

**THE DYNAMICS OF A SUBTROPICAL LAKE FISHERY IN
CENTRAL MOZAMBIQUE**

A thesis submitted in fulfilment of the requirements for the degree of

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To my family- Uli, Gaby, Julia, Anika, Michael and Philip

' As for certain truth, no man has known it

Nor shall he know...

And even if by chance he were to utter

The final truth, he would himself not know it

For all is but a woven web of guesses.'

(Xenophanes, 5th Century BC)

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ABSTRACT

Fisheries in African reservoirs are typically multi-species and in most cases the fish resource is harvested with a number of gears. These characteristics complicate their management and the development of management procedures. Typically, long time series of data on catch and effort and length- or age-based catch are not available for these fisheries. This precludes the use of data intensive methods such as multi-species virtual population analysis.

The principal aim of this thesis was to develop a management procedure for African reservoir fisheries that takes into account the pertinent biological characteristics of the target species and accounts for the multi-species and multi-gear interactions in such fisheries. An opportunity availed itself to undertake this work on Lake Chicamba (19°08'S 33°08'E) a man-made hydroelectric dam in subtropical Mozambique (Manica province). The specific objectives of this study were: to obtain locality specific biological parameters for the target species in Lake Chicamba; to assess gear utilisation trends in the fishery through the determination of gear-selectivity, catch rate and effort for each of the principal gears used in the fishery; to assess the fishery using traditional per-recruit models and to test existing and new per-recruit models that account for the multi-species and multi-gear nature of the fishery and to determine the adequacy of each of these approaches in the determination of suitable target reference point (TRP) exploitation rates.

The three principal species in Lake Chicamba are the introduced largemouth bass, *Micropterus salmoides*, and two cichlids the Mozambique tilapia, *Oreochromis mossambicus* and the redbreast tilapia, *Tilapia rendalli*. Sectioned otoliths were used for age and growth determination. Marginal zone analysis showed that annulus formation in all

three species occurred during winter. The maximum-recorded age was 5 years for *M. salmoides*, 16 years for *T. rendalli* and 10 years for *O. mossambicus*. Growth of the three species was best described by the 3 parameter von Bertalanffy growth model as $l_a = 465.51 (1 - e^{-1.175(a + 0.009)})$ mm FL for *M. salmoides*; $l_a = 238.74 (1 - e^{-0.636(a + 0.905)})$ mm TL for *T. rendalli*; and $l_a = 266.06 (1 - e^{-0.7904(a + 0.269)})$ mm TL for *O. mossambicus*. Female *T. rendalli* attained 50%-maturity at 2.89 years, while *O. mossambicus* matured at 2.83 years and *M. salmoides* at 0.9 years. Both cichlid species spawned throughout summer while *M. salmoides* had a very short spawning season from August to September. The total annual mortality rate (Z) for *M. salmoides* in Lake Chicamba was 1.27 yr^{-1} , the mean empirical estimate of natural mortality (M) was 0.73 yr^{-1} , and fishing mortality (F) was calculated at 0.54 yr^{-1} . For *T. rendalli* $Z = 0.31 \text{ yr}^{-1}$, $M = 0.20 \text{ yr}^{-1}$, $F = 0.11 \text{ yr}^{-1}$ and for *O. mossambicus* $Z = 0.62 \text{ yr}^{-1}$, $M = 0.38 \text{ yr}^{-1}$, $F = 0.24 \text{ yr}^{-1}$.

The three species exhibited reproductive traits, which implied a high reliance of recruitment on spawner stock (nest guarding in *T. rendalli* and *M. salmoides* and mouthbrooding in *O. mossambicus*). For this reason it was decided that the cichlid fisheries should be managed using TRPs which maintained the spawner biomass-per-recruit at 50% (F_{SB50}) of pristine levels. However, based on good evidence it was hypothesised that the high rate of fishing mortality helped to maintain the fast growth rate of *M. salmoides*. It was, therefore, decided to manage this species at a TRP of F_{SB40} .

The three most important fishing sectors were the gill-net, seine-net and hook-and-line fisheries. The total catch for 1996 was 223 t. The gill nets selected all three species at a size/age approximating 50%-maturity while the seine-net and hook-and-line fisheries

selected mainly juvenile fishes. There was strong evidence to suggest that seine net fishing also disrupted spawning.

It was shown that the 'traditional' single-species per-recruit models were unsuitable to assess multi-species and multi-gear reservoir fisheries. Since existing multi-species/multi-fishery yield-per-recruit models were not capable of defining $F_{SB(x)}$ TRPs, a new multi-species/multi-fishery spawner-biomass-per-recruit approach was developed. This approach allowed for the simulation of the response of spawner biomass-per-recruit to changes in effort in the three fishery sectors, simultaneously. The models showed that the spawner biomass-per-recruit, at current effort levels, was higher than the suggested TRP for the three species. However, it was shown that an increase of 10% in current total effort would reduce spawner biomass-per-recruit to below the recommended TRP levels. With the closure of the seine-net fishery, gill-net effort could be increased to 338 fishers (340 for management purposes) and effort in the hook-and-line fishery could be increased by 30% before the TRP was reached.

To maintain the fish stocks above TRP levels, effort control was considered to be the most effective management method. The main recommendations for Lake Chicamba were to close the seine-net fishery, to limit the gill-net fishery to 340 fishers (using 137-m long \times 3-m deep gill nets) and to maintain the open access nature of the hook-and-line fishery. The multi-species/multi-fishery per-recruit approach allows for the meaningful simulation of various scenarios and provides relatively robust management options. In the absence of long time series of effort and age- or length-based catch data, this approach was considered as the most suitable assessment method for multi-species/multi-gear African reservoir fisheries.

CHAPTER 1

Introduction

The fundamental purpose of fisheries management is to ensure the sustainable utilisation of fish stocks over time, thereby promoting the economic and social well being of the harvesting fisheries (Hilborn & Walters 1992). The proper assessment and management of a fishery requires an understanding of the biology, life history and distribution of the target species (King 1995). Given that most African reservoirs have existing fisheries, the use of assessment methods that allow for dynamic simulation analysis incorporating the response of the stock to changes in management strategy (e.g. a change in gill net mesh size or effort) is of utmost importance. Essentially, sustainable management is dependent on the ability of fisheries managers to determine at what levels of fishing effort and at which gear selectivity scenarios the catch of a target species is sustainable and the spawning stock remains adequate. The determination of these key features has given rise to a worldwide trend for fisheries management advice based on more quantitative methodologies. However, before considering the application of suitable models, the nature of African reservoir fisheries must be considered.

African reservoir fisheries

African reservoirs exceeding 10 km² cover an estimated area of 40 000 km² and contribute an estimated 150 000 t to the total inland fishery yield (Kapetsky & Petr 1984). Yields in inland fisheries range from 9 to 343 kg ha⁻¹yr⁻¹ (Marshall 1984). The largest of the African

reservoir fisheries (Kariba, Nasser, Kainji, Volta) have received the most attention from researchers in the past and, therefore, fisheries information for these reservoirs is relatively comprehensive (Kapetsky & Petr 1984, Crul & Roest 1995). This is in direct contrast to smaller African reservoir fisheries, when one considers that in thirteen medium-sized African reservoirs (300 km² to 4340 km²), catch rate data and biological data on the target species were available for only four fisheries (Lagado reservoir, Cameroon; Kafue flats/gorge dam, Zambia; Lake Kossou, Cote d'Ivoire and Jebel Aulia reservoir, Sudan) (Van Der Knaap 1994).

Directed catch and effort data and length- or age-based catch data for the application of fisheries management models and stock assessments are not available for most African reservoir fisheries. When catch and effort data are available, they are often temporally disjunct and of little quantitative value. This is directly attributable to the lack of government funds for fisheries research in African countries and the short-term nature of the support given by donor organisations.

In addition to the paucity of historical data, a number of other characteristics of African reservoir fisheries complicate management. Firstly, the diverse ichthyofauna in African freshwater systems leads to a mixed species catch composition in most fisheries. This ranges from fairly simple systems such as the Hartbeespoort dam in the North-West province of South Africa, in which the fishery is essentially based on three target species (Cochrane 1985), to complex systems such as the Lake Kariba inshore gill-net fishery, where various cyprinids, distichontids, cichlids and characins dominate the catch (Marshall

et al. 1982). Even in highly selective fisheries such as the Lake Kariba kapenta (*Limnothrissa miodon*) fishery there is considerable by-catch of other species, such as the tigerfish *Hydrocynus vittatus* (Cochrane 1976). Secondly, the biological parameters necessary for the application of age-based models, such as growth rate, length-at-maturity and spawning periodicity may vary considerably between localities (Lowe-McConnell 1958, Garrod 1959, Le Roux 1961, Hecht 1980a, DeMerona et al. 1988, Beamesderfer & North 1995). In addition, environmental variability has been found to further modify these biological parameters. For example, the growth rate of *O. mossambicus* in Hartbeespoort dam, South Africa, was found to increase after flooding in response to increased food availability (Cochrane 1985). In Sri Lankan reservoirs, fluctuations in lake level have been shown to influence the reproductive output of this species to such an extent that commercial catches were affected three years later (De Silva 1985). Finally, in most African reservoir fisheries the fish resource is harvested with multiple gears. These gears include gill nets, seine nets, cast nets, longlines, hook and line fishing and traps (Van der Knaap 1994). Although these gears have some inherent species- and size-selectivity, there is considerable overlap in the species composition and the size of fish harvested by each gear.

Management techniques

There has been an increasing realisation that small African reservoirs are of considerable importance for the maintenance of food security in the region (Kapetsky & Petr 1984, Marshall & Maes 1994, Van der Knaap 1994). The sustainable management of these resources should therefore be a high priority and there is a need for the development of appropriate methods for the rapid assessment of these fisheries.

Given the constraints in terms of the availability of biological and fisheries data for African reservoir fisheries, management has largely focused on the rapid assessment of potential yield. One of the earliest empirical approaches related fish yield to the mean depth of the lake (Rawson 1952). The morphoedaphic index was developed by Ryder (1965), to take into account the effect of lake fertility, indicated by total dissolved solids, as well as mean depth in the prediction of fish yields. The relationship of yield to morphoedaphic indices is probably the most widely applied rapid assessment method (Ryder et al. 1974, Henderson & Welcomme 1974, Ryder 1982, Schlesinger & Regier 1982, Bernacsek & Lopes 1984, Marshall 1984). Essentially the empirical relationship is described by the morphoedaphic index and the actual yield in existing fisheries, which can then be used to predict the potential yield for unexploited or unmanaged systems. The estimates of fish yield derived from these models are more than incidental (Ryder et al. 1974) and these models have some predictive utility on the total annual yield attainable from a system. However, since the comprehensive management of a fishery requires an understanding of the biological characteristics of the stock, its interaction with the environment and its response to fishing pressure, the use of morphoedaphic models as a management tool is limited.

More quantitative methodologies that are often mathematically and statistically complex and computationally intensive must therefore be applied. The lack of historical catch data and annual age-composition data negates the use of stock assessment methods which require these data, such as *ad hoc* tuned-Virtual Population Analysis (Pope & Shepherd 1985, Butterworth et al. 1990), integrated analysis (Deriso et al. 1985) and age-structured

production models (Punt & Japp 1994, Booth 1997). For these reasons, abbreviated versions of the full dynamic pool model, such as the yield-per-recruit model (Beverton & Holt 1956, 1957) which allows for the easy evaluation of yield-per-recruit to changes in fishing mortality and age-at-selectivity have been widely applied in both marine and lacustrine environments (Pulfrich & Griffiths 1988, Amarasinghe & De Silva 1992, Blay & Asabere-Ameyaw 1993, Booth & Buxton 1997, Thompson & Allison 1997). However, these models assume that the parameters considered are constant and that the system is in a steady state (Punt 1993b). In addition these models have traditionally treated the target species in isolation from the environment, as well as from other species and from other fisheries. Since most fisheries present a scenario where many species are caught by each gear in a multi-gear fishery and in which interactions exist between fish species and their environment, the use of single species models in managing these fisheries is inadequate.

There has been a growing consensus among fisheries scientists and managers of aquatic resources that traditional single-species approaches should be replaced by methods that account for the highly interactive nature of the fisheries resources. These methods include Multi-Species Virtual Population Analysis (MSVPA) (Sparre 1991, Magnusson 1995) and the ECOPATH approach (Polovina 1984). MSVPA utilises extensive time series of catch-at-age data to produce natural mortality rates and population estimates for exploited parts of the ecosystem and makes prognosis of the impact of changes in fishing intensity and gear-selectivity. However, the data complexity of this model and the need for historical catch-at-age data negates its use in the assessment of African reservoir fisheries. The ECOPATH approach (Polovina 1984, Christensen & Pauly 1992a & b, 1995) has been widely applied

to aquatic ecosystems (Christensen & Pauly 1995, Moreau et al. 1997). ECOPATH is highly data intensive requiring estimates of production, ecotrophic efficiency, relative food consumption and diet composition of all levels in the ecosystem as well as an accurate indication of fish yield (Moreau et al. 1997). For this reason it has only been applied in fisheries where comprehensive studies have led to the availability of input data, e.g. Lake Kariba (Moreau et al. 1997). In addition, the ECOPATH approach is essentially a tool for summarising available knowledge on a given ecosystem to derive various system properties and to compare these with properties derived from other systems. Therefore, ECOPATH provides only a static picture of the ecosystem trophic structure (Walters et al. 1997). To overcome this constraint, the ECOSIM approach was developed for using ECOPATH results to construct dynamic ecosystem models which were capable of dynamic simulation analysis and analysis of changing equilibria (Walters et al. 1997). Although no historical catch data is required for the application of ECOSIM, this model is also considered too data intensive for the assessment and management of most African reservoir fisheries.

The ability to manage African reservoir fisheries on a sustainable basis, therefore, depends on techniques that compromise between data intensity, predictive utility and environmental interactions. For these reasons, the per-recruit approach is considered as the most applicable management tool for African reservoirs. Although per-recruit models assume constant parameters and steady state equilibrium, these models take pertinent biological characteristics (i.e. growth rate, maturity and mortality) into account and allow for the prediction of the response of the stock to changes in gear-selectivity and effort. In marine fisheries, a number of authors have focused on the need of the traditional yield-per-recruit

models to incorporate either multi-species interactions (Murawski 1984, Pikitch 1987) or multi-gear interactions (Murawski 1984, Djama & Pitcher 1997). However, the application of these models in fisheries where multiple gears harvest multiple species has never been applied in reservoir fisheries. Since both multi-species and multi-gear interactions exist in African reservoir fisheries, there is a need for the development of models that can assess the fisheries with multi-species and multi-gear interactions.

Thesis outline

The principal aim of this thesis was to develop predictive management models that incorporate essential biological aspects of the target species, account for both multi-gear and multi-species interactions in the fishery and allow for the relatively rapid assessment of the fishery. Three characteristics made the Lake Chicamba fishery suitable for the development and testing of these models. Firstly, it is a large subsistence fishery in which different types of gear are used, including gill nets, seine nets, cast nets, traps, hook and line and longlines (Weyl 1994). Secondly, the fishery is multi-species, focusing on three major target species: the Mozambique tilapia *Oreochromis mossambicus*, the redbreast tilapia *Tilapia rendalli* and the largemouth bass *Micropterus salmoides*. Thirdly, no historical data were available on the fishery. Lake Chicamba is therefore very similar to other African reservoir fisheries and presented an opportunity to develop a management protocol for African reservoir fisheries as a whole.

To achieve these aims this thesis has been divided into seven Chapters, each addressing a step in the development of the management protocol. Chapter 2 describes the study area,

the sampling strategy and the materials and general methods used in this study. In Chapter 3, the biological parameters which are pertinent for the application of management models are assessed for the three target species. Chapter 4 considers how lake-level fluctuations affect recruitment and the life history of the three principal target species. In Chapter 5, the fishery is assessed in terms of size, gear utilisation, gear selectivity and yield. In Chapter 6, the fishery is assessed using traditional per-recruit models and the adequacy of these traditional models in the development of management advice is discussed. Following from this discussion a new set of models that account for the mixed species catch and multi-gear nature of the fishery were developed and management scenarios were tested. In Chapter 7, a set of guiding principles for the assessment of African reservoir fisheries is developed, a management strategy is recommended for the Lake Chicamba fishery and the utility of the new models as management tools in existing fisheries are considered.

CHAPTER 2

Description of the study area and general methodology

2.1 STUDY AREA

Physical characteristics

Lake Chicamba (19°08'S, 33°08'E), is a mesotrophic to meso-eutrophic hydroelectric impoundment (Robelus & Vissers 1984) with a drainage basin of 2800 km² on the Revue river of the Buzi river system in Manica Province, Mozambique (Figure 2.1). The 75-m high dam wall was constructed in two phases, beginning with the initial closure of the dam in 1959 at 604-m amsl and ending in 1970 when the dam wall was raised to 625 m amsl. The first year of full impoundment was 1975. At maximum capacity the lake covers an area of 116 km² and has a maximum and mean depth of 61 metres and 16 metres, respectively. The substratum is typically silt with stands of drowned trees extending down to the former river channels (Figure 2.2 a).

The lake level follows regional rainfall patterns with a flooding phase commencing during late December and ending in April and a gradual drawdown phase from May to December (Figure 2.3). However, droughts in the subregion caused a general decline in lake level from maximum capacity in 1989 to a low of 12.5 percent of the lakes surface area in 1995. Increased rainfall during the 1995 and 1996 rainy seasons allowed a recovery to 73 percent of total surface area.

During the drawdown phase large areas of silt soils are exposed and are rapidly overgrown with dense grassland vegetation dominated by *Melinis*, *Digitaria* and *Panicum* species (Figure 2.2 b) during the beginning of the rainy season. A substantial proportion of the exposed substratum is also used for subsistence agriculture by the rural community living on the lakeshore (Figure 2.2 c). During the flooding phase (January-April), these grassland and agricultural areas are inundated.

To estimate dry plant biomass submerged by flooding, ten random lakeshore areas (approximately 100-m long) were sampled using 1-m² quadrates (n = 10 per area) during December and January 1996. All plants within each quadrate were removed and dried at 70°C in an oven. It was subsequently determined that 820 ± 202 g m⁻² of dry plant biomass is inundated during the flooding phase. This was similar to the dry standing crop of 792 g m⁻² recorded in the drawdown zone of Lake Kariba (Skarpe 1997). The surface area inundated by flooding and the estimated total submerged plant biomass from 1989 to 1997 is summarised in Table 2.1. No aquatic macrophytes were present in the lake.

Table 2.1. Total area (km²) inundated during the flooding phase in Lake Chicamba between December and March and estimated submerged plant biomass (metric tons), from 1989 to 1997.

Flooding phase	Area inundated	Total biomass
1989/1990	10.9 km ²	8938 t
1990/1991	0.1 km ²	82 t
1991/1992	0 km ²	0 t
1992/1993	6.2 km ²	5084 t
1993/1994	3.4 km ²	2788 t
1994/1995	0.6 km ²	492 t
1995/1996	16.5 km ²	13530 t
1996/1997	51.7 km ²	42397 t

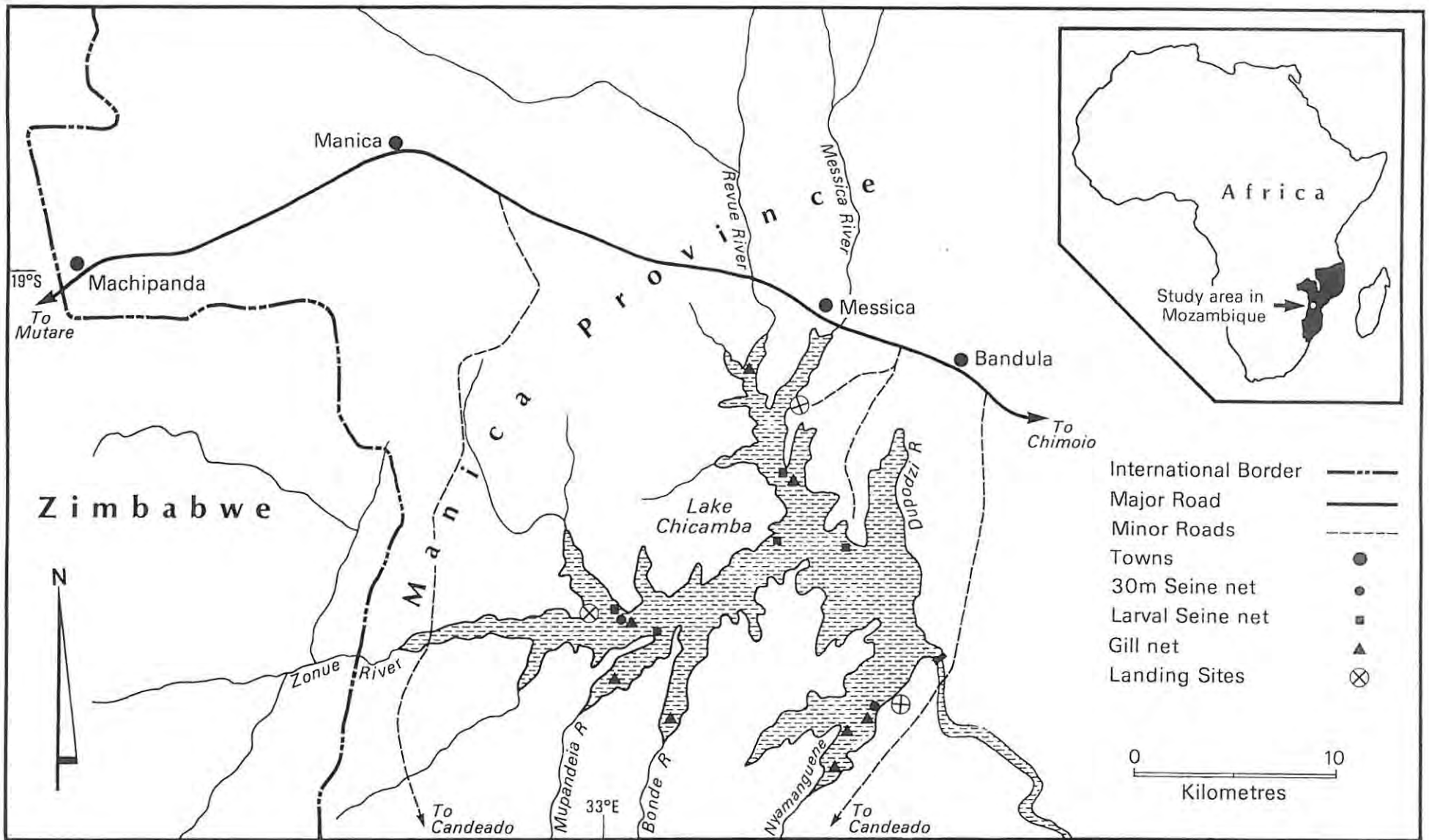


Figure 2.1. A map of Lake Chicamba, Mozambique, showing the seine net, fry seine net and gill net sampling sites and the landing sites where creel surveys were conducted.



