267	male	a	1
O. mortimeri	208	164	198.2	female	a	1
O. mortimeri	420	309	2380	male	s	0.1
O. mortimeri	296	231	540	male	s	-
O. mortimeri	237	184	339.8	female	nn	-
O. mortimeri	231	180	307.9	nn	n	-
O. mortimeri	310	237	453.5	male	a	-
O. mortimeri	325	253	633	male	a	-
O. mortimeri	353	271	842	male	a	-
O. mortimeri	352	276	834	male	a	-
O. mortimeri	287	221	503	male	a	-
O. mortimeri	288	226	504	male	a	-
O. mortimeri	281	216	482	female	r	2
O. mortimeri	274	214	509	male	t	-
O. mortimeri	279	209	419	female	a	2
O. mortimeri	244	180	286	male	a	-
O. mortimeri	260	202	254	male	nn	-
O. mortimeri	259	199	339	female	r	8
O. mortimeri	272	208	399	male	a	-
O. mortimeri	225	176	288	male	a	-
O. mortimeri	229	176	255	male	a	-
O. mortimeri	250	191	330	female	r	8

SPECIES	TOTAL LENGTH (mm)	STANDARD LENGTH (mm)	TOTAL WEIGHT (g)	SEX	GONAD STATE	GONAD WEIGHT (g)
O. niloticus	331	265	802	female	r	15
O. niloticus	322	259	657	female	r	9
O. niloticus	230	180	261	male	i	0.1
O. niloticus	235	181	293	male	i	0.1
O. niloticus	212	169	205	male	i	0.1
O. niloticus	260	209	385	female	r	7
O. niloticus	251	202	336	male	s	0.1
O. niloticus	234	183	244	male	a	1
O. niloticus	250	197	306	male	a	1
O. niloticus	243	190	284	male	s	0.1
O. niloticus	238	184	278	male	s	0.1
O. niloticus	240	190	275	female	r	3
O. niloticus	255	198	336	male	s	0.1
O. niloticus	230	181	255	female	a	1
O. niloticus	260	208	373	female	a	1
O. niloticus	249	195	310	male	s	0.1
O. niloticus	251	199	304	male	s	0.1
O. niloticus	265	207	400	female	a	1
O. niloticus	260	203	348	male	a	1
O. niloticus	250	210	370	male	s	0.1
O. niloticus	243	191	295	female	a	1
O. niloticus	241	192	304	female	a	1
O. niloticus	253	198	348	female	a	1
O. niloticus	255	200	377	female	r	6
O. niloticus	238	191	251	female	a	1
O. niloticus	260	207	391	male	s	1
O. niloticus	255	201	355	male	a	1
O. niloticus	268	210	401	male	a	1
O. niloticus	251	201	357	male	a	1

SPECIES	TOTAL LENGTH (mm)	STANDARD LENGTH (mm)	TOTAL WEIGHT (g)	SEX	GONAD STATE	GONAD WEIGHT (g)
O. niloticus	294	235	496	female	s	0.1
O. niloticus	248	195	300	-	-	-
O. niloticus	245	196	290	-	-	-
O. niloticus	436	338	1721	-	-	-
O. niloticus	347	278	761	-	-	-
O. niloticus	263	113	338	-	-	-
O. niloticus	262	210	371	-	-	-
O. niloticus	246	196	327	-	-	-
O. niloticus	284	231	511	-	-	-
O. niloticus	296	246	562	-	-	-
O. niloticus	192	140	906	-	-	-
O. niloticus	190	146	137	-	-	-
O. niloticus	279	219	413	-	-	-
O. niloticus	206	166	182	-	-	-
O. niloticus	253	200	326	-	-	-
O. niloticus	196	159	156	-	-	-
O. niloticus	291	231	472	-	-	-
O. niloticus	250	195	281	-	-	-
O. niloticus	261	213	338	-	-	-
O. niloticus	335	278	761	-	-	-
O. niloticus	124	77	15	-	-	-
O. niloticus	258	210	371	-	-	-
O. niloticus	251	196	327	-	-	-
O. niloticus	277	231	511	-	-	-
O. niloticus	301	246	562	-	-	-
O. niloticus	325	279	906	-	-	-
O. niloticus	230	175	185	-	-	-
O. niloticus	215	160	139	-	-	-
O. niloticus	271	229	417	-	-	-
O. niloticus	217	163	157	-	-	-
O. niloticus	246	200	284	-	-	-
O. niloticus	277	225	331	-	-	-
O. niloticus	291	245	498	-	-	-