Figure 2.2. Photographs of Lake Chicamba showing (a) the typical silt substratum and drowned trees (b) subsistence crop cultivation in the drawdown zone, (c) submerged grassland and (d) submerged maize during the flooding phase (January-April) in Lake Chicamba.

In a comprehensive study on the limnology of Lake Chicamba (Robelus & Vissers 1984) the lake was classified as being warm monomictic with the annual turnover occurring in July.

During the current study period, temperature, oxygen saturation, conductivity, pH and secchi depth were measured monthly at all experimental gill-net, seine-net and fry-seine-net sampling sites (Figure 2.1). Temperature and oxygen saturation were recorded at depths from 0.3 m to 15 m using a hand-held oxygen meter with a probe. Conductivity and pH were measured at a depth of 0.3 m using hand held conductivity and pH meters, which were calibrated daily.

During the present study, the mean summer water temperature was 27.6 °C with a range from 25.2 °C to 32.7 °C, while the mean winter water temperature was 22 °C with a range from 18.5 °C to 25.5 °C (Figure 2.4 a). The annual average water temperature during the period from July 1995 – March 1997 was 25.8 °C. A thermocline was present with an inflexion point shallower than 10 m during the summer months and deeper than 10 m from April to September. This was similar to the position of the thermocline recorded by Vissers & Robelus (1984).

Mean conductivity ranged from 60 $\mu\text{S. cm}^{-1}$ in the river inlets during the rainy season (December – April) to 160 $\mu\text{S. cm}^{-1}$ in the main body of the lake in July 1995. Mean conductivity was $97.4 \pm 19.4 \mu\text{S. cm}^{-1}$. There was no significant seasonal variation in pH (pH 8.3 ± 1.1) during the study period. Dissolved oxygen levels at the surface (0.3 m depth) and at 3m were relatively high and tended towards supersaturation in the surface

layers (Figure 2.4b). There was no evidence of anaerobic conditions up to a depth of 15 m (15 m = maximum depth of the oxygen probe). The temperature regime, conductivity, pH and dissolved oxygen levels during the study period were also similar to those recorded by Vissers and Robelus (1984). Mean secchi depth was 1.5 m, with a range from 10 cm in river inlets at the height of river discharge, to 4 m in the main body of the lake during winter (Figure 2.4 c).

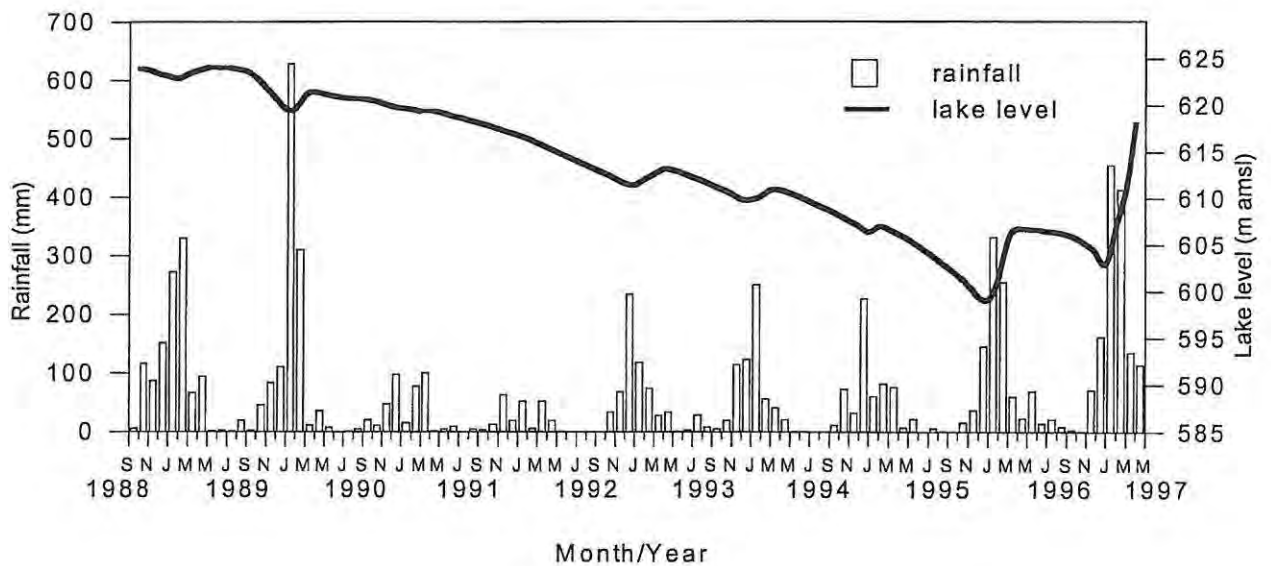


Figure 2.3. Lake Chicamba: monthly rainfall and lake level (m amsl) from September 1988 to April 1997.

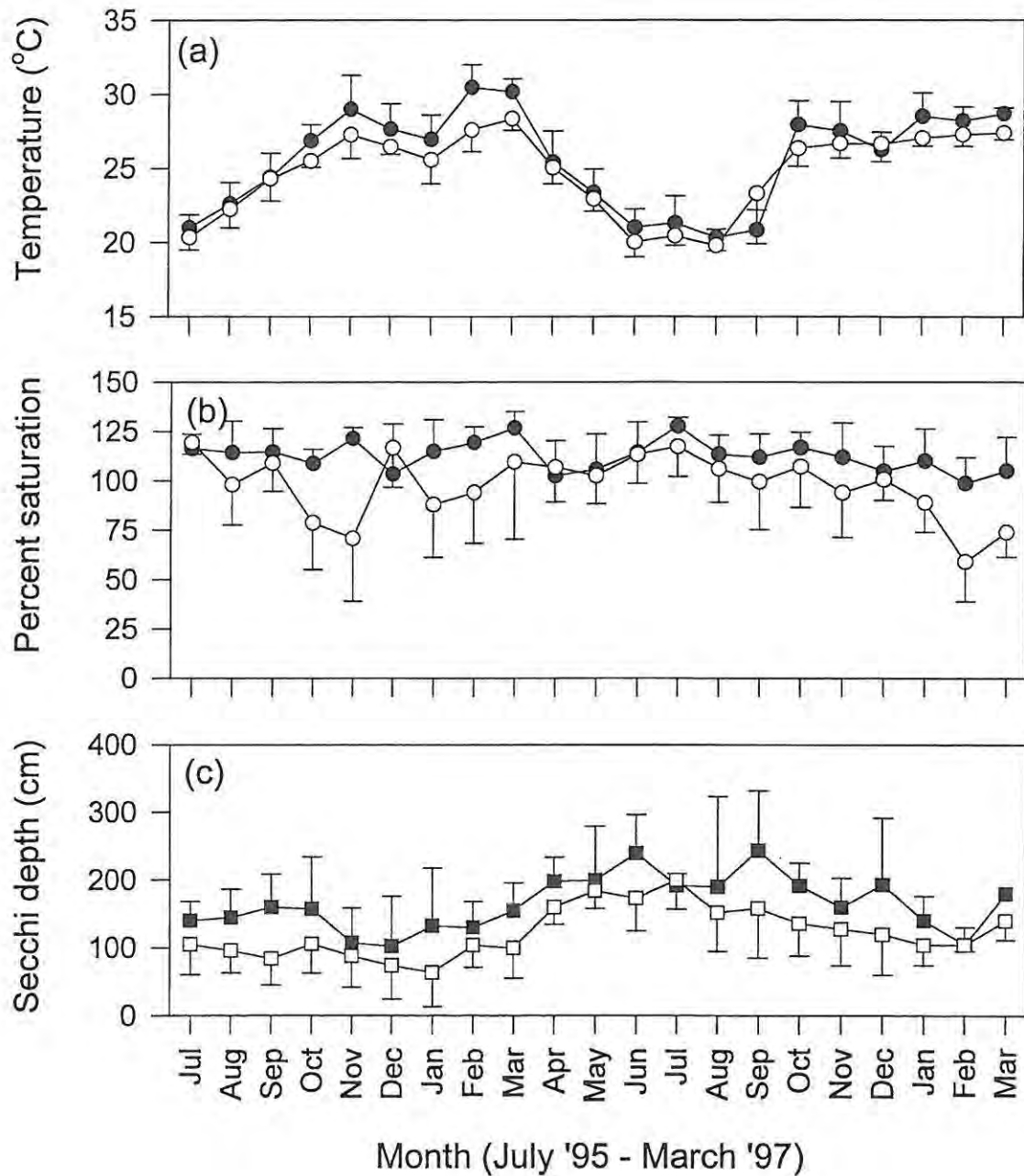


Figure 2.4. Monthly mean \pm standard deviation (a) water temperature at 0.3 m depth (closed circles) and at 3 m (open circles), (b) oxygen saturation levels at 0.3 m depth (closed circles) and at 3 m (open circles) and (c) secchi depth in riverine (open squares) and main lake sites (closed squares) in Lake Chicamba.

Fish fauna

Thirteen fish species were identified in Lake Chicamba during this study (Table 2.2). Included are three alien species, the cyprinid *Cyprinus carpio*, the centrarchid *Micropterus salmoides* and the cichlid *Oreochromis niloticus* (Table 2.2). These species were either introduced through active stocking programmes (*M. salmoides* in 1966 and *C. carpio* during 1992 and 1994) or are a consequence of invasion from upstream reservoirs in Zimbabwe, where they were stocked for angling purposes (*M. salmoides* since the early 1960s and *O. niloticus* from 1992 to the present). All other species are indigenous to the region (Skelton 1993). However, during the 1960s the lake was extensively stocked with *O. mossambicus* and *T. rendalli*.

Table 2.2. Fish species recorded in Lake Chicamba between July 1995 and March 1997 (* denotes alien species).

Species	Common name
ANGUILLIDAE	
<i>Anguilla mossambica</i>	Longfin eel
CYPRINIDAE	
<i>Barbus annectens</i>	Broadstriped barb
<i>Barbus radiatus</i>	Beira barb
<i>Barbus trimaculatus</i>	Threespot barb
<i>Barbus paludinosus</i>	Straightfin barb
<i>Labeo cylindricus</i>	Redeye labeo
<i>Cyprinus carpio</i> *	Carp*
CLARIIDAE	
<i>Clarias gariepinus</i>	African sharptooth catfish
CENTRARCHIDAE	
<i>Micropterus salmoides</i> *	Largemouth bass*
CICHLIDAE	
<i>Pseudocrenilabrus philander</i>	Southern mouthbrooder
<i>Tilapia rendalli</i>	Redbreast tilapia
<i>Oreochromis mossambicus</i>	Mozambique tilapia
<i>Oreochromis niloticus</i> *	Nile tilapia*

2.2. SAMPLING METHODS

The biological and fishery data used in this study were obtained using a variety of sampling methods (Table 2.3). These included experimental gill nets, experimental seine nets, creel surveys, canoe counts and questionnaire surveys. These methods are described in detail in the materials and methods section of the relevant chapters.

Table 2.3. Sources of data used in this study.

Data	Source
Biological data (July 1995 – March 1997)	Experimental gill nets, seine nets and fry seine nets
Fishery data (July 1995 – March 1997)	
Catch composition	Creel surveys
Length frequencies	Experimental gill nets and seine nets Creel surveys
Catch per unit effort	Creel surveys
Effort	Creel surveys Canoe counts Questionnaire surveys

Experimental gill nets

All experimental gill net fleets were composed of six randomly distributed panels of 6-ply multifilament gill netting with manufacturer quoted stretched mesh sizes of 25, 50, 70, 90, 110 and 130 mm, hung at a 60 % ratio. Actual stretched mesh sizes are shown in Table 2.4.

Table 2.4. Manufacturer-quoted stretched mesh size (MQS) and actual stretched mesh range, mean and standard deviation of the six net panels used in experimental gill net fleets on Lake Chicamba, Mozambique. (n = 200)

MQS	Strech mesh range	Mesh size \pm STD
25	22.8 – 25.6 mm	23.8 \pm 0.5 mm
50	46.5 – 49.2 mm	48.0 \pm 0.6 mm
70	66.1 – 69.2 mm	67.3 \pm 0.6 mm
90	86.2 – 93.5 mm	90.1 \pm 1.0 mm
110	110.0 – 120.2 mm	115.5 \pm 2.5 mm
130	125.2 – 140.0 mm	130.9 \pm 2.1 mm

All gill nets were set overnight, between 16h00 and 18h00 and lifted between 06h00 and 08h00. During this study, three gill netting procedures were employed:

- (1) Four main lake sites and five riverine sites (Figure 2.1) were sampled, on a monthly basis from July 1995 to March 1997, using one gill net fleet, with 33 m² (3 m deep \times 11 m long) panels, per sampling site. Additional samples, using the same fleet, were obtained from 49 random sites, which were fished between April 1996 and March 1997. Each gill net fleet was surface-set, parallel to the shore along the 3 m depth contour.

- (2) Ten random sites were sampled between January 1997 and March 1997 using gill net fleets with of 99 m² (3 m deep \times 33 m long) panels. This fleet was surface set along the 3-m depth contour.

(3) Twenty-four randomly selected sites were sampled using both surface-set (along the 3 m depth contour) and bottom-set experimental gill net fleets with 33 m² (3 m deep × 11 m long) panels, from April 1996 to March 1997. The bottom-set gill nets were deployed along contours at depths ranging from 6 to 15 metres.

Each species component in the gill net catch was weighed to the nearest gram and each fish was measured to the nearest millimetre fork length (FL) or total length (TL) depending on species.

Experimental seine nets

Two areas on the lake, approximately 2 km long, were selected for seine netting (Figure 2.1). These areas were relatively free of drowned trees, which would obstruct effective seine netting. Seine nets were 30 m long, 3 m deep and fitted with a bag. Two different mesh diameters, 10 and 25 mm were used. Each area was sampled with each seine net on one day per month, during the second week of each month. On each sampling day 10 seine net hauls were performed at random sites within the two sampling areas. Each species component in the catch was weighed collectively to the nearest gram. A sample of not less than 25 % of each species was measured to the nearest millimetre, FL or TL depending on species.

Experimental fry seine nets

Fry seines consisted of a 1m deep x 2 m long panel of mosquito netting with a mesh size of 1 mm. Monthly samples were taken between February 1996 and March 1997 from five main lake and three riverine sites (Figure 2.1). Five hauls were performed on each

site and each haul covered an area of 10 m². All fish sampled were measured for fork length (FL) or total length (TL) depending on species.

Fish samples for biological analysis were collected monthly from July 1995 to December 1996. All of these fish were measured to the nearest millimetre total length (TL), fork length (FL) and standard length (SL) and weighed whole to the nearest gram.

Questionnaire surveys

Between August 1995 and March 1997, 174 randomly selected fishers were surveyed by means of questionnaires to determine the gear they used, their patterns of utilisation and their resource awareness (Appendix 1).

Creel surveys and canoe counts

Two creel survey methods were used to obtain catch composition, length frequency, catch per unit effort and total effort data for the subsistence fishery. These were landing site surveys and roving creel surveys (Pollock et al. 1994). Landing site creel surveys were conducted at three major landing sites (Figure 2.1). Data were collected on five consecutive days per landing site per month, from August 1995 to March 1997. The date of each sampling period was randomly selected. All fishermen returning to the landing site on the sampling day were interviewed and the gear type, effort and the total mass of each species component in each catch was recorded. A sample of not less than 10 % of each species component in each catch was measured to the nearest millimetre FL or TL, depending on species.

Roving creel surveys were conducted on 15 days per month from January 1996 to March 1997. The lake was divided into 10 sampling areas of equal shoreline length. The sampling day for each area was randomly selected. On each sampling day, an instantaneous activity count was conducted. At least 20 % of the fishers were interviewed in the sampling area and the catch, effort and catch composition were recorded as for the landing site surveys. Total effort was estimated by counting canoes from an aircraft and from a boat moving parallel to the shoreline. The creel surveys and canoe counts are further described in Chapter 5.

CHAPTER 3

The biology of *Micropterus salmoides*, *Tilapia rendalli* and *Oreochromis mossambicus* in Lake Chicamba.

3.1. INTRODUCTION

The life history of fishes in different water bodies is highly variable with respect to growth rate, size at sexual maturity and reproductive periodicity (Lowe-McConnell 1958, 1982, Garrod 1959, Le Roux 1961, Hecht 1980a, DeMerona et al. 1988, Beamesderfer & North 1995). It has been proposed that fishes may tend towards an altricial or precocial life-history style, depending upon environmental conditions (Balon 1979, 1981, Noakes & Balon 1982). The precocial life-history style which includes traits such as delayed maturity, is favoured in large, deep, stable habitats such as reservoirs and lakes. Fish from unstable or harsh environments, which undergo unpredictable and near cataclysmic physico-chemical changes, on the other hand, tend towards the altricial life-history style of early maturation at a small body size (Noakes & Balon 1982). Therefore, the proper assessment and management of a fishery requires an understanding of locality specific growth and reproductive life-history parameters of the species.

The accurate determination of age in fishes is a fundamental requirement for calculating the population age structure and population growth rate (Beamish & McFarlane 1987) upon which reliable stock assessments can be based. Both otoliths and scales have been used with varying degrees of success in ageing studies (Summerfelt & Hall 1987, Weatherly & Gill 1987), but scales have been found to underestimate longevity and thus over-estimate

growth rate (Fagade 1974, Pannella 1974, Hecht 1980a, 1980b, Goeman et al. 1984, Boxrucker 1986, Hammers & Miranda 1991, Booth et al. 1995). Sectioned otoliths are currently considered the most suitable hard tissue for age and growth determination in tropical and subtropical areas (Hecht 1980a, 1980b, Beamish & McFarlane 1987, Hammers & Miranda 1991, Booth et al. 1995).

Since Lake Chicamba is a man-made impoundment and the target species in the fishery are either of riverine origin (*O. mossambicus* and *T. rendalli*) or are alien to this area (*M. salmoides*), the rational exploitation and management of these populations depends on locality-specific biological information. The primary objective of this part of the study was to provide a full biological synthesis of the three principal fishery species in the lake (*M. salmoides*, *T. rendalli* and *O. mossambicus*), upon which management proposals and recommendations can be based.

3.2. METHODS AND MATERIALS

General

Samples of *M. salmoides*, *T. rendalli* and *O. mossambicus* were collected monthly from Lake Chicamba between October 1995 and December 1996 using the experimental seine netting and experimental gill netting procedures described in Chapter 2. *M. salmoides* were measured to the nearest millimetre fork length (FL) and standard length (SL) and weighed whole to the nearest 0.1 g. The two cichlids were measured to the nearest millimetre total length (TL) and standard length (SL) and also weighed whole to the nearest 0.1 g. The fish were subsequently dissected and sexed. The gonads were removed, weighed and categorised according to five developmental stages described in Table 3.1. The eviscerated

mass of the fish was then recorded. The sagittal otoliths were removed and stored dry in manilla envelopes for subsequent sectioning and age estimation.

Table 3.1. Macroscopic criteria used to stage gonadal development in *Micropterus salmoides* and the two cichlids *Tilapia rendalli* and *Oreochromis mossambicus* from Lake Chicamba.

Stage	Development	Macroscopic appearance
I	Juvenile	Not possible to visibly distinguish sex. Gonad appears as a translucent gelatinous strip.
II	Resting	Ovaries white or slightly yellowish. Oocytes are macroscopically distinguishable. Testes are discernible as thin white bands.
III	Developing	Ovaries enlarged, oocytes readily visible and yellow. Testes broadened, distended and cream in colour.
IV	Ripe	Oocytes of maximum size. Yellow and hydrated and readily extruded under abdominal pressure from females of <i>M. salmoides</i> . Oocytes yellow to green and hydrated in <i>O. mossambicus</i> and <i>T. rendalli</i> . Testes swollen to maximum size.
V	Spent	Ovaries flaccid and sac-like with few vitellogenic oocytes visible. Testes reduced in size and dirty grey in colour.

Age and growth

To enhance the visibility of otolith rings, the otoliths were burnt over a low-intensity ethanol flame until they turned pale brown. Care was taken not to char the otoliths, as this tends to obscure the internal structure and margin of the otolith (Booth & Merron 1996). The otoliths were mounted medial side down in clear polyester casting resin and sectioned transversely through the nucleus using a double-bladed diamond-edged saw and mounted on slides with DPX mountant.

The number of opaque zones was read on two occasions with a dissecting microscope under transmitted light using variable magnification. If the two readings were the same then the age estimate was accepted. If the two readings were not the same, a third reading was taken and the age estimate was accepted if two of the three readings were the same. If the three readings differed by two years then the mean of the three estimates was taken. If the readings differed by more than two years then the otolith was rejected.

To determine the periodicity of ring formation, the outer margin of otoliths sampled at monthly intervals was examined. A total of 176 *M. salmoides*, 141 *T. rendalli* and 185 *O. mossambicus* sagittal otoliths was examined. In the otoliths, growth was reflected as alternating opaque and translucent zones (Figure 3.1). The composition of the outer margin (either opaque or translucent) was noted and expressed as a percentage of the monthly sample (Figure 3.2).

In *M. salmoides* the spawning season and annulus formation were discrete (Figure 3.2a, 3.5a, 3.6a). Accurate monthly-age determinations could, therefore, be obtained for the species by back calculating the age of the sampled fish to the last spawning season. The assumption was made that all fish were born in the mode of the spawning season. Due to a protracted spawning season in the Cichlidae, this back-calculation procedure was not possible for *T. rendalli* and *O. mossambicus*.

Recommendations by Punt and Hughes (1992) for determining and fitting appropriate growth models were followed. The non-parametric one-sample runs test for randomness

and the Bartlett's test for homoscedascity (Hughes 1986) were applied. Variance estimates were calculated using the (conditioned) parametric bootstrap resampling method (Efron 1982) with 500 bootstrap iterations. Standard errors and 95% confidence intervals were constructed from the bootstrap data using the percentile method described by Buckland (1984). PC-YIELD 2.2 (Punt & Hughes 1992) was used to execute the above procedure. This software uses a non-linear minimisation routine (simplex method) to obtain parameter estimates for the selected growth model. The selected model was the specialised von Bertalanffy growth model of the form:

$$l_a = L_{\infty}(1 - e^{-K(a - a_0)}) \quad (\text{Equation 3.1})$$

where a_0 is the age at "zero" length; L_{∞} is the predicted asymptotic length and K is the Brody growth co-efficient (Ricker 1975, Punt & Hughes 1992).

To determine the growth rate of juvenile *M. salmoides*, monthly samples of fish were collected from October 1995 to May 1996 (n=1592). The fish were measured to the nearest millimetre fork length (FL). Juvenile growth rate was determined by cohort analysis using linear regression.

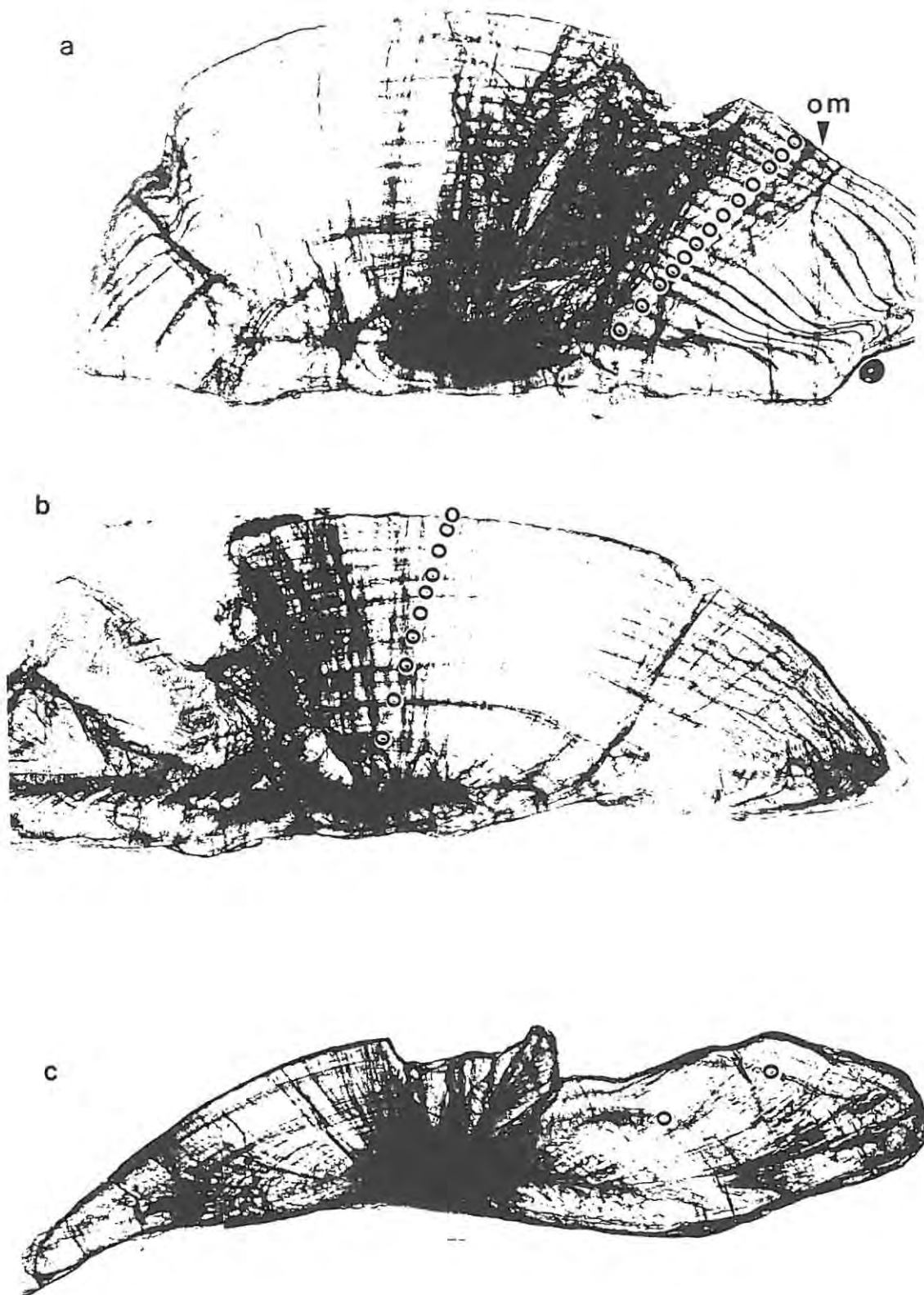


Figure 3.1. Photomicrographs of sagittal otoliths from (a) a 231 mm TL, 14 year-old *Tilapia rendalli*, (b) a 320 mm TL, 10 year-old *Oreochromis mossambicus* and (c) a 405 mm FL, 2 year-old *Micropterus salmoides* from Lake Chicamba. Note the opaque margin (om) on the *T. rendalli* otolith.

Maturity and spawning periodicity

Mean length at sexual maturity was determined from 111 male and 80 female *M. salmoides*, collected in August and September 1995 and 1996, 328 male and 401 female *T. rendalli* and 125 male and 442 female *O. mossambicus* collected during the peak reproductive season between October 1995 and February 1996. The proportion of sexually mature individuals (ψ) by length (L) was fitted to the logistic curve:

$$\psi = \frac{1}{1 + e^{-(L-Lm_{50})/\delta}}, \quad (\text{Equation 3.2})$$

where Lm_{50} is the mean length-at- 50%- sexual maturity and δ is the width of the logistic ogive. Since the highest proportion of mature *O. mossambicus* females was 76.9% the logistic curve for this plot (Figure 4d) was fitted to data which were multiplied by a correction factor of 1.3. This correction factor was applied since fitting the logistic curve directly to data from populations where not all mature individuals are in reproductive condition at the same time leads to an overestimation of Lm_{50} (King 1995). Age-at-50%-maturity was determined by converting length frequency data to age frequency and fitting the same logistic ogive.

Temporal patterns in reproductive activity were assessed on a monthly basis using a gonadosomatic index (GSI) and development stages of the gonads. A total of 225 female *M. salmoides*, 201 female *T. rendalli* and 228 female *O. mossambicus* was sampled. All fish in the sample were above the mean size at sexual maturity. The gonadosomatic index was expressed as:

$$\text{GSI} = \left[\frac{\text{Gonad mass (g)}}{\text{Eviscerated mass (g)}} \right] \times 100 \quad (\text{Equation 3.3})$$

Eviscerated mass was used to minimise bias from variable gut fullness.

To assess whether spawning was dependent on flooding, the proportion of ripe females and GSI values were grouped into three categories according to season. These were summer flooding periods (January to April), winter drawdown periods (May to August) and summer drawdown periods (October to December). The seasonal distribution of ripe females was analysed using a 2 X 3 contingency table. Seasonal variation in GSI values was compared using the non-parametric Kruskal-Wallis one-way analysis of variance (ANOVA) on ranks. To isolate the group or groups that differed from the others an all-pairwise multiple comparison procedure (Dunn's Method) was performed. A significance level of $p < 0.05$ was chosen for all tests.

Feeding

Initial observations showed that the diet of *O. mossambicus* and *T. rendalli* in Lake Chicamba did not differ from detritivory and macrophytic browsing recorded in other populations (Le Roux 1956, Munro 1967, Wagner & Rowe-Rowe 1972, Bruton & Boltt 1975, Caulton 1976, 1977 a & b, Whitfield & Blaber 1978, Bowen 1979, De Moor et al. 1986, Chifamba 1990). For this reason the diet of these two cichlid species was not investigated further. To gain an understanding of the diet of the predator, *M. salmoides* in Lake Chicamba the diet of the fish was analysed. Fish were collected from October 1995 to September 1996. The total sample consisted of 173 young-of-the-year and 179 adult *M.*

salmoides. Stomachs were dissected out of the fish and preserved in 10% formalin. Stomach contents were examined and the individual items were counted and weighed wet, to the nearest 0.05g. The stomach contents were assessed using the index of relative importance (IRI), as described by Hyslop (1980):

$$IRI = (\%N + \%M) \times \%F \quad \text{(Equation 3.4)}$$

where $\%N$ is the number of individuals in each food category expressed as a percentage of the total individuals in all food categories; $\%M$ is the mass of all individuals in each food category expressed as a percentage of the total mass of all food categories; and $\%F$ is the frequency of occurrence of a particular dietary item i.e. the number of stomachs containing a certain food item expressed as a percentage of all stomachs in the sample. Stomach contents were compared with prey abundance data outlined in Chapter 4.

Mortality estimates

A first approximation of the instantaneous rate of total mortality (Z) for *M. salmoides*, *O. mossambicus* and *T. rendalli* was estimated by catch-curve analysis (Ricker 1975). Catch-curve analysis was applied to length frequency distributions, which were converted to age frequency distributions by means of a normalised age-length key (Butterworth et al. 1989). The length frequency distributions for *O. mossambicus* and *T. rendalli* were obtained from experimental gill net fleet samples (see Chapter 2) and from the subsistence seine net and hook and line fisheries (see Chapter 5). Length frequency data for *M. salmoides* were obtained from two angling tournaments held in October 1995 and August 1996 respectively

as well as from the subsistence seine-net and hook-and-line fishery. In addition, further estimates of Z were obtained by using the Butterworth et al. (1989) equation:

$$Z = \ln \left[1 + \frac{1}{(a_r - a_f)} \right] \quad \text{(Equation 3.5)}$$

where a_f is the mean age at full recruitment and a_r is the age of fully recruited fish sampled. A first approximation of Z was obtained by averaging the slope estimates from catch-curves and from the estimates obtained using the Butterworth et al. (1989) equation on age-converted data collected from the subsistence gill-net, seine-net and hook-and-line fisheries.

Of the life history parameters used in fisheries models, natural mortality (M) is one of the most elusive. Whilst in unexploited populations the natural mortality rate can be estimated by catch curve analysis, this is not possible in exploited fish populations. As a result, the estimation of natural mortality most commonly relies on empirical relationships. Correlating natural mortality rates from unexploited populations with biotic and abiotic parameters pertaining to the stock, derives these relationships (Pauly 1980, Rihkter & Efanov 1977, Gunderson & Dygert 1988, Hoenig 1983). Since these empirical relationships represent approximations of the natural mortality rate, four empirical equations were used to obtain an estimate of M for the three stocks, namely:

(1) Pauly's (1980) empirical equation:

$$\ln M = -0.0152 - 0.279 \ln L_\infty + 0.6543 \ln K + 0.463 \ln T \quad \text{(Equation 3.6)}$$

where L_∞ and K are the von Bertalanffy growth parameters and T is the mean annual water surface temperature ($^{\circ}\text{C}$);

(2) the Rihkter and Efanov (1977) equation:

$$M = \frac{1.521}{a_m^{0.72}} - 0.155 \quad (\text{Equation 3.7})$$

which uses the age-at-50 % maturity (a_m) as a parameter;

3) the Gunderson and Dygert (1988) equation:

$$M = 0.03 + 1.68 \times \text{GSI} \quad (\text{Equation 3.8})$$

which uses the GSI of ripe female fish as the input parameter; and

4) the Hoenig (1983) equation:

$$\ln Z = 1.46 - 1.01 \ln(a_{\max}) \quad (\text{Equation 3.9})$$

which uses the maximum age sampled (a_{\max}) as a parameter in order to estimate Z in *O. mossambicus* and *T. rendalli*. Although the Hoenig (1983) equation was developed to approximate total mortality, it was derived from empirical data that pertained to unexploited or lightly fished stocks. Since, considerable effort was made to sample a wide age-range of *O. mossambicus* and *T. rendalli* individuals (Chapter 3), the value derived from the Hoenig (1983) equation is probably closer to M than to Z . Since the oldest M .

salmoides sampled was relatively young (5 years), the Hoenig (1983) equation was not used in the estimation of M in this species. Having obtained Z and M , fishing mortality was derived by subtraction ($F = Z - M$).

3.3. RESULTS

Age and growth

Morphometric relationships between FL, weight and SL are summarised in Table 3.2. Of the 304 *M. salmoides*, 300 *T. rendalli* and 199 *O. mossambicus* otoliths examined, 7.2%, 3%, and 7%, respectively, were rejected as unreadable. The monthly examination of otolith margins revealed that one translucent and one opaque zone were deposited in the otoliths each year (Figure 3.2). These were validated as annuli and could be used to estimate the age of the species. *M. salmoides*, *T. rendalli* and *O. mossambicus* reached a maximum age of 5, 16 and 10 years respectively. Length-at-age keys for *M. salmoides*, *T. rendalli* and *O. mossambicus* are presented in Tables 3.3, 3.4 and 3.5 respectively.

Table 3.2. Morphometric relationships of *Micropterus salmoides*, *Tilapia rendalli* and *Oreochromis mossambicus* from Lake Chicamba. Wt = weight, FL = fork length, SL = standard length.

Relationship		r^2	P	n
<i>M. salmoides</i>				
Wt (g)	= $0.000013 \times \text{FL (mm)}^{3.043}$	0.99	< 0.001	616
SL (mm)	= $- 8.049 + 0.880 \times \text{FL (mm)}$	0.99	< 0.001	194
<i>T. rendalli</i>				
Wt (g)	= $0.000012 \times \text{TL (mm)}^{3.136}$	0.99	< 0.001	821
SL (mm)	= $- 2.290 + 0.797 \times \text{TL (mm)}$	0.95	< 0.001	366
<i>O. mossambicus</i>				
Wt (g)	= $0.000021 \times \text{TL (mm)}^{2.984}$	0.99	< 0.001	602
SL (mm)	= $- 1.722 + 0.802 \times \text{TL (mm)}$	0.98	< 0.001	250

Length-at-age for *M. salmoides*, *T. rendalli* and *O. mossambicus* was adequately described by the von Bertalanffy growth model. This model was chosen since its parameters are commonly used in empirical estimates of natural mortality (Pauly 1980), in per-recruit modelling (Ricker 1975) and for ease of comparison with growth studies conducted in other localities and on other species. The von Bertalanffy growth parameters, their associated estimates of variation and confidence intervals are summarised in Table 3.6 and Figure 3.3.

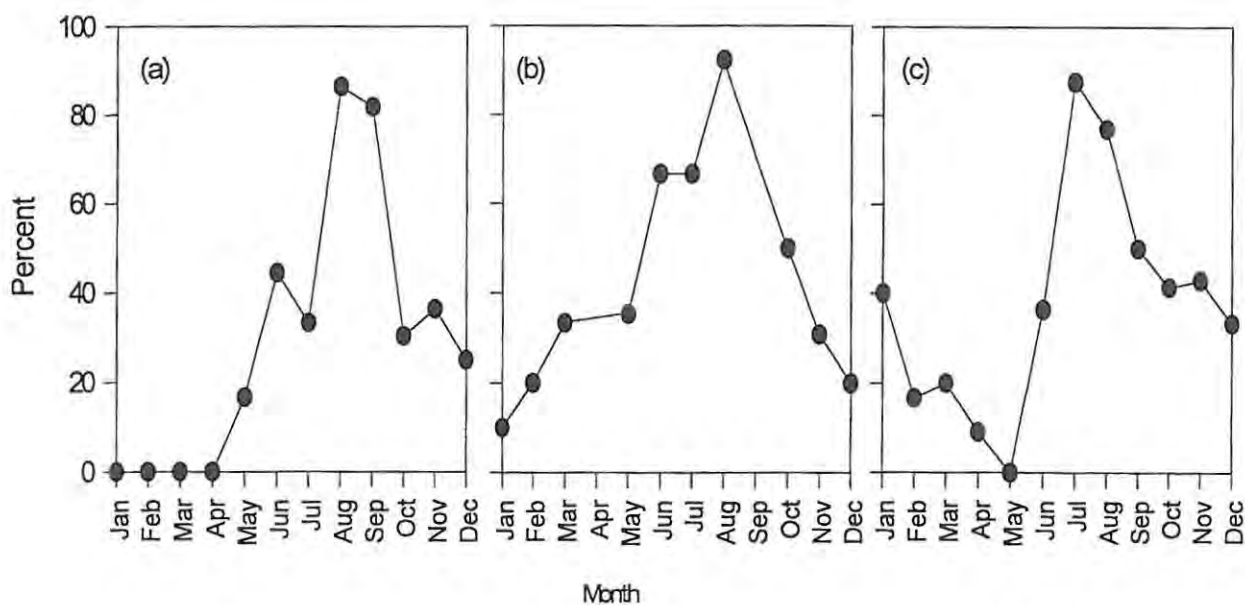


Figure 3.2. The monthly percent occurrence of an opaque margin in otoliths of (a) *Micropterus salmoides*, (b) *Tilapia rendalli* and (c) *Oreochromis mossambicus*, sampled from Lake Chicamba.

Table 3.3. Length-at-age (FL) key for *Micropterus salmoides* in Lake Chicamba. Age was estimated from readings of sectioned sagittal otoliths.

Length (mm FL)	Age (years)					
	0	1	2	3	4	5
41-290	78					
291-300	5	1				
301-310	3	6				
311-320	3	2				
321-330	2	8				
331-340		16	1			
341-350		18	4			
351-360		17	1			
361-370		3				
371-380			3			
381-390			2			
391-400			8			
401-410			10	2		
411-420			11	5	1	
421-430			9	5		
431-440			9	1	1	
441-450			8	6		
451-460			4	5	2	
461-470			2		1	1
471-480			4	3	1	
481-490			3	2		
491-500				3	1	
501-510						1
511-520			1		1	
521-530						
531-540						1
n	91	71	80	32	8	3

Table 3.4. Length-at-age (TL) key for *Tilapia rendalli* in Lake Chicamba. Age was estimated from readings of sectioned sagittal otoliths.

Length (mm TL)	Age (years)																
	0	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16
1-70	1																
71-80	14																
81-90	14																
91-100	21	1															
101-110	29																
111-120	22	2															
121-130	11																
131-140	4	1		1													
141-150	1	2				1											
151-160	5	8															
161-170	4	2															
171-180		2		1		1											
181-190		3	1	1	1	1											
191-200	1	2		5	4	1	1										
201-210	1		4	4	3	1											
211-220	1	1	5	5	2	5	1	1	1	2			1				
221-230		1	2	4	2	6	5	1	2	1		4	2				1
231-240			3	4	2	5	1	3	1		1				1	1	
241-250				1	3		6	1	1	1	2		1				
251-260			1	1	1	2	1	3						1			
261-270				1		2	2	2			1						
271-280						1						1					
281-290						1				1			1				
291-300																	
301-310								1									
n	130	25	16	28	18	27	17	12	5	5	4	5	5	1	1	1	1

Table 3.5. Length-at-age (TL) key for *Oreochromis mossambicus* in Lake Chicamba. Age was estimated from readings of sectioned sagittal otoliths.

Length (mm TL)	Age (years)										
	0	1	2	3	4	5	6	7	8	9	10
1-70	2										
71-80	18										
81-90	21	1									
91-100	17										
101-110	19	3									
111-120	23	1									
121-130	20	2									
131-140	8	8	2	1							
141-150	2	1	1	1							
151-160	2	1	1								
161-170	2	1			1						
171-180	3	1	1								
181-190	1	3	2	1							
191-200		1		1		2					
201-210		2	1	1	2						
211-220			2	1	1	4	1				
221-230		1	1	5	1	2					
231-240		2	4	9	5	2	1	1			
241-250			3	7	3	3	2				
251-260				6	8	3	3				
261-270			1	3	4	6		1			
271-280				1	1			1			
281-290			1	2	3	1	1				
291-300				2	2	1	1		1		
301-310			1	4	3						1
311-320				2	3	1				1	
321-330			1					1			
331-340											
341-350											
351-360											
361-370							1				
n	138	28	22	47	37	25	10	4	1	1	1

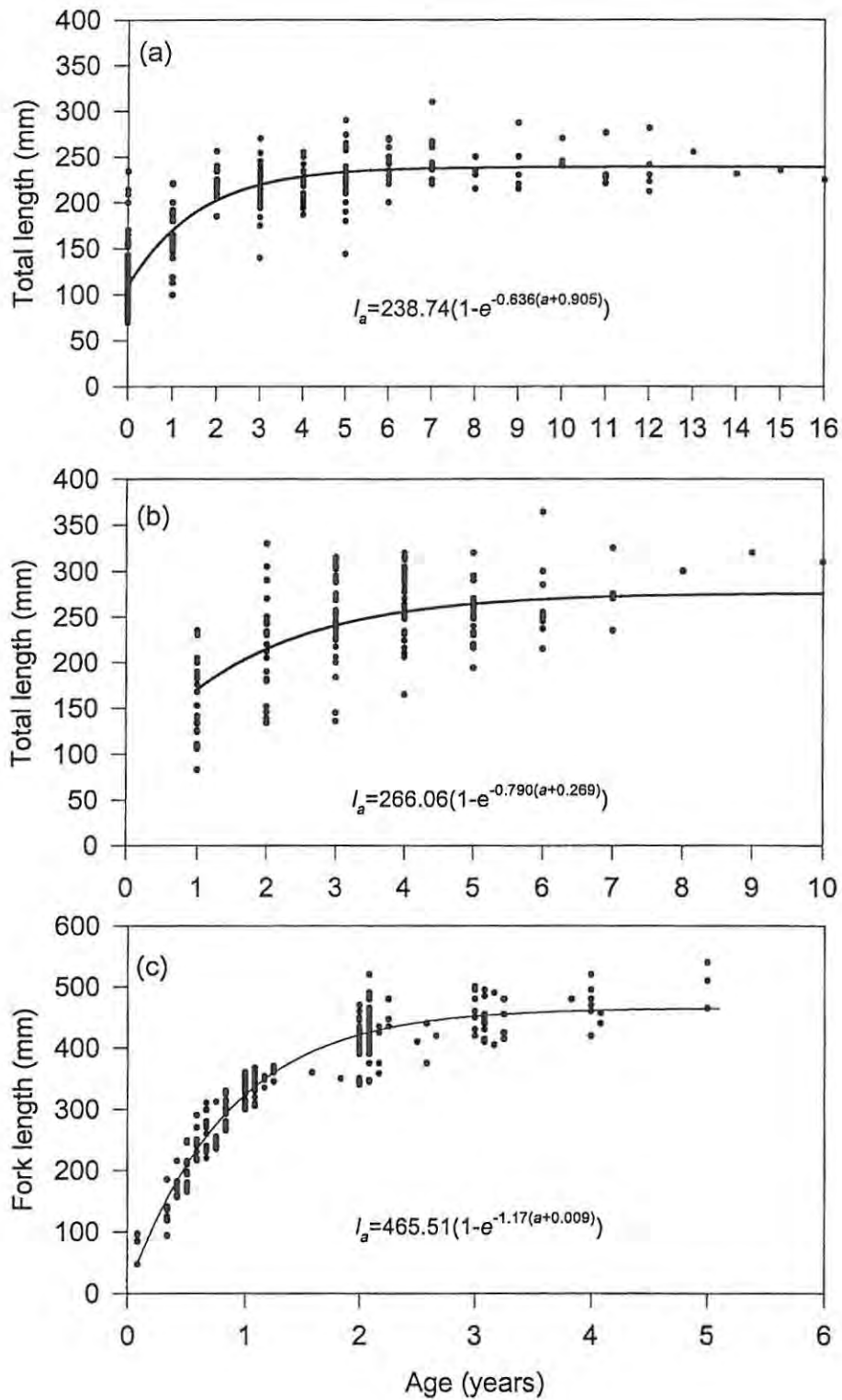


Figure 3.3. Observed individual lengths-at-age of (a) *Tilapia rendalli*, (b) *Oreochromis mossambicus* and (c) *M. salmoides* determined using sagittal otoliths. Samples were collected between October 1995 and September 1996. The growth curves were fitted to combined sex data using the von Bertalanffy growth model with an absolute error structure.