SPECIES	TOTAL LENGTH (mm)	STANDARD LENGTH (mm)	TOTAL WEIGHT (g)	SEX	GONAD STATE	GONAD WEIGHT (g)
O. niloticus	166	114	223	-	-	-
O. niloticus	267	215	387	-	-	-
O. niloticus	282	240	481	-	-	-
O. niloticus	287	240	486	-	-	-
O. niloticus	291	235	478	-	-	-
O. niloticus	227	179	220	-	-	-
O. niloticus	258	207	314	-	-	-
O. niloticus	278	226	392	-	-	-
O. niloticus	299	251	519	-	-	-
O. niloticus	286	238	378	-	-	-
O. niloticus	379	329	1122	-	-	-
O. niloticus	257	207	260	-	-	-
O. niloticus	265	217	385	-	-	-
O. niloticus	364	312	985	-	-	-
O. niloticus	224	174	263	-	-	-
O. niloticus	218	169	188	-	-	-
O. niloticus	216	167	192	-	-	-
O. niloticus	219	169	202	-	-	-
O. niloticus	223	175	213	-	-	-
O. niloticus	246	202	288	-	-	-
O. niloticus	272	221	298	-	-	-
O. niloticus	203	154	172	-	-	-
O. niloticus	299	247	521	-	-	-
O. niloticus	347	278	761	-	-	-
O. niloticus	263	113	338	-	-	-
O. niloticus	365	286	1230	male	r	0.8
O. niloticus	428	340	1550	male	s	0.1
O. niloticus	375	299	1230	male	r	0.7
O. niloticus	419	336	1450	male	r	0.9
O. niloticus	409	325	1310	male	r	0.8

SPECIES	TOTAL LENGTH (mm)	STANDARD LENGTH (mm)	TOTAL WEIGHT (g)	SEX	GONAD STATE	GONAD WEIGHT (g)
O. niloticus	306	245	710	male	a	1
O. niloticus	395	315	1240	male	s	0.1
O. niloticus	326	255	770	male	s	0.1
O. niloticus	377	303	1180	male	r	0.9
O. niloticus	383	302	1300	male	r	0.9
O. niloticus	383	302	1210	female	r	29.5
O. niloticus	412	333	1570	male	r	0.9
O. niloticus	345	276	800	male	s	0.1
O. niloticus	344	273	910	male	r	0.7
O. niloticus	327	275	920	male	a	1
O. niloticus	371	291	1260	male	s	0.1
O. niloticus	383	308	1270	male	r	1
O. niloticus	382	316	1380	female	r	14.5
O. niloticus	363	235	1320	male	r	0.9
O. niloticus	367	292	1270	male	r	0.9
O. niloticus	402	326	1450	male	a	0.7
O. niloticus	370	303	1230	female	a	3
O. niloticus	291	231	550	female	r	4.1
O. niloticus	266	214	292.9	male	s	0.1
O. niloticus	253	206	370.1	female	a	1.1
O. niloticus	372	320	1051	-	nn	-
O. niloticus	294	233	530	-	nn	-
O. niloticus	299	232	490	-	nn	-
O. niloticus	261	204	355.5	male	a	-
O. niloticus	267	212	393.7	female	r	10.8
O. niloticus	332	261	890	female	r	11.6
O. niloticus	307	244	630	-	-	-
O. niloticus	311	247	560	-	-	-
O. niloticus	301	239	610	-	-	-
O. niloticus	374	293	940	-	-	-
O. niloticus	323	247	640	-	-	-
O. niloticus	316	248	790	-	-	-