Table 3.6. The von Bertalanffy growth parameters, standard error (SE) and 95% confidence intervals for *Micropterus salmoides*, *Tilapia rendalli* and *Oreochromis mossambicus* in Lake Chicamba.

Parameter	Estimate	SE	95 % confidence
<i>M. salmoides</i>			
<i>K</i>	1.17 year ⁻¹	0.05	[1.07, 1.25]
<i>L</i> _∞	465.51 mm FL	4.87	[456.50, 476.08]
<i>a</i> ₀	-0.009	0.021	[-0.058, 0.026]
<i>T. rendalli</i>			
<i>K</i>	0.636 year ⁻¹	0.06	[0.539, 0.76]
<i>L</i> _∞	238.74 mm TL	3.16	[232.21, 245.18]
<i>a</i> ₀	-0.905	0.079	[-1.059, -0.762]
<i>O. mossambicus</i>			
<i>K</i>	0.790 year ⁻¹	0.23	[0.470, 1.361]
<i>L</i> _∞	266.06 mm TL	8.01	[253.67, 285.11]
<i>a</i> ₀	-0.269	0.340	[-1.048, 0.245]

The observed length-at-age (FL) for *M. salmoides* juveniles are presented in Table 3.7. The linear regression model:

$$FL \text{ (mm)} = 31.1 + 22.8 \times \text{age (months)} \text{ (} r^2 = 0.91 \text{)}$$

best described the growth of juvenile largemouth bass during the first 7 months of life.

Table 3.7. Sample size, observed length range and observed lengths-at-age (FL \pm standard deviation) of young-of-the-year *Micropterus salmoides* sampled between October 1995 and April 1996 from Lake Chicamba.

Age (months)	n	Observed length range (mm FL)	Mean \pm STD
1	815	30 – 97	57.5 \pm 6.8
2	302	57 – 115	69.5 \pm 17.6
3	149	69 – 120	86.1 \pm 8.7
4	211	104 – 180	121.7 \pm 10.8
5	31	90 – 212	161.5 \pm 22.6
6	40	155 – 217	176.0 \pm 14.7
7	44	95 – 260	201.0 \pm 26.5

Reproductive biology

O. mossambicus and *T. rendalli*

Of the 729 mature *T. rendalli* sampled 45% were male and 55% were female. The sex ratio was 1 male : 1.22 females, differing significantly from unity ($\chi^2 = 7.31$, $df = 1$, $p < 0.05$). Male *T. rendalli* attained L_{m50} at 218 mm TL (Figure 3.4a) and females at 205 mm TL (Figure 3.4b). Of the 527 mature *O. mossambicus* sampled 24% were male and 76% were female. The sex ratio was 1 male : 3.16 female, differing significantly from unity ($\chi^2 = 143.23$, $df = 1$, $p < 0.05$). *O. mossambicus* males and females attained L_{m50} at 251 mm TL, and 223 mm TL respectively (Figure 3.4c & d). The mean age-at-50% maturity was calculated at 2.83 years for *O. mossambicus* and 2.89 years for *T. rendalli*.

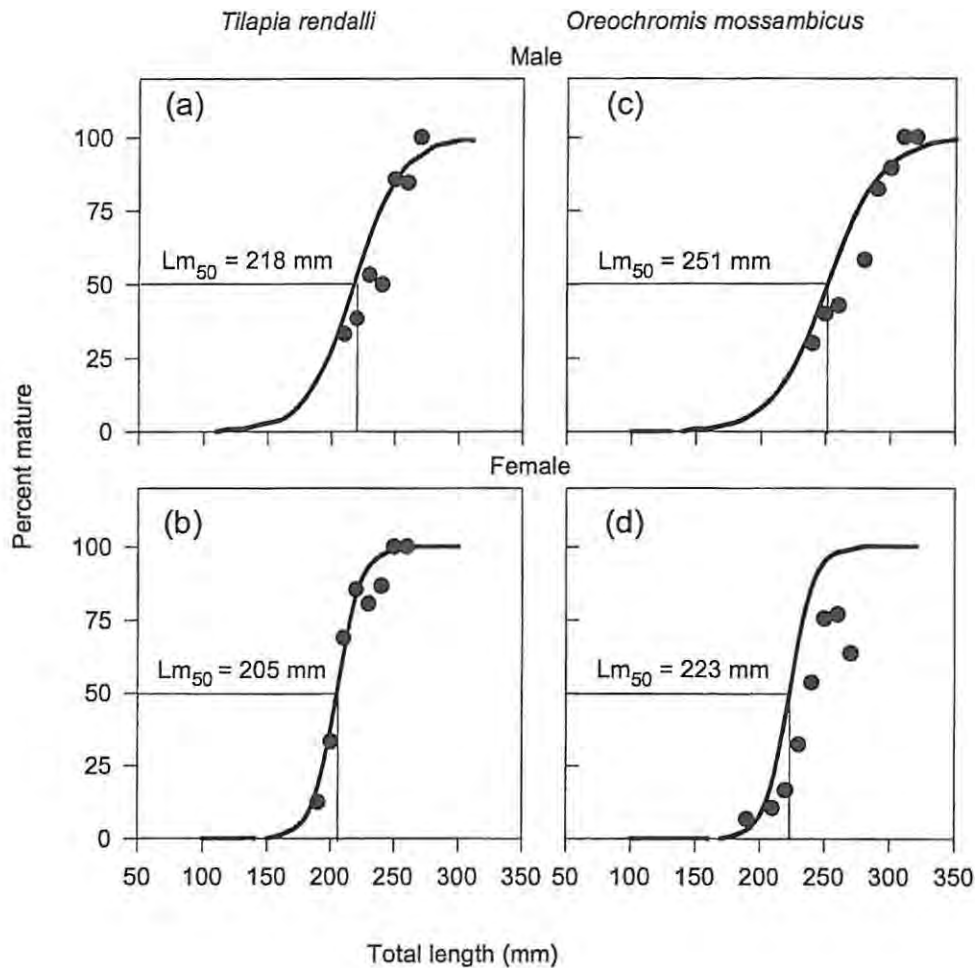


Figure 3.4. Sexual maturity in (a) *Tilapia rendalli* males ($n = 328$), (b) *T. rendalli* females ($n = 401$), (c) *Oreochromis mossambicus* males ($n = 125$) and (d) *O. mossambicus* females ($n = 401$) in Lake Chicamba. The length-at-50%-maturity (Lm_{50}) was calculated by fitting a logistic ogive to the data. In *O. mossambicus* females (d) a maximum of 76.9% mature females was recorded and the logistic ogive was fitted to data which was multiplied by a correction factor of 1.3.

From October to January, over 60% of female *T. rendalli* were in the ripe condition (Figure 3.5b). The proportion of ripe female *T. rendalli* decreased sharply in February to 15%, with the majority of females (69%) being in the “spent” condition (Figure 3.5b). During July 1996 and August 1996 no ripe females were recorded (Figure 3.5b). By September, the proportion of ripe females increased to 38% (Figure 3.5 b). The proportion of ripe

females was significantly dependent on season ($\chi^2 = 62.08$, $df = 2$); however, there was no difference in the proportion of ripe females between the 1995 drawdown summer and 1996 flooding summer periods ($\chi^2 = 0.267$, $df = 1$).

O. mossambicus were in a ripe condition between October and March (Figure 3.5c). By April this proportion had dropped to 45% and in May, July and August no ripe female *O. mossambicus* were sampled (Figure 3.5c). The proportion of ripe females was significantly dependent on season ($\chi^2 = 49.63$, $df = 2$). Similarly, there was no significant difference between the 1995 drawdown and 1996 flooding summer periods ($\chi^2 = 0.200$, $df = 1$).

In both *T. rendalli* and *O. mossambicus* the mean GSI values in summer (October to March) were significantly higher than in winter (May to August) ($p < 0.05$; Figure 3.6 b & c). GSI values during the drawdown and flooding summer did not differ significantly from each other.

Micropterus salmoides

Of the 168 mature *M. salmoides* collected during the period August 1995 to October 1996, 50.6% were male and 49.4 % female. The adult sex ratio did not differ from unity ($\chi^2 = 0.023$, $df = 1$, $p > 0.05$). No immature male or female *M. salmoides* were recorded in September. The smallest mature male measured 305 mm FL and the smallest mature female measured 290 mm FL. Maturity in this species is, therefore, attained within the first year, at a calculated age of 0.9 years.

M. salmoides ovaries were in a developing phase from April to July (Figure 3.5 a). By August, 43% were ripe and all ovaries were ripe in September (Figure 3.5 a). Over 95% of the October sample and the entire November and December samples were in the spent condition (Figure 3.5 a). This trend was reflected by rapidly increasing GSI from May (1.2%) to September (9.4%) and a marked fall to a GSI of 1.4% in October (Figure 3.6 a). The August and September GSI values were significantly higher than in any of the other months ($p < 0.05$).

Feeding

The diet of *M. salmoides* in different age classes is summarised in Table 3.7. Initially (October 1995), the diet of the 1995 cohort of *M. salmoides* was dominated by *Daphnia* sp., *Corixa* sp. and aquatic insects (Table 3.8, Figure 3.7 a). After November, there was a steady transition towards piscivory (Table 3.8). Cichlids were the most important dietary item from February to April; thereafter a distinct shift towards cyprinid prey in July and August was recorded (Table 3.8, Figure 3.7 a). In adult largemouth bass collected between October 1995 and December 1995 where primarily cannibalistic (Table 3.8, Figure 3.7 b), while cichlids dominated the diet of the 1995 cohort from September to November 1996 (Table 3.8, Figure 3.7a).

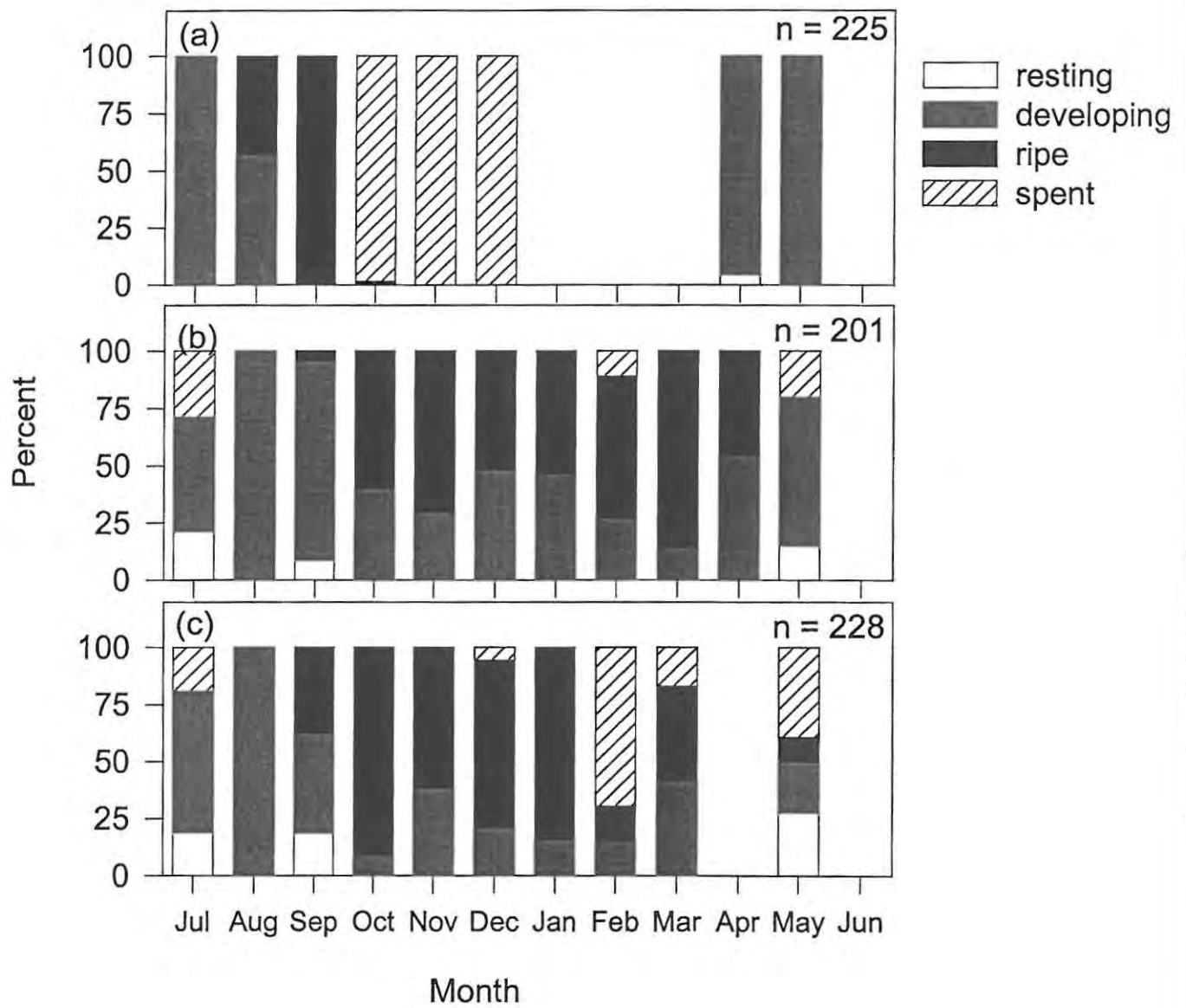


Figure 3.5. Gonad maturity in female (a) *Micropterus salmoides*, (b) *Tilapia rendalli* and (c) *Oreochromis mossambicus* collected from Lake Chicamba.

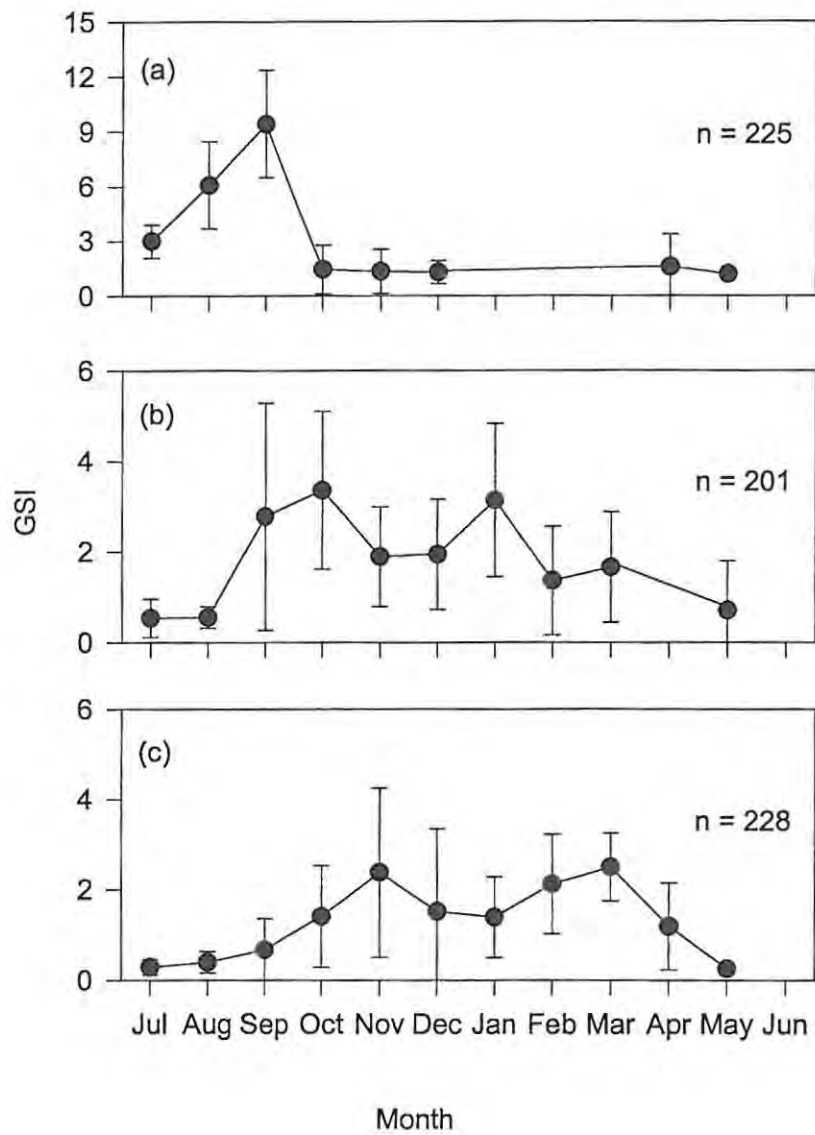


Figure 3.6. Monthly gonadosomatic indices (GSI) \pm standard deviation for female (a) *Micropterus salmoides*, (b) *Tilapia rendalli* and (c) *Oreochromis mossambicus* in Lake Chicamba.

Table 3.8. Monthly index of relative importance (IRI) of prey items in the diet of different mean length (mm fork length) and monthly age of *Micropterus salmoides* collected between October 1995 and November 1996 from Lake Chicamba.

Month	Index of relative importance (IRI)														
	Oct 95	Nov 95	Jan 96	Feb 96	Mar 96	Apr 96	May 96	Jul 96	Aug 96	Sep 96	Oct 95	Oct 96	Nov 95	Nov 96	Dec 95
	58 mm	70 mm	122 mm	162 mm	176 mm	201 mm	250 mm	>290 mm	>290 mm	>300 mm	>300 mm	>300 mm	>300 mm	>300 mm	>300 mm
Age (months)	(1)	(2)	(4)	(5)	(6)	(7)	(8)	(>10)	(>11)	(>12)	(>13)	(>13)	(>14)	(>14)	(>15)
Prey item															
<i>Daphnia</i> sp.	13803	3983	0	38	0	0	0	0	0	0	0	0	0	0	0
<i>Corixa</i> sp.	578	0	6009	476	155	0	0	0	0	0	0	0	0	0	0
Aquatic insects	0	3536	0	3386	5807	0	492	217	155	449	1	0	7	0	0
Terrestrial insects	0	0	25	1095	1890	0	0	0	0	0	21	0	0	0	13
Mollusca	0	6	0	0	0	0	0	0	0	0	0	0	0	0	0
Crabs	0	0	0	2	0	0	0	0	0	86	0	0	0	0	0
Reptiles	0	0	0	0	0	0	0	0	0	0	3	0	0	0	0
Fish remains	5	6	1619	236	1390	658	203	341	432	88	495	82	192	0	1587
Cichlidae	0	1	165	1029	4264	27922	5309	393	1752	5034	301	12183	260	0	503
Cyprinidae	0	0	0	0	69	12	57	1847	2934	782	600	0	29	66	45
<i>C.gariepinus</i>	0	0	0	41	51	0	70	0	0	0	0	0	0	0	0
<i>M.salmoides</i>	0	0	0	0	0	0	0	0	0	0	2334	472	6541	0	2279

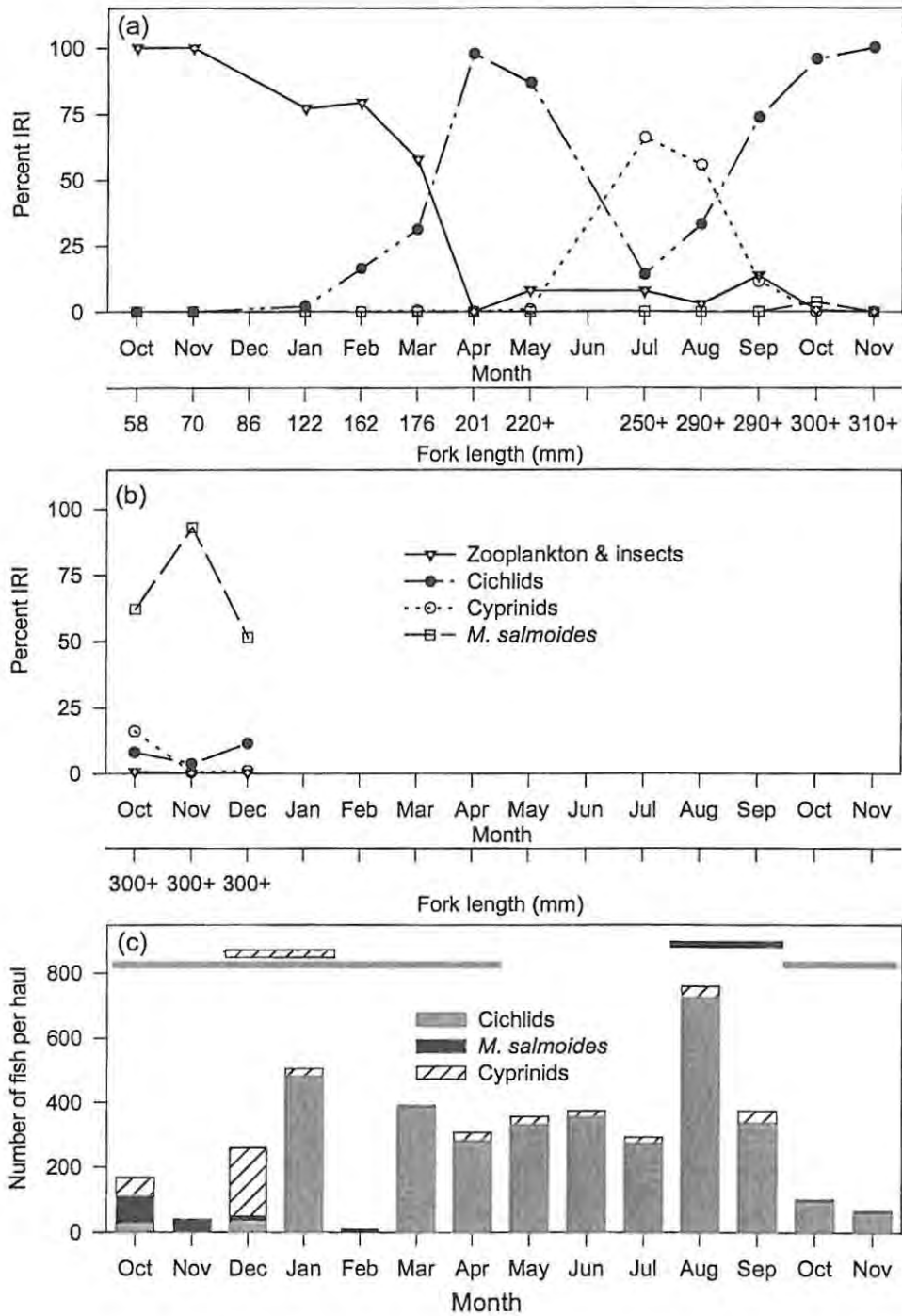


Figure 3.7. (a) Monthly percent index of relative importance (IRI) of zooplankton and insects, cichlids, cyprinids and conspecifics in the diet of the September 1995 cohort of *Micropterus salmoides* collected from October 1995 to November 1996 and (b) of adults collected from October 1995 to December 1995 in Lake Chicamba. (c) The spawning period (horizontal bars) and the abundance (vertical bars) of *M. salmoides*, juvenile cichlids and small cyprinids in the lakes littoral area (samples were obtained using a 30 m seine net).

Mortality estimates

Age-based catch curves for *M. salmoides* sampled from the October 1995 and August 1996 angling tournaments and the subsistence seine net and hook and line fisheries are illustrated in Figure 3.8. Age-based catch curves from experimental gill net, experimental seine net and the subsistence seine-net and hook-and-line fisheries for *O. mossambicus* and *T. rendalli* are illustrated in Figure 3.9. First estimates of Z from the catch curves and the Butterworth et al. (1989) equation are shown in Table 3.9. The mean value for Z from all estimates was $1.27 \pm 0.16 \text{ yr}^{-1}$ for *M. salmoides*, $0.62 \pm 0.15 \text{ yr}^{-1}$ for *O. mossambicus* and $0.31 \pm 0.07 \text{ yr}^{-1}$ for *T. rendalli*. The point estimates for M derived from the Pauly (1980), Rihkter & Efanov (1977), Gunderson & Dygert (1988) and Hoenig (1983) equations are presented in Table 3.9. For a first estimate of M , a mean of the four empirical estimates was calculated as $M = 0.71 \pm 0.33 \text{ yr}^{-1}$ for *M. salmoides* and $0.38 \pm 0.16 \text{ yr}^{-1}$ for *O. mossambicus*. Although the Pauly (1980) estimate is considered the most suitable estimate for M due to the large sample size and rigorous and robust multiple regression technique employed in its derivation, it produced an unrealistically high estimate of natural mortality ($M > Z$) for *T. rendalli*. This estimate was, therefore, excluded from the determination of M for *T. rendalli* and an estimate of $M = 0.20 \pm 0.13 \text{ yr}^{-1}$ accepted. Therefore F was estimated as ($F = Z - M$) at 0.56 yr^{-1} for *M. salmoides*, 0.24 yr^{-1} for *O. mossambicus* and 0.11 yr^{-1} for *T. rendalli*.

Table 3.9. First estimates of the instantaneous rate of total mortality (Z) and natural mortality (M) for *Micropterus salmoides*, *Oreochromis mossambicus* and *Tilapia rendalli*. Estimates of Z were obtained from catch curves and the Butterworth et al. (1989) equation using age frequencies from experimental gill net fleets, experimental seine nets and the subsistence seine net and hook and line fishery in Lake Chicamba. Estimates of M were derived using the Pauly (1980), Rihkter & Efanov (1977), Gunderson & Dygert (1988) and Hoenig (1983) equations.

	Z		M	
	Catch curve	Butterworth et al. 1989	Method	M
<i>M. salmoides</i>				
October 1995 tournament	1.33 yr ⁻¹	1.22 yr ⁻¹	Pauly (1980)	0.76 yr ⁻¹
August 1996 tournament	0.86 yr ⁻¹	0.73 yr ⁻¹	Rihkter & Efanov (1977)	1.49 yr ⁻¹
Subsistence seine net	1.19 yr ⁻¹	2.24 yr ⁻¹	Gunderson & Dygert (1988)	0.13 yr ⁻¹
Subsistence line fishing	1.25 yr ⁻¹	1.30 yr ⁻¹	Hoenig (1983)	0.45 yr ⁻¹
<i>O. mossambicus</i>				
Experimental gill net	0.44 yr ⁻¹	0.78 yr ⁻¹	Pauly (1980)	0.60 yr ⁻¹
Experimental seine net	0.68 yr ⁻¹	0.68 yr ⁻¹	Rihkter & Efanov (1977)	0.73 yr ⁻¹
Subsistence seine net	0.45 yr ⁻¹	0.47 yr ⁻¹	Gunderson & Dygert (1988)	0.07 yr ⁻¹
Subsistence line fishing	0.78 yr ⁻¹	0.71 yr ⁻¹	Hoenig (1983)	0.14 yr ⁻¹
<i>T. rendalli</i>				
Experimental seine net	0.34 yr ⁻¹	0.42 yr ⁻¹	Pauly (1980)	0.46 yr ⁻¹
Subsistence seine net	0.27 yr ⁻¹	0.34 yr ⁻¹	Rihkter & Efanov (1977)	0.71 yr ⁻¹
Subsistence line fishing	0.26 yr ⁻¹	0.25 yr ⁻¹	Gunderson & Dygert (1988)	0.08 yr ⁻¹
			Hoenig (1983)	0.05 yr ⁻¹

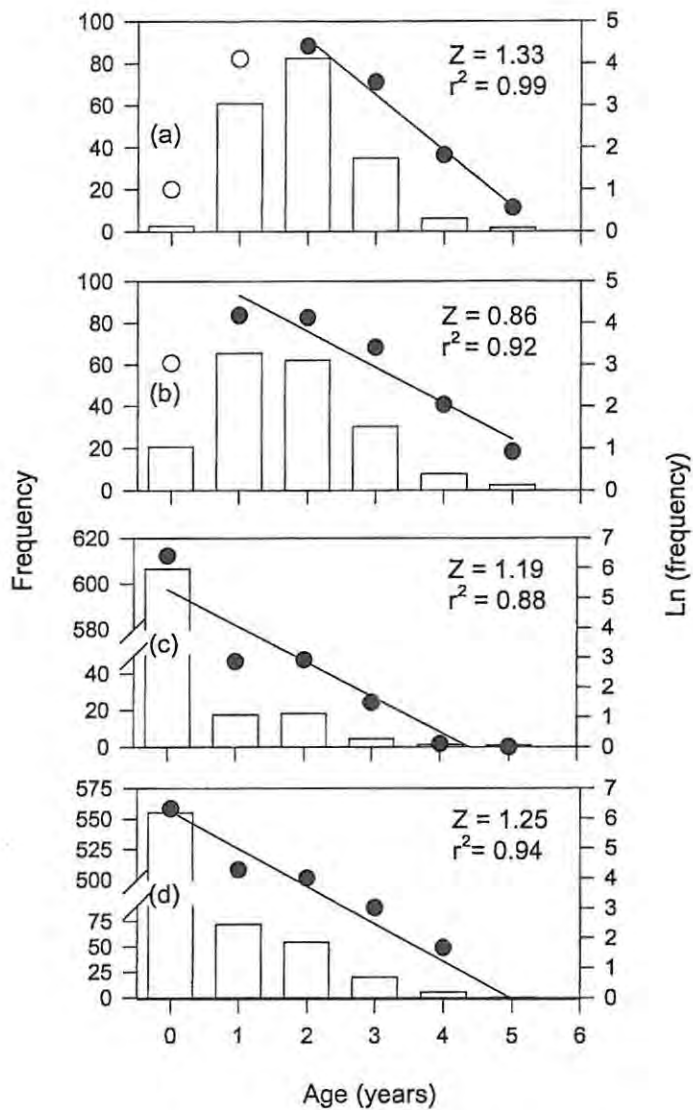


Figure 3.8. First estimates of the total annual mortality rate (Z) for *M. salmoides* in Lake Chicamba. The Z estimates were obtained by fitting linearised catch curves (closed circles) to age-frequency distributions (bars) obtained from angling tournaments held in (a) October 1995 and (b) August 1996, and from the subsistence (c) seine-net fishery and (d) hook-and-line fishery on Lake Chicamba.

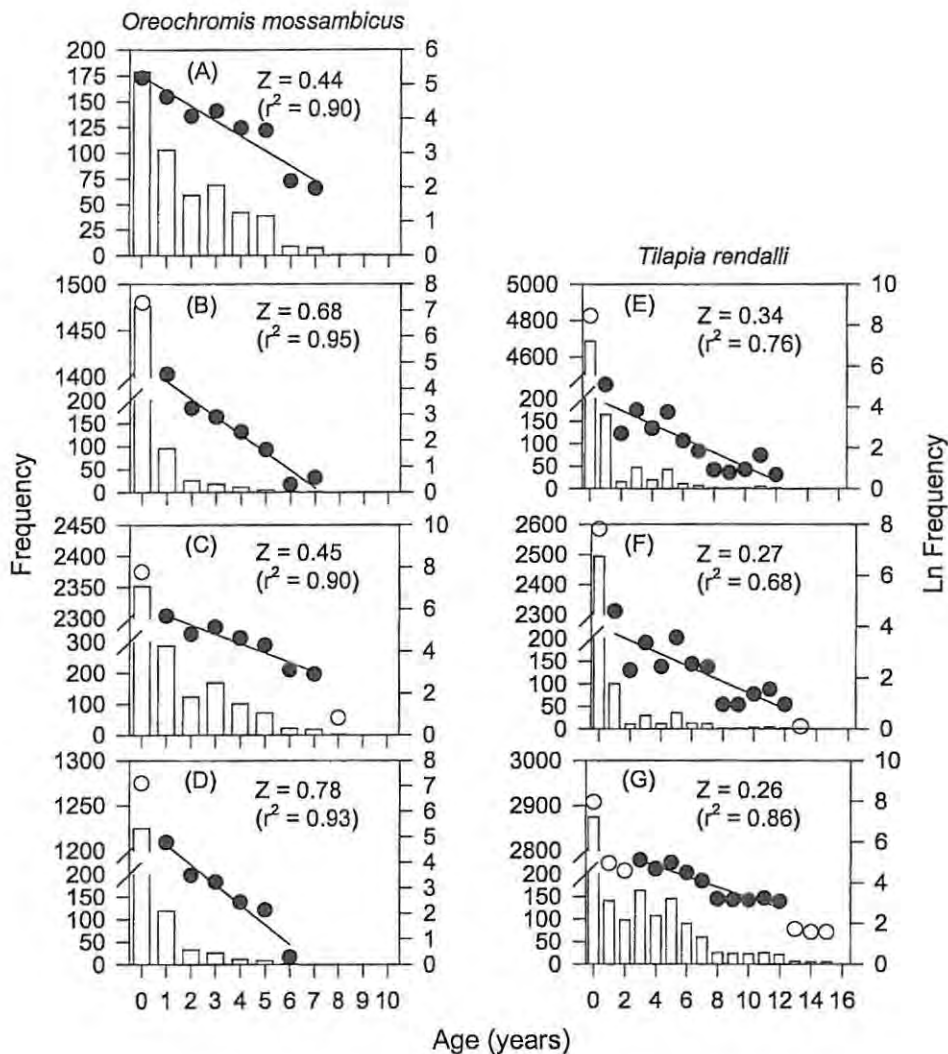


Figure 3.9. First estimates of the total annual mortality rate (Z) for *Oreochromis mossambicus* and *Tilapia rendalli* in Lake Chicamba. The Z estimates were obtained by fitting linearised catch curves (closed circles) to age-frequency distributions (bars) obtained for *Oreochromis mossambicus* in (A) experimental gill-net fleets, (B) experimental seine nets, (C) the subsistence seine-net and (D) subsistence hook-and-line catches and for *Tilapia rendalli* in (E) experimental seine net, (F) subsistence seine net and (G) subsistence hook-and-line fishing catches.

3.4 DISCUSSION

Since there are substantial differences in the life history traits of *M. salmoides* and the two cichlid species, *T. rendalli* and *O. mossambicus*, their life histories are discussed separately.

Micropterus salmoides

The success of a species in a 'foreign' environment is dependent on its ecological and behavioural distinction from native species and a reproductive strategy that confers an unusual degree of 'fitness' and a pre-adaptation to distinctive environmental conditions (Moyle 1986). The combination of these factors leads to the establishment of a viable population, which can be used as a measure of success (De Moor 1996).

The growth performance of a fish species reflects the ability of a species to meet nutritional requirements and its adaptation to prevailing abiotic conditions such as the temperature regime (Jobling 1981). Beamesderfer & North (1995) summarised the von Bertalanffy growth parameters K and L_{∞} for various *M. salmoides* populations in 34 North American states. Since populations with different growth parameters may have a similar growth performance, the parameter ϕ' (phi prime) (Pauly & Munro 1984), which takes into consideration the interaction and dependence between the von Bertalanffy growth parameters, K and L_{∞} , was used to compare the Lake Chicamba population with the North American populations. This information and the calculated ϕ' values are shown in Table 3.10. The growth performance of largemouth bass in Lake Chicamba was significantly higher than the growth performance of the American populations (students t-test; $p < 0.05$).

Table 3.10. The von Bertalanffy growth parameters and calculated ϕ' (phi-prime, Pauly & Munro 1984) for *Micropterus salmoides* from Lake Chicamba, Mozambique, and 34 North American states (adapted from Beamesderfer & North 1995).

Locality	K	L_{∞}	ϕ'
Lake Chicamba	1.17	402	5.28
Alabama	0.28	521	4.88
Virginia	0.26	530	4.86
Florida	0.26	516	4.84
Illinois	0.30	478	4.84
Oklahoma	0.31	472	4.84
North Carolina	0.24	534	4.83
Utah	0.06	1054	4.82
Louisiana	0.36	425	4.81
Tennessee	0.21	555	4.81
Maryland	0.34	430	4.80
Arkansas	0.29	453	4.77
Delaware	0.29	452	4.77
Iowa	0.19	551	4.76
Kentucky	0.22	504	4.75
New York	0.22	494	4.73
Rhode Island	0.22	483	4.71
Georgia	0.23	470	4.70
Oregon	0.17	543	4.70
Connecticut	0.22	471	4.69
Ohio	0.14	582	4.68
Missouri	0.21	475	4.67
Idaho	0.16	532	4.66
Massachusetts	0.18	505	4.66
New Mexico	0.08	760	4.66
Maine	0.22	449	4.65
Michigan	0.20	562	4.63
Ontario	0.19	467	4.62
Washington	0.15	522	4.61
Wisconsin	0.19	459	4.60
British Columbia	0.16	493	4.59
Mississippi	0.16	495	4.59
South Dakota	0.11	597	4.59
Montana	0.07	744	4.58
Pennsylvania	0.11	580	4.57

The high growth rate of the Lake Chicamba population is, in part, likely to be a response to water temperature. Lake Chicamba's water temperatures lie within the thermal preferendum for *M. salmoides* i.e. between 26°C and 32°C (Coutant 1977, Jobling 1981), for eight months of the year. It is known that as long as the fish are not food-limited,

maximum growth of fishes occurs within the range of its thermal preferendum (Crawshaw 1977, Jobling 1981). In this respect, the Lake Chicamba population is similar to the *M. salmoides* population in Flint Creek, Arkansas, which has a similar temperature regime (Galloway & Kilambi 1988). The mean lengths-at-age of bass in Lake Chicamba and Flint creek reservoir (Galloway & Kilambi 1988) are summarised in Table 3.11. However, to understand the success of *M. salmoides* in Lake Chicamba, one must consider the life history of the species in this lake in detail and consider it in relation to the only other predator in the lake, viz. *Clarias gariepinus*.

Table 3.11. Length-at-age, von Bertalanffy growth parameters and calculated ϕ' (phi-prime; Pauly & Munro 1984) for *Micropterus salmoides* in Lake Chicamba, Mozambique and Flint Creek reservoir, Arkansas (Galloway & Kilambi 1988). For comparison all lengths were adjusted to standard length (mm). In both lakes, the mean annual water temperature was within the range preferred by bass.

Locality	Mean standard length (mm) at age (years)						Growth parameters		
	1	2	3	4	5	6	K	L_{∞}	ϕ'
Flint Creek	194	309	379	419	444	458	0.52	480	5.1
Lake Chicamba	290	354	383	396	402	-	1.17	402	5.3

The Lake Chicamba population of largemouth bass has a short spawning period, which is generally triggered by increasing day length and temperature (Dadzie & Aloo 1990, Rosenblum et al. 1994). Although extended spawning seasons have been recorded in warm climates (Dadzie & Aloo 1990), the two-month spawning period in Lake Chicamba was

similar to that of populations in its native range (Miller & Stork 1984, Isley et al. 1987). Spawning in Lake Chicamba (August to September) occurs just after the winter period.

The inherent 'early' spawning season of this species differs distinctly from that of the indigenous fishes in the lake. These are either flood-dependent spawners or have reproductive periods confined to the summer months. Flood-dependent spawners in Lake Chicamba include *C. gariiepinus* (Bruton 1979a) and the cyprinids such as *L. cylindricus* (Bowmaker 1973, Weyl & Booth in press). In these species spawning occurs only during the flooding phase of the lake (January to March). Thus, juveniles of these two species occur only after flooding from January to April. Spawning of *T. rendalli* and *O. mossambicus* in Lake Chicamba is restricted to the summer months from October to April. However, juvenile cichlid (TL < 50 mm) density in the shallow littoral areas has been shown to be significantly lower in September (0.1 fish m⁻²) and October (0.3 fish m⁻¹) than during other months (2.2 – 8.9 fish m⁻², see Chapter 4).

Zooplankton biomass in the lake during October and November has been shown to be lower than in other months (Vissers & Robelus 1984). Since zooplankton is a major constituent in the diet of juvenile *M. salmoides* (Table 3.8), juvenile cichlids and juvenile *C. gariiepinus* (Le Roux 1956, Munro 1967, Holl 1968, Wagner & Rowe-Rowe 1972, Caulton 1976, Whitfield & Blaber 1978, De Moor et al. 1986), and given that the juveniles of all these species occupy the same habitat, inter-specific competition for food may be reduced by 'early' spawning. By the time the main recruitment phase of the indigenous fish species occurs in January (Figure 3.7 c), the juvenile *M. salmoides* are no longer dependent on zooplankton, but rather feed on larger prey items such as corixids, aquatic and terrestrial

insects and fish (Table 3.8). Therefore, spawning during the time of decreased juvenile cichlid abundance allows the initial growth of juvenile largemouth bass to take place when competition for zooplankton is low. In contrast to *M. salmoides*, spawning of *C. gariepinus* takes place after rain in recently inundated marginal areas (Bruton 1979a). In Lake Chicamba the spawning period of *C. gariepinus* occurs during January and February (pers. obs.) and coincides with peak cichlid abundance in the lake's littoral zone. Competition for zooplankton in the littoral zone during this time may be intense enough to limit the recruitment of *C. gariepinus*.

The length at which largemouth bass become piscivorous ranges from 35 mm (Turner and Kraatz 1920) to 140 mm (Bettoli et al. 1992). In Lake Chicamba, the young-of-the-year largemouth bass attain a fork length of 121.7 mm (Table 3.7) by January, when the main recruitment phase of juvenile cichlids occurs (Figure 3.7 c). This is reflected by an increase in the importance of the fish component in the diet from January onwards (Table 3.8, Figure 3.7 a). However, the juvenile bass did not become fully piscivorous until April (Table 3.7) at a length of 201 mm FL (Table 3.7). This was likely to be due to the increased availability of alternative food items, such as terrestrial and aquatic insects, as a consequence of the inundated lake margins from January to April. It appears that spawning of largemouth bass in August and September not only reduces inter-specific competition for zooplankton, but allows the juvenile bass to grow to a size large enough to be piscivorous before the main recruitment phase of the indigenous species. During July and August 1996, cyprinids were the most important prey item in the diet of largemouth bass (Figure 3.7 a). Since cichlids were still the most abundant fish in the littoral zone during the winter months (Figure 3.7 c), the dominance of cyprinids in the diet of largemouth bass may be a

consequence of their moving to deeper water where cyprinids dominated small-meshed gill net catches (Weyl & Hecht, in press a).

Since spawning of *M. salmoides* in Lake Chicamba takes place four months before the main recruitment phase of the indigenous fishes, the young-of-the-year largemouth bass may be the most abundant, suitably sized, prey item for the previous year classes from October to December. This was illustrated by the high rates of cannibalism which were recorded during October and November 1995 (Figure 3.7 b), when juvenile bass made up 48.5% and 77.1% of the littoral ichthyofauna, respectively (Figure 3.7 c). Conversely, lower rates of cannibalism were recorded during October and November 1996 when cichlids dominated the littoral ichthyofauna (Figure 3.7 c).