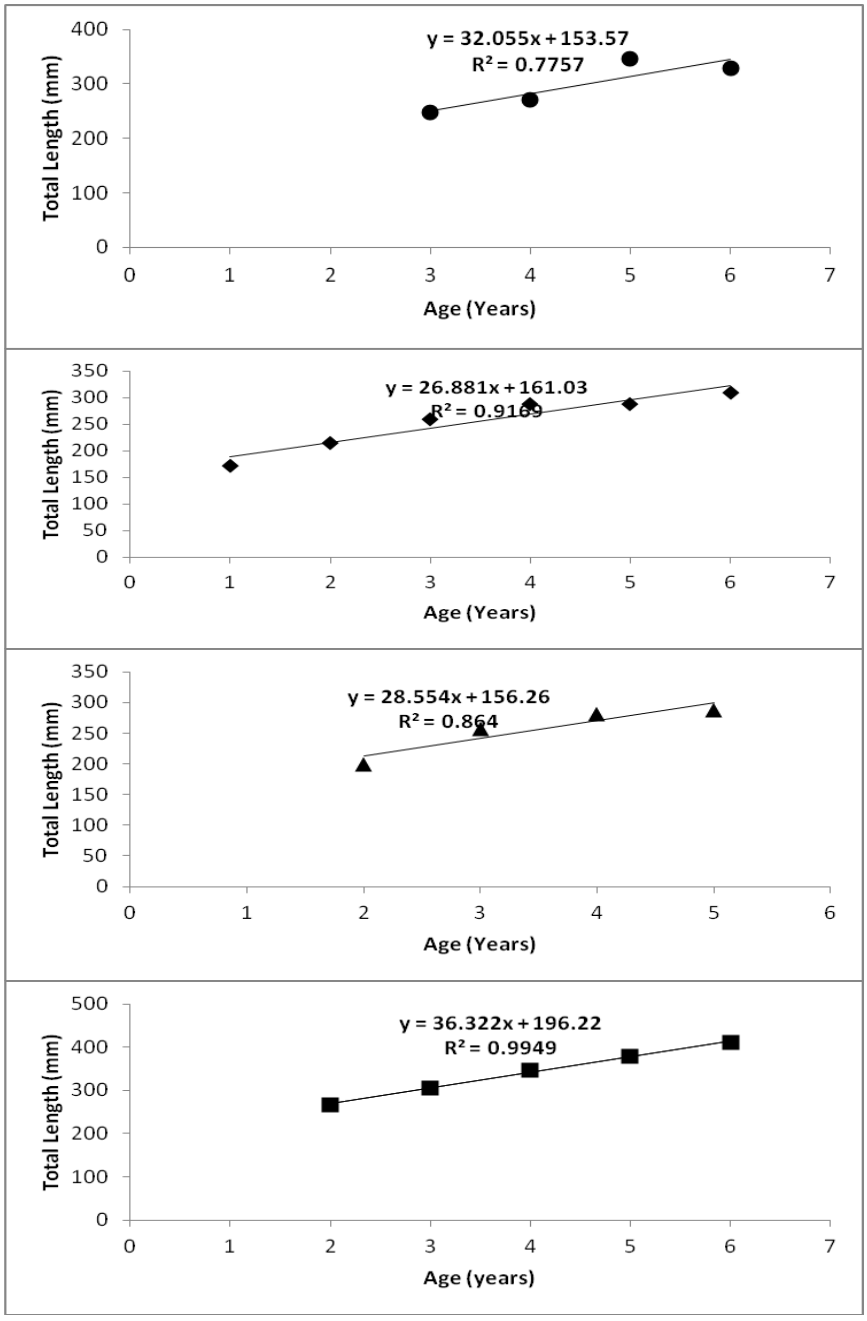
SPECIES	TOTAL LENGTH (mm)	STANDARD LENGTH (mm)	TOTAL WEIGHT (g)	SEX	GONAD STATE	GONAD WEIGHT (g)
O. niloticus	308	242	720	-	-	-
O. niloticus	297	234	540	-	-	-
O. niloticus	287	227	530	-	-	-
O. niloticus	280	219	560	-	-	-
O. niloticus	336	204	830	male	r	-
O. niloticus	373	295	1100	female	r	20.3
O. niloticus	282	224	441	female	r	20
O. niloticus	304	242	565	male	a	-
O. niloticus	279	221	481	male	a	-
O. niloticus	281	221	446	male	a	-
O. niloticus	342	271	831	male	a	-
O. niloticus	266	209	418	female	a	1
O. niloticus	286	226	576	male	a	-
O. niloticus	350	258	902	nn	-	-
O. niloticus	242	147	972	nn	-	-
O. niloticus	242	154	303	nn	-	-
O. niloticus	366	299	1021	-	-	-
O. niloticus	416	324	1350	-	-	-
O. niloticus	291	236	548	-	-	-
O. niloticus	297	239	599	-	-	-
O. niloticus	274	219	418	-	-	-
O. niloticus	339	272	913	-	-	-
O. niloticus	424	335	1246	-	-	-
O. niloticus	381	301	1029	-	-	-
O. niloticus	277	222	488	-	-	-
O. niloticus	324	252	737	-	-	-
O. niloticus	386	305	1088	-	-	-
O. niloticus	397	316	949	-	-	-
O. niloticus	424	333	975	-	-	-
O. niloticus	333	265	584	-	-	-
O. niloticus	401	325	1370	-	-	-
O. niloticus	311	246	659	-	-	-