Increases in the rate of cannibalism with decreased availability of alternative food have been widely documented (Fox 1975, Davis 1985, Hughes 1986, Hecht & Appelbaum 1988, Ogari & Dadzie 1988, Ogutu-Ohwayo 1990). In Lake Victoria, the introduction of the piscivorous Nile perch *Lates niloticus* led to the depletion of the indigenous fish species and subsequently high rates cannibalism were reported in this species (Hughes 1986, Ogari & Dadzie 1988, Ogutu-Ohwayo 1990). However, in Lake Chicamba, cannibalism among *M. salmoides* appears to be a response to a short-term decrease in prey availability coupled with the concomitant high relative abundance of conspecific juveniles after the spawning period. Therefore, the timing of the spawning event of largemouth bass in Lake Chicamba has the added advantage of providing an abundant food supply during a period when alternate prey is limited.

The population controlling effect of cannibalism has been discussed for many fish species (Santander et al. 1983, Lleonart et al. 1985, Hecht & Appelbaum 1988, Smith & Reay 1991, Hecht & Pienaar 1993) and in some populations cannibalism is the main cause of natural mortality (Lleonart et al. 1985). For example, cannibalism by one year-class can cause poor recruitment in subsequent year classes (Goldspink & Goodwin 1979), and in low nutrient lakes, a single year class can dominate European perch populations for as long as 15 years (Alm 1952). However, in Lake Chicamba, the juvenile bass are not depleted to the extent that older age classes dominate (Figure 3.8). This is considered to be an effect of the high total mortality rate ($Z = 1.27 \text{ yr}^{-1}$). Although the calculated natural mortality for *M. salmoides* in Lake Chicamba was high ($M = 0.73 \text{ yr}^{-1}$), it is similar to the highest rate of natural mortality ($M = 0.70 \text{ yr}^{-1}$) recorded for the species in its native environment (Beamesderfer & North 1995), and is considered to be a relatively accurate indication of natural mortality in this population. The high fishing mortality ($F = 0.54 \text{ yr}^{-1}$) may be a major factor in controlling the adult population to levels at which the juvenile stock is not completely depleted by cannibalism. The high total mortality rate is further supported by the low recorded maximum age of 5 years (Table 3.3) compared to the maximum recorded age of over 20 years of largemouth bass in some North American lakes (Green & Heidinger 1994).

Cannibalism may perform a vital function in regulating the juvenile largemouth bass population to levels below which intra-cohort competition becomes a limiting factor. Since young-of-the-year largemouth bass are highly cannibalistic (DeAngelis et al. 1979), the lack of recorded coeval sibling cannibalism in juveniles from Lake Chicamba (Table 3.8) is an indicator of low intra-cohort competition. Since density dependent processes such as

cannibalism (Dong & Polis 1992, Hecht & Pienaar 1993) only take effect when density increases to levels at which food availability is depleted to below individual needs (Dong & Polis 1992), the lack of coeval sibling cannibalism is indicative of juvenile densities below a level that results in competition. In addition, the high total mortality rates may contribute towards keeping the adult stock at levels low enough to avoid food depletion and competition.

The success of largemouth bass in Lake Chicamba is therefore considered to be a sum effect of early spawning that eliminates inter-specific competition among juveniles, successive feeding on the most abundant food organisms, cannibalism during periods of low alternative food availability and the thinning out of juveniles through cannibalism which limits intra-cohort competition. The balance between the adult and juvenile stock is maintained by high mortality rates, which reduces the adult stock to levels at which recruitment of juveniles is not restricted. The concomitant high year-round abundance of prey for all size classes, coupled with the high water temperatures prevalent throughout the year leads to rapid growth in this population.

The life history and reproductive strategy of *M. salmoides* make this species highly competitive in the subtropical African environment where the reproductive activity and recruitment of the indigenous species takes place in summer and may explain its dominance over *C. gariepinus* in Lake Chicamba.

Tilapia rendalli and *Oreochromis mossambicus*

The initial growth rate of both cichlid species was rapid, with asymptotic length being attained within three years (Figure 3.3). Since both species mature at lengths corresponding to ages of 2+ years, the attainment of asymptotic length occurs soon after sexual maturation and reflects a shift from somatic growth to reproductive energy requirements. This growth pattern is typical of many cichlid populations (Bruton & Allanson 1974, Hecht 1980 a, van der Waal 1985) and allows the juvenile fishes to quickly attain a size large enough to avoid predation and to simultaneously cause the rapid attainment of sexual maturity to enable reproduction in unstable environments.

The high variability in growth rate and the length-at-50 % maturity in cichlids are evident when the data from this study are compared to other populations (Table 3.12). The variability in growth rate has been linked to reservoir size (De Silva 1986), habitat stability (Noakes & Balon 1982) and food availability (Balon & Coche 1974). James & Bruton (1992) recorded lengths at maturity ranging from 110 mm SL to 265 mm SL for male *O. mossambicus* in water bodies in the Eastern Cape Province of South Africa. The large variation in the length-at-50% maturity was attributed to the response of the fish to environmental variability. Greater lengths at maturity have been recorded in stable environs (De Silva 1986, James & Bruton 1992) and smaller lengths at maturity have been found in harsher habitats, such as small dams in which food is limiting and large temperature fluctuations are common (James & Bruton 1992).

The growth rate of *O. mossambicus* and *T. rendalli* in Lake Chicamba is relatively fast when compared to other populations in the southern African region (Table 3.12). The

growth rate of *O. mossambicus* in Lake Chicamba was faster than in Lake Sibaya (Bruton & Allanson 1974) but was similar to the population from the Luphephe/Nwanedzi impoundment described by Hecht (1980a) for the first three years of life. However, slower growth and smaller maximum size of *O. mossambicus* in Lake Sibaya can be attributed to early maturity and precocious breeding in this abiotically harsh environment (Bruton 1979b). When the Lake Chicamba population was compared to temperate populations in the Eastern Cape of South Africa (James 1989), it was slower growing than the Mill farm dam population where feeding conditions were highly favourable, but faster growing than the Bradshaw's mill dam population where feeding conditions were less favourable (James 1989). In addition, the Lake Chicamba population was only slightly slower growing than the Hartbeesport dam population in the North-West province of South Africa (Cochrane 1985).

The growth rate of *T. rendalli* in Lake Chicamba was similar to that in Lake Liambezi (van der Waal 1985) and Lake Kariba (Kolding et al. 1992) for the first three years, whereafter the growth in Lake Chicamba was slower (Table 3.12). However, the Lake Liambezi *T. rendalli* population was aged using scales, which have been shown to be poor indicators of age after asymptotic length has been attained (Hecht 1980 a, Booth et al. 1995). Since the oldest *T. rendalli* sampled in Lake Chicamba was 16 years and the oldest fish in Lake Liambezi was 7 years old, it is possible that the larger lengths-at-age in this locality are an effect of age underestimation.

T. rendalli and *O. mossambicus* from Lake Chicamba are relatively large when they reach L_{m50} (Table 3.12). The large size at maturity is similar to the lengths at maturity recorded

for *T. rendalli* in Lake Kariba (Kolding et al. 1992) and *O. mossambicus* in Sri Lankan reservoirs (De Silva 1986). Lake Kariba and the Sri Lankan reservoirs tend towards environmental stability. In contrast, the abiotically harsh environment of Lake Sibaya has led to early maturation and precocious breeding in *O. mossambicus*, despite the large area of the lake (Bruton 1979b). Similarly, *T. rendalli* in the shallow Lake Liambezi also mature at a relatively smaller size although the temperature regime and surface area (Seaman et al. 1978) are similar to Lake Chicamba. The relatively large length-at-50% maturity of *T. rendalli* and *O. mossambicus* in Lake Chicamba is indicative of a precocial life-history style associated with environmental favourability (Noakes & Balon 1982, James & Bruton 1992).

T. rendalli falls within the reproductive guild of guarders while *O. mossambicus* are mouthbrooders (Balon 1975). *T. rendalli* excavate pits in shallow areas, including submerged anthills in Lake Chicamba (pers. obs.). The eggs are deposited into these pits and are guarded and fanned by both parents (Bruton & Kok 1980). Subsequently the fry form independent shoals often around submerged plant beds (Bruton & Kok 1980). *O. mossambicus* build nests, which are simple hollows, often grouped together in arenas, and are defended by the male (Bruton & Bolt 1975, Bruton 1979b, Bruton & Kok 1980). After a brief courtship, the female leaves the nest and mouthbroods the eggs and fry for 14 to 22 days (De Moor & Bruton 1988).

Table 3.12 Length-at-50 % maturity (L_{m50}), calculated length-at-age (SL) and the von Bertalanffy growth parameters for *Oreochromis mossambicus* and *Tilapia rendalli* in southern African water bodies based on published data. All data have been standardised to standard length (SL) (m = male, f = female, t = both sexes).

Locality	Sex	L_{m50}	Length (mm SL)-at-age (years)						Growth parameters			
			0	1	2	3	4	5	a_0	L_∞	K	
<i>O. mossambicus</i>												
Chicamba ¹	m	171										
	f	161										
	t			134	176	198	207	198	-0.269	212	0.790	
Luphephe ²	t	nd		110	168	206	225	234	-0.299	273	0.425	
Sibaya ³	m	120		85	124	148	177	187	-0.360	217	0.358	
	f	100		83	113	134	147	166	-1.054	217	0.240	
Mill farm dam ⁴	m	265	185	224	256	282	304	322	-3.154	406	0.193	
	f	263	132	200	246	278	300	315	-1.272	348	0.376	
Bradshaw's Mill dam ⁴	m	168	51	122	173	211	239	260	-0.578	317	0.306	
	f	186	50	166	212	230	238	240	-0.248	242	0.924	
Hartbeespoort dam ⁵	m			89	191	237	290	322	-0.360	372	0.420	
	f			90	179	228	280	292	-0.300	309	0.510	
<i>T. rendalli</i>												
Chicamba ¹	m	171										
	f	161										
	t		82	132	158	172	180	184	-0.905	188	0.636	
Liambezi ⁶	m	109	108	119	129	181	203	216	-1.953	240	0.479	
	f	109		117	173	190	198	207	-0.935	366	0.128	
Kariba ⁷	m	184										
	f	168										
	t			72	115	151	183	211	-0.419	387	0.145	

¹Present study – Lake Chicamba, Mozambique.

²Hecht (1980a) – Luphephe/Nwanedzi impoundment, South Africa.

³Bruton & Allanson (1974) – Lake Sibaya, South Africa.

⁴James (1989) – Eastern Cape, South Africa.

⁵Cochrane (1985) - Hartbeespoort dam. South Africa.

⁶van der Waal (1985) – Lake Liambezi, Namibia

⁷Kolding et al. (1992) – Lake Kariba, Zimbabwe.

Spawning periodicity in cichlids is often independent of flooding but has been linked to other factors such as water temperature and day length (Fryer & Iles 1972, Bruton & Allanson 1974, van der Waal 1985, James & Bruton 1992, Lowe-McConnell 1991, Merron et al. 1993). This is illustrated in the Phongolo floodplain, South Africa, where *O. mossambicus* dominates after a period of flood failure (Merron et al. 1993). Similarly, in

Lake Liambezi, Namibia, spawning of *T. rendalli* was not dependent on flooding (van der Waal 1985). In Lake Chicamba, the reproductive activity of both cichlids was confined to the summer period from September to May (Figure 3.5 & 3.6), when mean water temperatures were higher than 24°C. Since the gonadosomatic indices and the proportion of ripe individuals in both species did not differ significantly throughout summer, it was concluded that gonad development and spawning were independent of flooding in this locality.

Fisheries considerations

High growth rates, a long lifespan, late maturity and precocial breeding habits imply that the two cichlid populations are likely to have relatively stable population sizes and future catch levels if effort is constant (Adams 1980). However, once the fishery is overfished, it would require a long period for the stock to rebuild to levels that could support future sustainable catches. The life history of the two cichlid species, therefore, may indicate a susceptibility to overexploitation. The highly skewed *O. mossambicus* sex ratio in Lake Chicamba may be an indication of overexploitation. In Lake Chicamba females dominate the population by a ratio of 1 male : 3.16 females. This contrasts with lightly exploited populations in the Eastern Cape Province of South Africa where males are 1.2 to 1.9 times more abundant than females (James 1989, James & Bruton 1992). It is possible that this highly skewed sex ratio may be a result of selective harvesting of mature male *O. mossambicus* from nesting sites by seine nets. However, the determination of sex-specific selectivity patterns in the fishery was beyond the scope of this thesis.

Conversely *M. salmoides* is a fast-growing, relatively short-lived species with a high rate of natural mortality. Typically these traits lead to a more productive fishery where fish can be harvested at younger ages. However, the precocial reproductive behaviour adopted by all three species including nest spawning, guarding and mouthbrooding, implies that recruitment in these species may be highly dependent on spawner stock levels. A management strategy for Lake Chicamba, therefore, has to place emphasis on the maintenance of the spawning stock of all three species.

CHAPTER 4

The effect of lake-level fluctuations on the life history and recruitment of *M. salmoides*, *T. rendalli* and *O. mossambicus*.

4.1. INTRODUCTION

Two views exist regarding the effects of lake-level fluctuations on fish populations. On the one hand, fluctuations in lake level are often cited as being undesirable in a reservoir fishery (Harding 1966, Jackson 1966, Coche 1974, Kohler et al. 1993). Flooding and drawdown events affect spawning success (Martin et al. 1981, Karengé & Kolding 1995, Jackson 1966), feeding conditions (Heman et al. 1969, Karengé & Kolding 1995) and prey evasion (Jackson 1961, Martin et al. 1981) which collectively affect recruitment. The deleterious effects of lake-level fluctuations on fish production are related mainly to the drawdown periods, which expose areas that are used for spawning, thereby disrupting spawning activity and resulting in egg and fry mortality (Jackson 1966, Coche 1974). In centrarchids, mortality of eggs and larvae stranded by drawdown events has been well documented (Heman et al. 1969, Ploskey 1986) and rapidly decreasing water levels have been shown to lead to poor hatching success as a result of nest desertion, poor egg survival and disrupted spawning (Walburg 1972, Ploskey 1986, Kohler et al. 1993).

On the other hand, rising water levels and inundation of lake margins are considered to have a number of beneficial effects for a reservoir fishery. Rising water level and the inundation of terrestrial vegetation creates cover and a favourable environment for fish

which inhabit the shallow littoral zone (Keith 1975, Martin et al. 1981). The nutrients released from the newly flooded vegetation and bottom soils may increase the productivity of the impoundment (Wood 1951). In non-cichlid species such as *Perca flavescens*, *Morone chrysops* and centrarchids, reproductive success was found to be enhanced when inundated vegetation was available during the spawning and nursery period (Martin et al. 1981). Similar trends have been shown for cichlids. In the Kafue floodplain, Zambia, the breeding success and reproductive output of *Oreochromis andersonii* and *O. macrochir* was enhanced during years with high flood levels (Dudley 1972). In Lake Kariba, shortly after the closure of the dam in 1958/1959 the spawning success of *O. mortimeri* was enhanced due to increased food production and the increased availability of refuges for juvenile fish in the newly impounded areas (Jackson 1961, Donnelly 1971).

In floodplain fisheries the flooding regime is considered of major importance to fish yields (Welcomme 1975, 1976, 1978, 1979 & 1986, Welcomme & Harborg 1977, Welcomme & Merona 1988). Welcomme & Harborg (1977), using a simulation model of a floodplain fishery, found that catches were highly correlated with the mean surface area of flooded areas in the same year. Leveque & Quensiere (1988) rank hydrology among the most important factors affecting community structure in shallow lakes. For example, in Lake Chilwa, a shallow lake in Malawi, fish yields and species composition were found to vary as a response to lake level (Furse et al. 1979). Similarly, in the Lake Malawi multi-species cichlid trawl fishery, Tweddle & Magasa (1989) found a significant correlation between lake level and catch. Kolding (1989, 1992) reported correlations between the previous year's lake level and commercial catches in Lake Turkana, Kenya, over a 16-year period.

Similarly, in Sri Lankan reservoirs, fluctuations in lake level have been shown to influence the reproductive output of *O. mossambicus* to such an extent that the commercial catches were affected three years later (De Silva 1985). Recent work on Lake Kariba has also shown that catch rates in artisanal and experimental gill nets were positively correlated with the flooding regime of the previous year (Karengere & Kolding 1995).

No long-term fishery data are available for the Lake Chicamba fishery with which to assess the effect of lake-level fluctuation on yield. Therefore, a new approach was required to determine the relationship between lake level fluctuations and the growth, reproductive success and recruitment of the major fish species. This approach is described in this chapter and tests the hypothesis that flooding of the lake margins enhances overall fish production by increasing food and cover, which could increase growth rate, survival and recruitment.

4.2. MATERIALS AND METHODS

Abundance estimates

An estimate of abundance of the juvenile cichlids (*T. rendalli* and *O. mossambicus*) in the shallow littoral (depth < 2 m) was obtained using a specially designed fry seine net, 2 m long by 1 m deep with a mesh size of 1 mm. Monthly samples were taken from 5 sites on the lake (see Chapter 2; Figure 2.1) with 5 hauls being performed at each site per month. Each haul covered an area of 10 m². Hauls were performed between drowned trees in sites where these were present. The possibility that juvenile cichlids occurred at depths greater than the 0.5-m depth effectively sampled with the fry seine-net was assessed by sampling lakeshore areas up to 2 m deep using a 30-m long by 3-m deep seine-net with a mesh size

of 10 mm. Ten seine net hauls were conducted in two sampling areas per month (Chapter 2; Figure 2.1). Each haul covered an area of approximately 140 m². In both sampling methods only *M. salmoides* less than 100 mm FL and cichlids less than 50 mm TL were used for subsequent analysis. Seasonal abundance data were grouped into three periods in each calendar year for comparison. These were 'flooding summer' (from January to April), 'winter' (from May to September) and 'drawdown summer' (from October to December). Abundance data and catch rates were compared using the non-parametric Kruskal-Wallis ANOVA on ranks. Groups that differed from others were isolated using an all-pairwise multiple comparison procedure (Dunn's method). The 'flooding' and 'drawdown' summers in successive years were compared by means of the non-parametric Mann-Whitney rank sum test. A significance level of $p < 0.05$ was chosen for all tests.

Growth rate

Growth rate of *M. salmoides*, *T. rendalli* and *O. mossambicus* as a response to changes in lake level was investigated by examining sectioned otoliths. Whole saggittal otoliths were measured for otolith length (OL) along the longitudinal axis and otolith diameter (OD) along the transverse axis. Saggital otolith sections were prepared according to the procedures described in Chapter 3; they were examined under transmitted light using a 20 X magnification. Some sections were selected for further analysis using the criterion that all annuli had to be clearly defined along the measuring plane from the medial margin to the lateral margin across the nucleus (Figure 4.1). These sections were scanned into the software package Sigma Scan with a 1-mm calibration bar; subsequent measurements were taken using a resolution of 0.001 mm. The number of annuli on the otolith was read and

the otolith was assigned an age. Finally, the sectioned otolith thickness was measured from the medial margin to the lateral margin across the nucleus, and the annulus width (AW) was measured as the distance between the first and second annulus from the beginning of the translucent zone to the end of the next opaque zone along the same plane as the sectioned otolith thickness (Figure 4.1). All measurements were taken twice and a mean measurement was accepted if the two measurements did not differ by a distance of more than 0.005 mm. If the two measurements did not meet this criterion the otolith was rejected. The annulus width was back-calculated to the year of deposition. Since the exact centre of the nucleus could not be determined in all sections and the fact that spawning in the cichlids occurred over an 8-month period in Lake Chicamba, comparisons of growth were confined to the period of deposition between the first and second annulus as this period represented the first measurable parameter before the fish had attained asymptotic length (Chapter 3; Figure 3.3).

Linear regression analysis was used to determine the relationship between annulus width and the following variables:

DDL (Δ drawdown level): the change in lake level (m amsl) due to drawdown.

DFL (Δ flood level): the change in lake level (m amsl) as a result of flooding.

DDSA (Δ drawdown surface area): the change in surface area (km^2) as a result of drawdown.

DFSA (Δ flood surface area): the change in surface area (km^2) as a result of flooding.

%DDSA (percent Δ drawdown surface area): the change in surface area as a result of drawdown expressed as a percentage of lake level prior to drawdown.

%DFSA (percent Δ flood surface area): the change in surface area as a result of flooding expressed as a percentage of lake level prior to flooding.

Age: Age of the fish sampled (years).

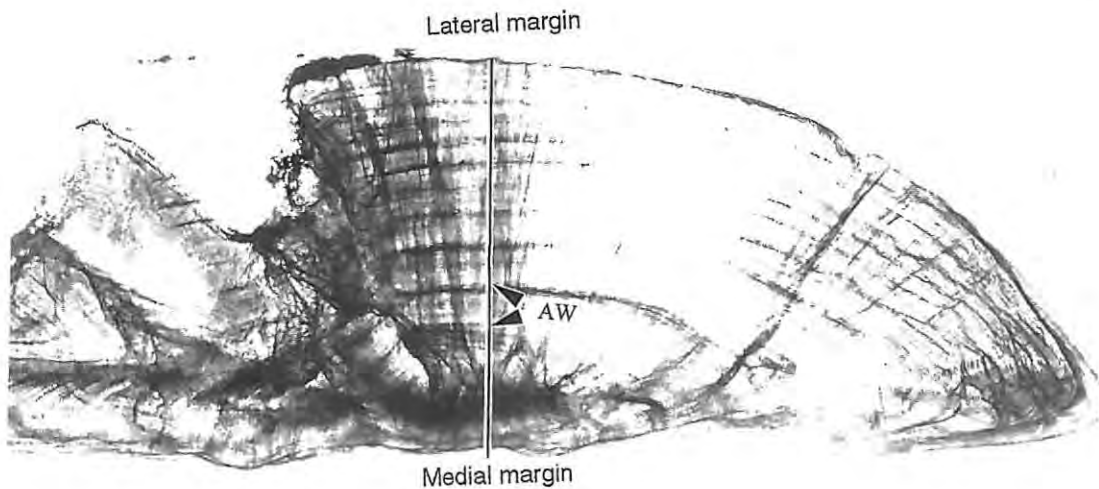


Figure 4.1. Photomicrograph of a sectioned *O. mossambicus* otolith showing the measurement plane used in the determination of the sectioned otolith thickness from the medial margin to the lateral margin across the nucleus and the annulus width (AW). Annulus width (AW) = the distance between the first and second annulus from the beginning of the translucent zone to the end of the next opaque zone.

The lake level variables from the 1985/1986 season to the 1995/1996 season are tabulated in Table 4.1. Data for annulus width in *T. rendalli* otoliths were log transformed to conform to normality and homoscedasticity criteria in regression analysis. Multiple linear regression analysis was applied if otolith width could be predicted by more than one independent variable.

Table 4.1. Lake-level variables used in regression analysis with annulus width in *M. salmoides*, *T. rendalli* and *O. mossambicus*. DDL = Δ drawdown level; DFL = Δ flood level; DDSA = Δ drawdown surface area; DFSA = Δ flood surface area; %DDSA = percent Δ drawdown surface area; %DFSA = percent Δ flood surface area.

Season	Drawdown			Flood		
	DDL	DDSA	% DDSA	DFL	DFSA	% DFSA
85/86	1.4	9.2	7.8	2.4	16.1	14.8
86/87	2.3	15.7	12.5	0.5	0.5	0.5
87/88	2.0	12.1	10.7	3.8	39.3	39.1
88/89	1.2	8.5	6.8	1.1	24.9	21.3
89/90	4.4	28.5	22.8	1.8	10.9	11.3
90/91	1.9	12.2	11.3	0.2	0.1	0.1
91/92	3.0	15.5	16.3	0.0	0.0	0.0
92/93	4.9	19.9	25.0	1.7	6.2	10.4
93/94	3.3	11.5	17.5	1.0	3.4	6.2
94/95	4.5	13.6	23.5	0.6	0.6	1.4
95/96	7.8	17.2	37.4	7.6	16.5	57.4

Fish condition

To assess the effect of flooding and drawdown on fish condition, monthly condition factors for *M. salmoides* (200 - 500 mm FL), *T. rendalli* (150 - 300 mm TL) and *O. mossambicus* (150 -350 mm TL) sampled between July 1995 and September 1996 were calculated using the equation recommended by Bolger & Connolly (1989):

$$\text{Condition factor (K)} = \frac{\text{Fish weight (g)}}{\text{Fish length (mm)}} \times 10^5$$

M. salmoides were measured to fork length (FL) and *T. rendalli* and *O. mossambicus* were measured to total length (TL).

4.3. RESULTS

Abundance estimates

The abundance and length distribution of juvenile cichlids sampled with the fry seine net in the shallow littoral areas is shown in Figure 4.2. Due to the small TL of these fish, it was not possible to accurately distinguish between the different cichlid species. However, in the 30-m seine net samples it was possible to distinguish between the two cichlid species and, therefore, abundance and length data are presented for *O. mossambicus* and *T. rendalli* separately (Figure 4.3 & 4.4).

In the shallow littoral areas (< 0.5 m depth) sampled using the fry seine net, juvenile cichlid densities were highest in January (8.4 fish m⁻²) and April (8.9 fish m⁻²) and lowest in

September (0.1 fish m⁻²) and October (0.3 fish m⁻²; Figure 4.2 a). During the other months juvenile cichlid densities ranged from 2.2 fish m⁻² (August) to 5.8 fish m⁻² (February)(Figure 4.2 a). Juvenile cichlid densities in the lake margins were significantly higher during the summer flooding phase of the dam than during the winter and summer drawdown phases (ANOVA, $p < 0.05$; Figure 4.2 a).

The abundance of each species component in the 30-m seine net catch is shown in Figure 4.3 and the monthly length distributions of *M. salmoides*, *T. rendalli* and *O. mossambicus* are shown in Figure 4.4. Four small cyprinids, *Barbus radiatus*, *Barbus trimaculatus*, *Barbus paludinosus* and *Labeo cylindricus*, and the two cichlids, *Tilapia rendalli* and *Oreochromis mossambicus* and *M. salmoides* dominated the fish assemblage of the littoral areas. The CPUE of juvenile cichlids was lowest from October to December during both 1995 (5 – 36 fish haul⁻¹) and 1996 (60 – 96 fish haul⁻¹; Figure 4.3). Juvenile *M. salmoides* made up 48.5% and 77.1% of the littoral ichthyofauna in October and November 1995, respectively. Juvenile cichlids made up over 90% of the ichthyofauna during the same months in 1996. Cichlids were the most abundant component of the ichthyofauna in the littoral areas from January to September (63.0% - 98.6%). Juvenile *C. gariepinus* abundance was low, with only 32 individuals recorded during the entire sampling period.

There was no difference in the relative abundance of juvenile *O. mossambicus* (TL < 50 mm) in seine net catches during the 1995 and 1996 drawdown summers (21.2 ± 11.6 fish haul⁻¹). There was no difference in *O. mossambicus* abundance during the 1996 and 1997 flooding summers (56.6 ± 26.6 fish haul⁻¹). In summer, *O. mossambicus* were significantly

more abundant than during winter. *O. mossambicus* abundance during flooding summer did not differ significantly from that recorded in the drawdown summer period.

The abundance for juvenile *T. rendalli* was significantly lower (Mann-Whitney rank sum test, $p < 0.05$) during the 1995 drawdown summer (6.0 ± 4.0 fish haul⁻¹) than during the 1996 drawdown summer (48.4 ± 13.9 fish haul⁻¹). Juvenile *T. rendalli* abundance during the 1996 flooding phase and the 1997 flooding phase did not differ significantly (23.4 ± 9.5 fish haul⁻¹). Juvenile *T. rendalli* were significantly more abundant during the flooding summer than during the drawdown summer.

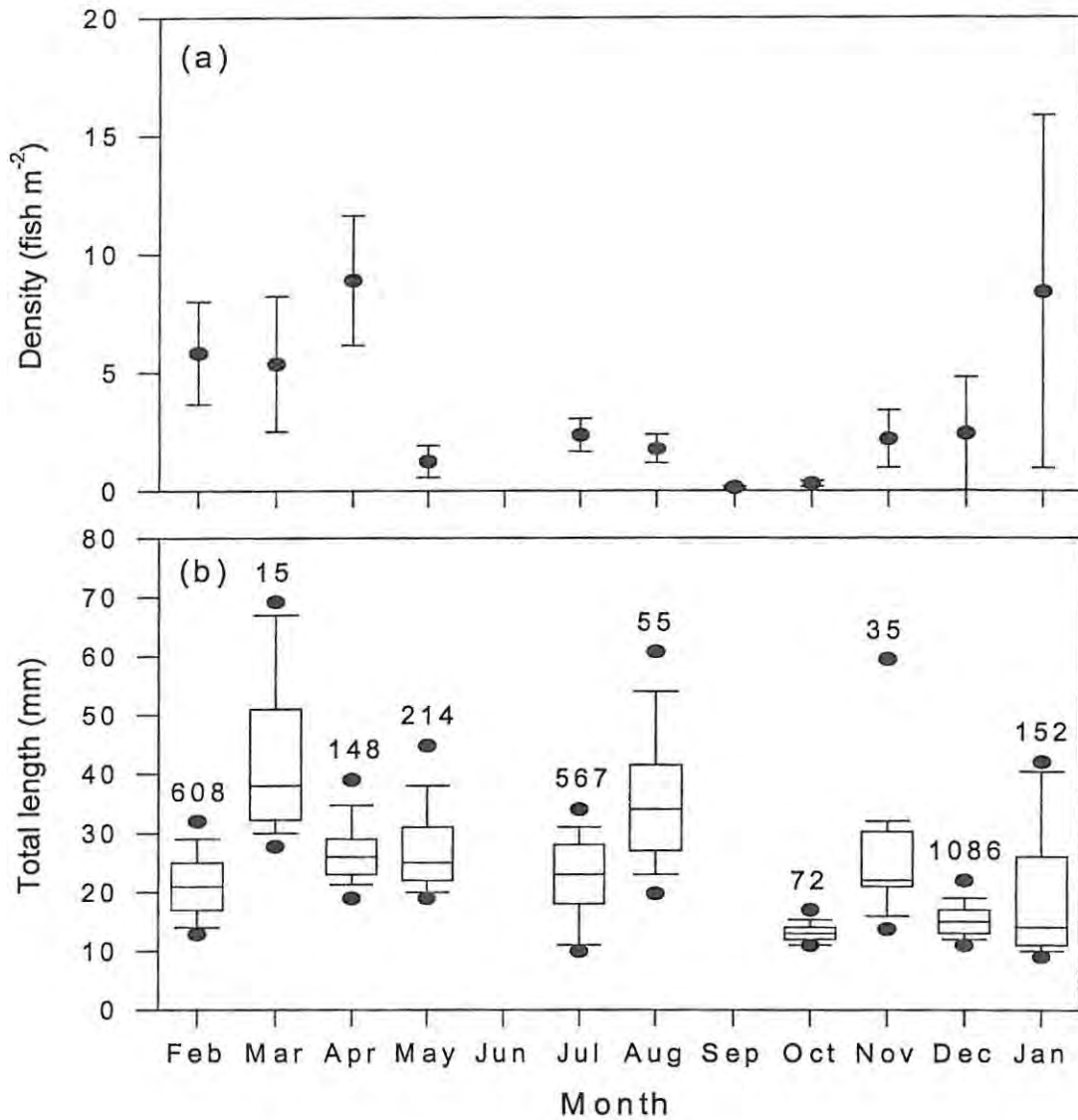


Figure 4.2. (a) Monthly juvenile cichlid densities expressed as number of fish per m^2 and (b) box and whisker plots showing the length distribution of juvenile cichlids sampled in the shallow littoral areas of Lake Chicamba using a 2-m long x 1-m deep fry seine net with a mesh size of 1 mm. Closed circles denote the 5th and 95th percentiles. Numbers above 95th percentile points indicate sample size.

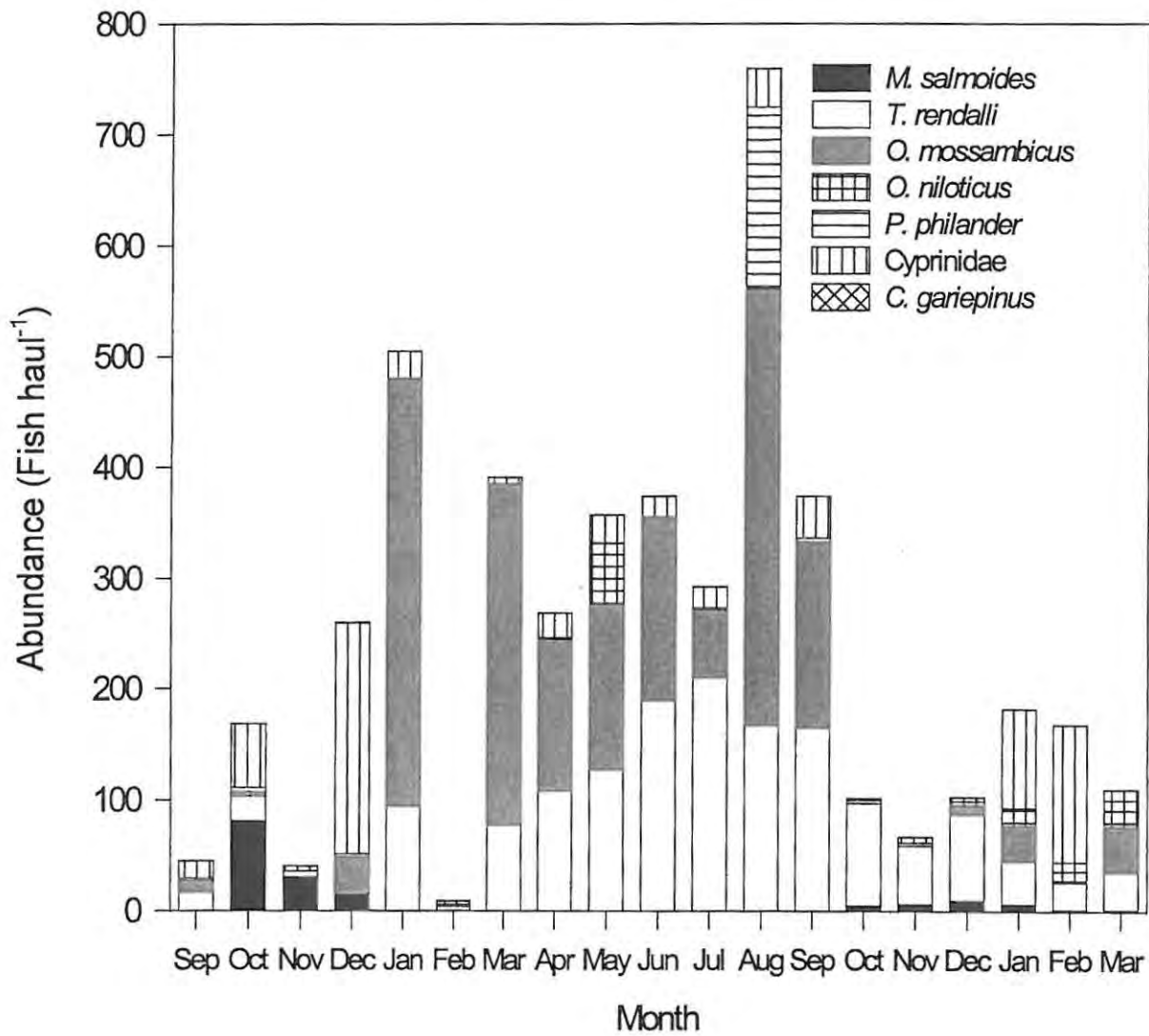


Figure 4.3. Monthly abundance of fish species (number of fish haul⁻¹) in the littoral areas of Lake Chicamba from September 1995 to March 1997 using 30-m seine-net hauls.

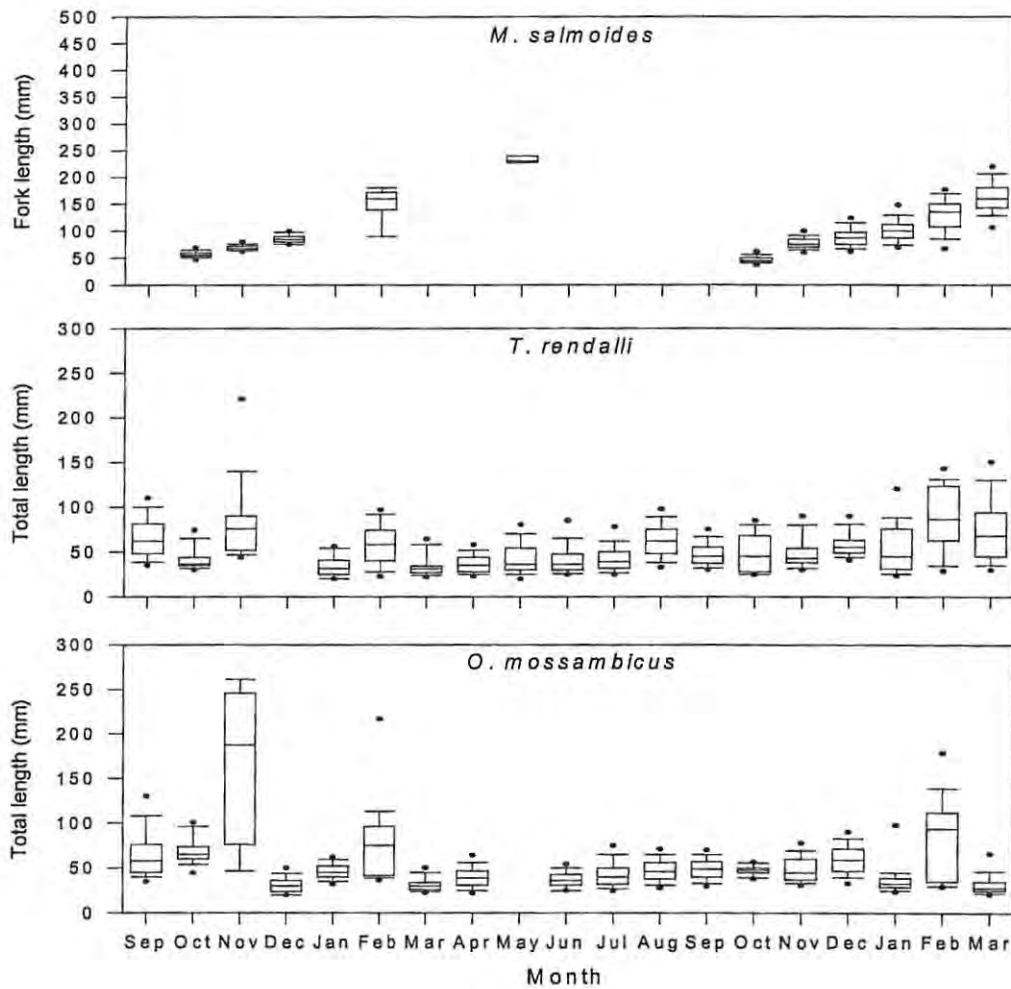


Figure 4.4. Box and whisker plots showing the length distribution of *M. salmoides*, *T. rendalli* and *O. mossambicus* in seine-net samples from September 1995 to March 1997. Closed circles denote the 5th and 95th percentiles.

Growth rate

The relationship between fish length and otolith length, otolith diameter and sectioned otolith thickness in *M. salmoides*, *T. rendalli* and *O. mossambicus* are summarised in Table 4.2. The probabilities of using lake level parameters to predict annulus width in the otoliths of these three species are summarised in Table 4.3.

Table 4.2. Morphometric relationships of *M. salmoides*, *Tilapia rendalli* and *Oreochromis mossambicus* sampled in Lake Chicamba, Mozambique. TL = total length, FL = fork length, OL = otolith length along the longitudinal axis, OD = otolith diameter along the transverse axis, OT = otolith thickness from the medial to the lateral margin.

Relationship		r ²	p	n
<i>M. salmoides</i>				
FL (mm)	= 99.9 OT (mm) + 135.1	76.1	< 0.0001	59
FL (mm)	= 22.96 OL (mm) ^{1.184}	94.1	< 0.0001	100
FL (mm)	= 40.39 OD (mm) ^{1.295}	91.8	< 0.0001	100
<i>T. rendalli</i>				
TL (mm)	= 147.5 OT (mm) + 48.7	48.6	< 0.0001	62
TL (mm)	= 23.28 OL (mm) ^{1.184}	98.0	< 0.0001	100
TL (mm)	= 36.57 OD (mm) ^{1.217}	96.0	< 0.0001	100
<i>O. mossambicus</i>				
TL (mm)	= 80.7 OT (mm) + 135.1	50.6	< 0.0001	85
TL (mm)	= 18.84 OL (mm) ^{1.224}	96.6	< 0.0001	100
TL (mm)	= 31.41 OD (mm) ^{1.270}	95.0	< 0.0001	100

In *M. salmoides* annulus width showed positive a trend with %DDSA (Figure 4.5; see table 4.1 for abbreviations). *T. rendalli* annulus width showed a positive trend with DDL and %DDSA (Figure 4.6), while *O. mossambicus* annulus width showed positive trends with DFL and %DFSA (Figure 4.7). In both *M. salmoides* and *O. mossambicus* annulus width showed a significant trend in which increments of younger fish were larger than those of older fish (Table 4.3). Annulus width in *T. rendalli* did not show this trend (Table 4.3). Annulus width in *O. mossambicus* could be predicted from the linear combination of DDSA ($p = 0.0002$) and DFL ($p = 0.0027$). Thus, annulus width could be described by the multiple linear regression equation:

$$\text{Annulus width (mm)} = 0.174 - (0.00327 \times \text{DDSA}) + (0.0131 \times \text{DFL}),$$

$$(r^2 = 16.4, p = 0.002)$$

The response of *O. mossambicus* annulus width to DDSA and DFL is shown in Figure 4.8.

Table 4.3. The effect of lake level parameters on annulus width in otoliths of *M. salmoides*, *T. rendalli* and *O. mossambicus*. * denotes a significant relationship at the chosen $p < 0.05$ level. DDL = Δ drawdown level; DFL = Δ flood level; DDSA = Δ drawdown surface area; DFSA = Δ flood surface area; %DDSA = percent Δ drawdown surface area; %DFSA = percent Δ flood surface area; Age = age in years of the sampled fish determined by annulus counts.

Parameter	r^2	p
<i>M. salmoides</i>		
DDL	5.6	0.054
DDSA	0.3	0.639
%DDSA*	5.8	0.050
DFL	3.7	0.119
FSA	2.6	0.196
%FSA	3.4	0.134
Age*	8.2	0.019
<i>T. rendalli</i>		
DDL*	7.0	0.021
DDSA	4.2	0.072
%DDSA*	6.9	0.021
DFL	2.0	0.223
FSA	0.0	0.906
%FSA	1.2	0.346
Age	3.1	0.120
<i>O. mossambicus</i>		
DDL*	4.0	0.046
DDSA	3.5	0.062
%DDSA	3.6	0.060
DFL*	8.4	0.004
FSA	0.6	0.421
%FSA	7.5	0.006
Age	9.7	0.002

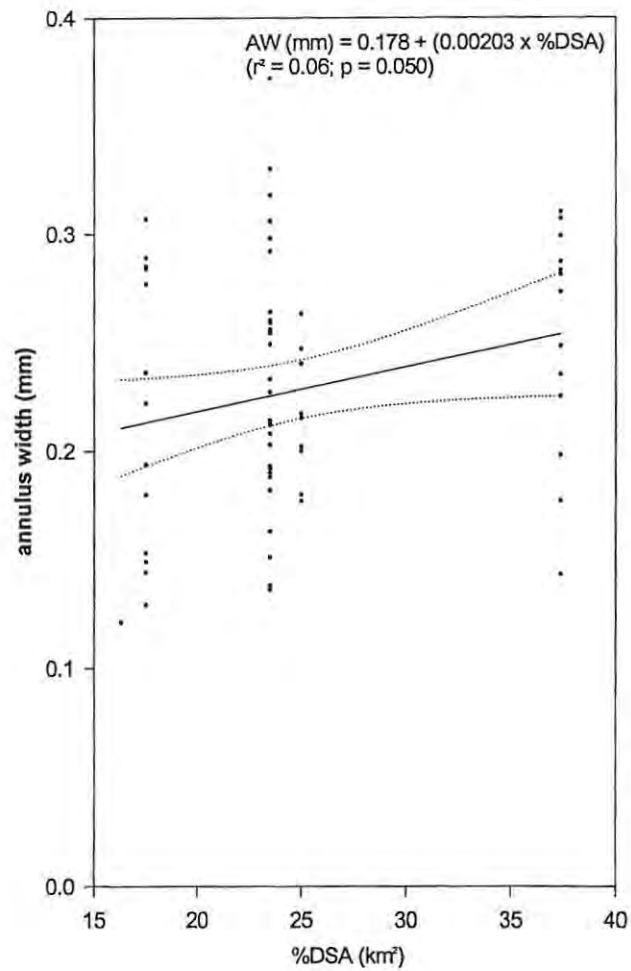


Figure 4.5. The relationship between annulus width (AW) (between the first and second annulus) in sectioned otoliths of *M. salmoides* and the percent change in surface area during the annual drawdown period (%DSA) (n = 67). Solid line = regression; dotted lines = 95% confidence intervals.