SPECIES	TOTAL LENGTH (mm)	STANDARD LENGTH (mm)	TOTAL WEIGHT (g)	SEX	GONAD STATE	GONAD WEIGHT (g)
T. rendalli	315	246	776	male	s	0.1
T. rendalli	235	182	306	male	i	0.1
T. rendalli	250	189	333	male	s	0.1
T. rendalli	248	193	322	male	a	1
T. rendalli	286	224	544	female	r	10
T. rendalli	275	219	504	female	r	17
T. rendalli	278	215	419	female	r	13
T. rendalli	267	205	388	female	a	1
T. rendalli	215	167	216	female	a	1
T. rendalli	225	174	254	female	a	1
T. rendalli	241	180	285	male	r	1
T. rendalli	220	172	223	male	r	1
T. rendalli	288	223	478	female	a	1
T. rendalli	273	213	469	female	a	1
T. rendalli	292	236	533	female	r	8
T. rendalli	281	226	495	female	a	1
T. rendalli	255	199	282	female	r	3
T. rendalli	260	203	451	male	r	1.5
T. rendalli	251	197	340	female	r	9
T. rendalli	160	109	54	-	-	-
T. rendalli	241	187	287	-	-	-
T. rendalli	221	166	230	-	-	-
T. rendalli	209	156	226	-	-	-
T. rendalli	276	219	528	-	-	-
T. rendalli	293	237	485	-	-	-
T. rendalli	222	171	248	-	-	-
T. rendalli	223	175	197	-	-	-
T. rendalli	141	99	57	-	-	-
T. rendalli	149	95	72	-	-	-
T. rendalli	234	179	262	-	-	-

SPECIES	TOTAL LENGTH (mm)	STANDARD LENGTH (mm)	TOTAL WEIGHT (g)	SEX	GONAD STATE	GONAD WEIGHT (g)
T. rendalli	317	266	625	-	-	-
T. rendalli	287	236	429	-	-	-
T. rendalli	184	137	117	-	-	-
T. rendalli	292	240	407	-	-	-
T. rendalli	262	212	444.4	male	r	0.6
T. rendalli	315	255	830	male	r	0.9
T. rendalli	200	169	189.5	male	i	0.1
T. rendalli	211	165	234.2	female	a	1
T. rendalli	288	209	418.3	male	a	1
T. rendalli	209	162	213.4	male	a	1
T. rendalli	282	225	580	male	r	1
T. rendalli	316	252	750	male	r	1
T. rendalli	232	184	295.4	female	r	2.6
T. rendalli	328	266	920	female	a	1
T. rendalli	307	236	650	male	r	0.8
T. rendalli	248	196	388.2	male	a	0.7
T. rendalli	273	225	540	female	r	21
T. rendalli	282	234	500	-	-	-
T. rendalli	242	191	358.6	male	a	-
T. rendalli	275	209	460	female	r	10.8
T. rendalli	279	225	600	-	-	-
T. rendalli	317	241	640	-	-	-
T. rendalli	303	230	650	-	-	-
T. rendalli	273	219	540	-	-	-
T. rendalli	333	257	680	male	r	-
T. rendalli	294	234	690	-	-	-
T. rendalli	283	222	490	-	a	-
T. rendalli	333	249	730	male	s	-
T. rendalli	316	239	710	male	a	-
T. rendalli	302	233	620	male	-	-
T. rendalli	265	212	357	-	-	-
T. rendalli	239	186	242	-	-	-
T. rendalli	236	184	191	-	-	-
T. rendalli	223	169	126	-	-	-
T. rendalli	223	172	144	-	-	-
T. rendalli	228	169	139	-	-	-
T. rendalli	210	162	167	-	-	-
T. rendalli	216	168	217	-	-	-
T. rendalli	214	168	223	-	-	-
T. rendalli	200	158	175	-	-	-
T. rendalli	296	236	460	-	-	-

a=Active; i= immature; q= Quiescent; r=Ripe; s=Spent; nn= Not Known

APPENDIX F: Age-Length Keys for Tilapiines studied at Lake Kariba, Sinazongwe.



Age-Length Keys: *Oreochromis andersoni* ▲ (*n*=43); *Oreochromis mortimeri* ● (*n*=16); *Oreochromis niloticus* ■ (*n*=73); *Tilapia rendalli* ♦ (*n*=147);