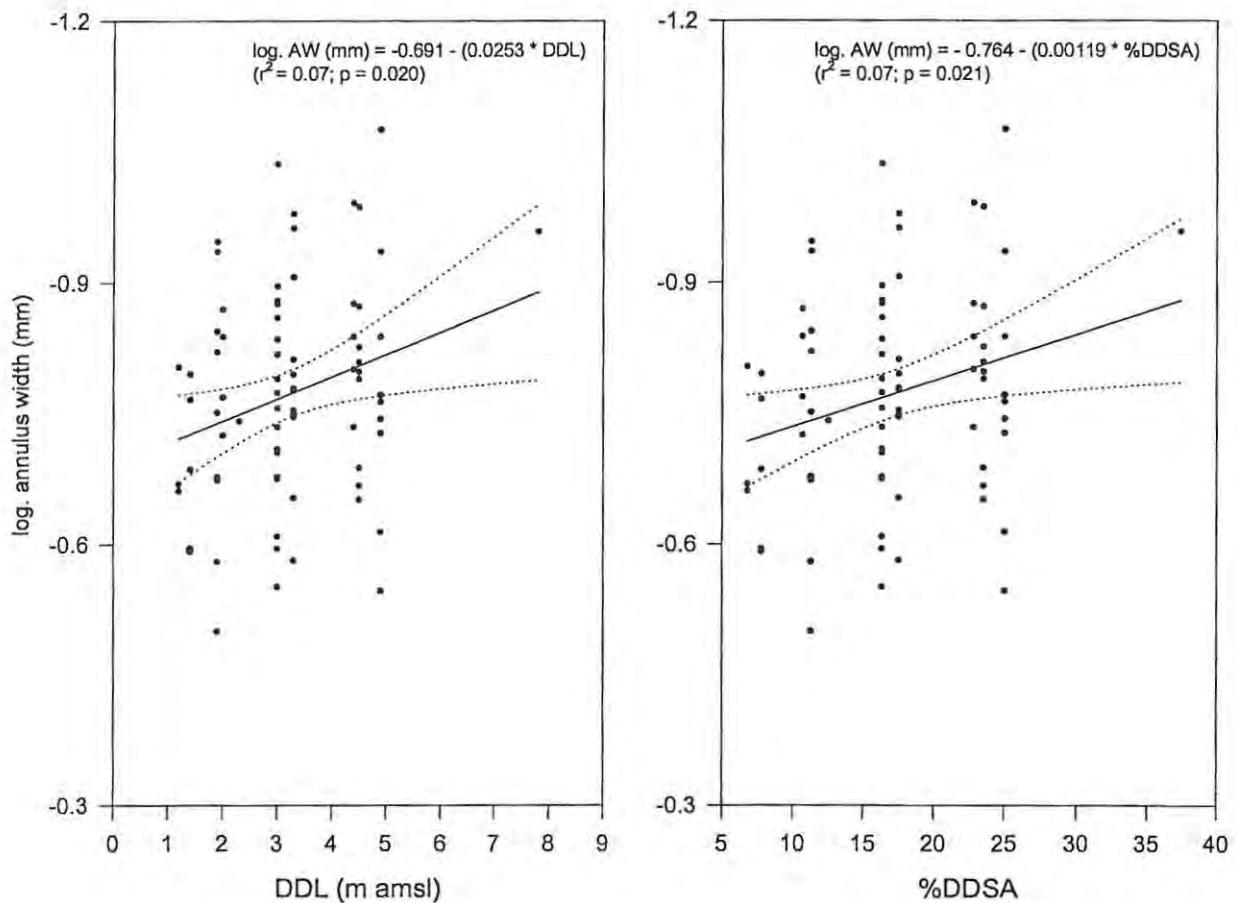


Figure 4.6. The relationship between the natural log of annulus width (AW)(between the first and second annulus) in sectioned *T. rendalli* otoliths and (a) Δ drawdown level (DDL) (change in lake level m amsl during drawdown) and (b) percent Δ drawdown surface area (DDSA)(change in lake surface area expressed as a percentage of lake surface area prior to drawdown) (n = 77). Solid line = regression; dotted lines = 95% confidence intervals.

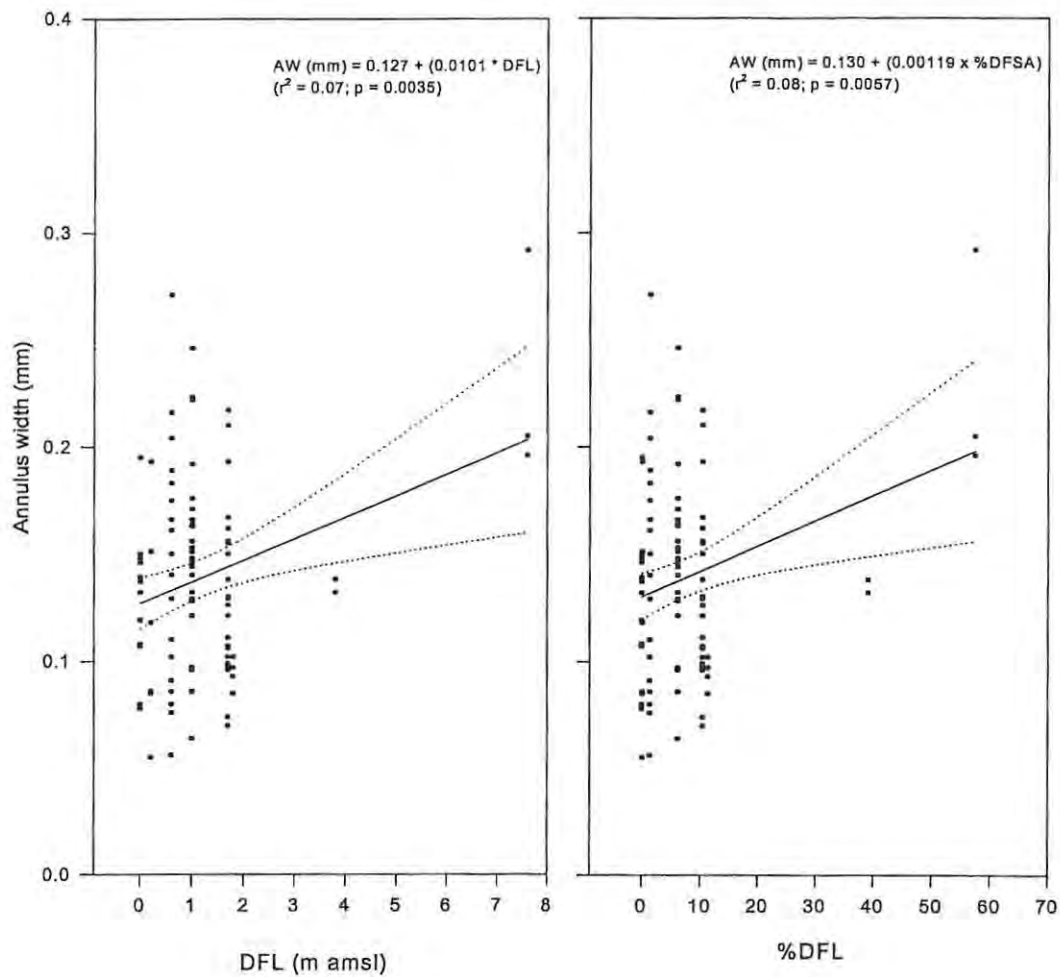


Figure 4.7. The relationship between annulus width (between the first and second annulus) in sectioned otoliths of *O. mossambicus* and (a) Δ flood level (DFL) (the increase in lake level (m amsl) as a result of flooding) and (b) percent Δ flood level (%DFL)(increase in surface area as a result of flooding expressed as a percentage of the lake surface area prior to flooding) ($n = 98$). Solid line = regression; dotted lines = 95% confidence intervals.

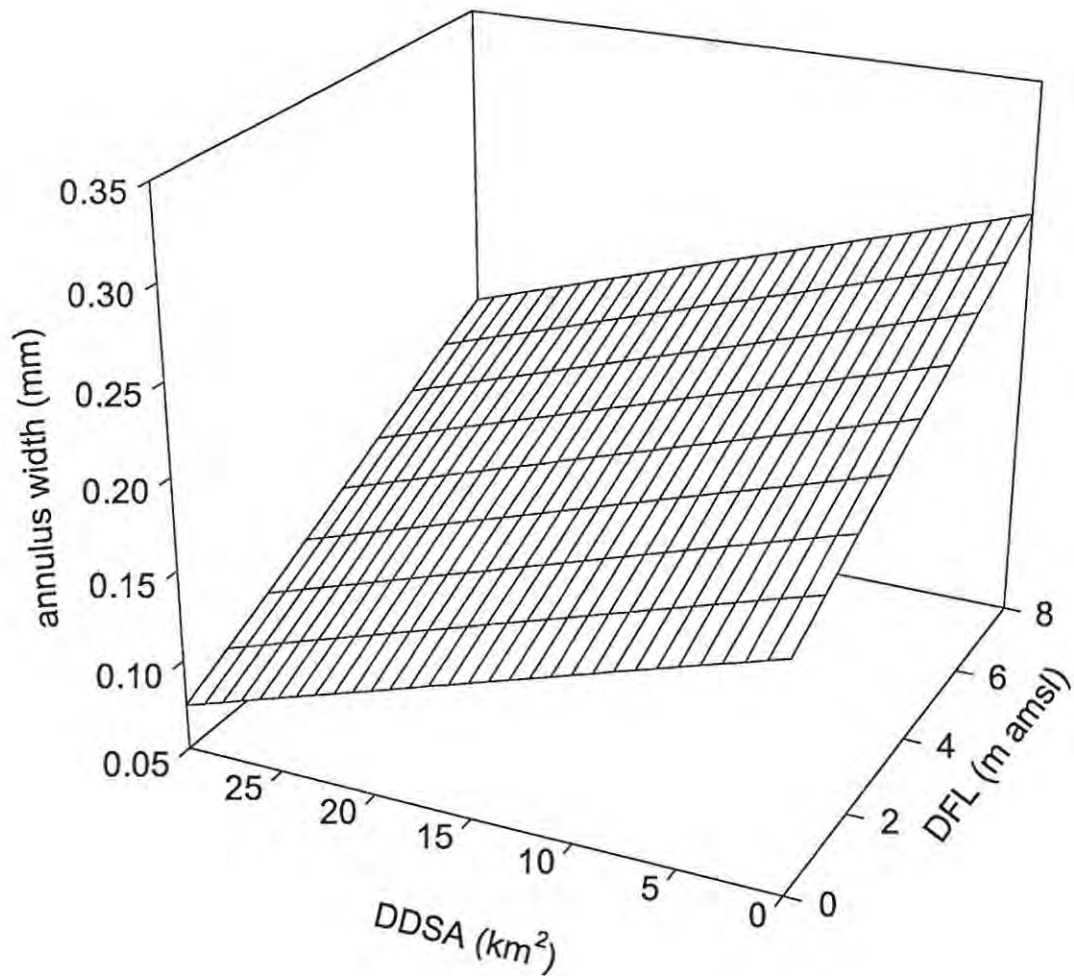


Figure 4.8. Three-dimensional representation of the relationship between annulus width of sectioned *O. mossambicus* otoliths (between the first and second annulus) and Δ drawdown surface area DDSA) and Δ flood level (DFL). ($r^2 = 16.4\%$; $p = 0.0002$).

Fish condition

The condition factors for *M. salmoides*, *T. rendalli* and *O. mossambicus* are illustrated in Figure 4.9. Condition factor (K) for *M. salmoides* was highest from February to September ($K = 1.63 - 1.81$) and lowest from October to January ($K = 1.48 - 1.60$; Figure 4.9). In *T. rendalli* condition factor showed a steady rise during flooding, from January ($K = 2.39$) to

June ($K = 2.81$), and a decrease in condition factor from July ($K = 2.60$) to December ($K = 2.29$; Figure 4.9). In *O. mossambicus*, condition factor was lowest during February and March ($K = 1.81 - 1.79$) and the highest value was recorded in June ($K = 2.11$; Figure 4.9).

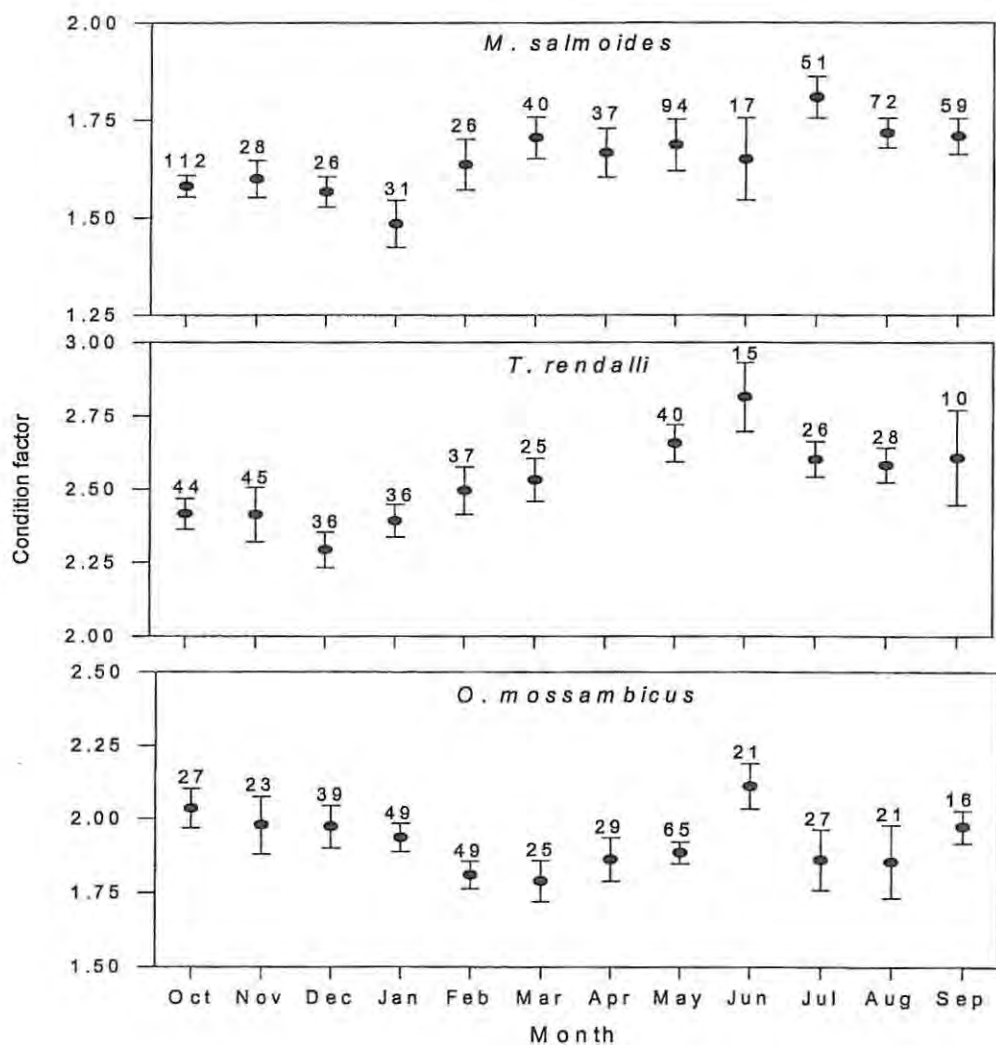


Figure 4.9. Monthly mean condition factor \pm 95% confidence intervals of *M. salmoides*, *T. rendalli* and *O. mossambicus* collected between October 1995 and September 1996 in Lake Chicamba. Numbers above error bars indicate sample number.

4.4. DISCUSSION

There is little doubt that fluctuations in lake level have a marked effect on fish populations (Jackson 1961 & 1966, Harding 1966, Heman et al. 1969, Coche 1974, Martin et al. 1981, De Silva 1985, Karengé & Kolding 1995). In Lake Chicamba, the abundance of juvenile fish, growth rate and condition factor were intricately linked to flooding of the lake margins. To understand this response, juvenile abundance, growth and condition factor must be viewed in relation to the effects that flooding and drawdown events have on spawning success, feeding, predator avoidance and growth rate.

Effects on spawning

Spawning periodicity in cichlids is often independent of flooding events in their habitat but flooding has been linked to other factors such as increasing water temperature and day length (Fryer & Iles 1972, Bruton & Allanson 1974, van der Waal 1985, Lowe-McConnell 1991, James & Bruton 1992, Merron et al. 1993). This is illustrated in the Phongolo floodplain, South Africa, where *O. mossambicus* dominated after a period of flood failure (Merron et al. 1993) and in Lake Liambezi, Namibia, where the spawning of *T. rendalli* was found to be independent of flooding (van der Waal 1985). In Lake Chicamba, the reproductive activity of both cichlid species was confined to the summer period from September to May, when mean water temperatures were in excess of 24°C (Chapter 3). Since flooding occurs only between late December and April, the spawning period of the cichlids in Lake Chicamba was independent of flooding. However, tilapias have evolved under riverine conditions (Fryer & Iles 1972, Greenwood 1974) where fluctuating water

levels are common. Therefore, these fish may retain the ability to successfully utilise flooded habitats in lacustrine conditions.

The higher density of juvenile cichlids in the shallow littoral zone (depth < 2 m) during the flooding phase of the lake (January to April), than during the drawdown phase (September to December) (Figure 4.2 a & 4.3) suggests that the abundance of juvenile cichlids in the lake's littoral area was enhanced by flooding. The rapid drawdowns during the summer period from October to December in Lake Chicamba, illustrated in Figure 4.10, may in part explain the decreased abundance of juvenile cichlids in the littoral areas during drawdown summer phase (Figure 4.2 a & 4.3). While *T. rendalli* juveniles were less abundant during severe drawdowns in October (1.05 m) and November 1995 (1.22 m) than during the same period in 1996 when drawdowns were less severe (0.69 m and 0.52 m in October and November 1996, respectively), the abundance of juvenile *O. mossambicus* was unaffected by drawdown and flooding events during summer (Figure 4.2 a & 4.3). These differences may be attributed to the different reproductive strategies employed by the two species.

T. rendalli are nest spawners which guard their eggs and fry for extended periods while *O. mossambicus* is a mouthbrooder which uses the nest only as a breeding arena (Fryer & Iles 1972, Bruton & Boltt 1975, Bruton 1979b, Caulton 1979, Bruton & Kok 1980, Trewawas 1983). *T. rendalli* prefer to spawn in shallow weeded areas (Fryer & Iles 1972, Caulton 1979) in simple nests consisting of a series of shallow pits or brood chambers (approximately 79 mm in diameter) (Bruton 1979b) which are excavated by the pair. Prenuptial courtship activities may last from 4 days to two weeks and after spawning the

eggs hatch in 3 to 4 days, depending on water temperature (Fryer & Iles 1972, Caulton 1979). The fry remain on the bottom of the nest for a further 4 to 5 days while the yolk sac is resorbed (Caulton 1979) and the parents may move the fry between brood chambers (Fryer & Iles 1972). Under semi-natural conditions in the Congo, a pair of *T. rendalli* was observed to raise seven successive broods with a minimum time interval between broods of 22 days (Fryer & Iles 1972). During October and November 1995 the water level in Lake Chicamba dropped by 0.87 m during a 22-day period. Given that the minimum depth of *T. rendalli* nests recorded in the lake was 0.3 m (pers. obs.), nests would initially have to be constructed at depths exceeding 1.27 m for the successful raising of a brood. However, most nests were in areas less than 1 m deep throughout the spawning season (often occurring on submerged ant hills; pers. obs.) and it is therefore likely that these nests were deserted as a consequence of exposure by receding water levels during October and November 1995. For example, during October and November 1995, 0.9 and 1.4 km² of potential *T. rendalli* spawning sites were exposed. Therefore, the abundance of juvenile *T. rendalli* was significantly higher during flooding periods (6.0 fish per haul⁻¹) than during the 1995 drawdown period (23.4 fish per haul⁻¹) and it is likely that spawning in this species was severely disrupted by rapid drawdowns.

In the mouthbrooder *O. mossambicus*, there is little risk of egg desiccation or stranding of the fry (Fryer & Iles 1972, Bruton 1979b, Caulton 1979, Trewawas 1983). Male *O. mossambicus* have been reported to take 4 to 6 days to construct the nest (Caulton 1979). In Lake Sibaya, South Africa, *O. mossambicus* nests were recorded at depths of between 41 cm and 8.1 m during low water level (Bruton 1979b). The ability of *O. mossambicus* to

spawn in deep water and its mouthbrooding reproductive strategy may therefore make spawning success in this species less susceptible to rapid rates of drawdown in Lake Chicamba. This is similar to observations made by Merron et al. (1993) in the Phongolo floodplain, South Africa, where *O. mossambicus* dominated the fish assemblage after periods of flood failure.

M. salmoides, like *T. rendalli*, are nest spawners and a stable lake level is considered to be essential for spawning success (Kohler et al. 1993). However, juvenile *M. salmoides* in Lake Chicamba were more abundant after severe drawdowns over the 1995 spawning season than in 1996 when the drawdown rate was less extreme (Figure 4.10). Therefore, drawdown during the spawning season of *M. salmoides* in Lake Chicamba does not lead to recruitment failure in this species, even at maximum drawdown rates. However, since spawning in this species is restricted to August and September, it was not possible to determine whether water-level stability or flooding during the spawning season enhances survival and thus recruitment. It is possible that spawning may only occur at a depth where receding water levels neither cause nest desertion by the male nor the stranding of eggs and fry. Although there is little quantitative data, the hypothesis that deep spawning occurs in this species is supported by the complete absence of *M. salmoides* nests in areas shallower than one metre during August and September, while hook and line fishing data indicated that ripe male *M. salmoides* were prolific in dense stands of drowned trees at depths greater than one metre (pers. obs.).

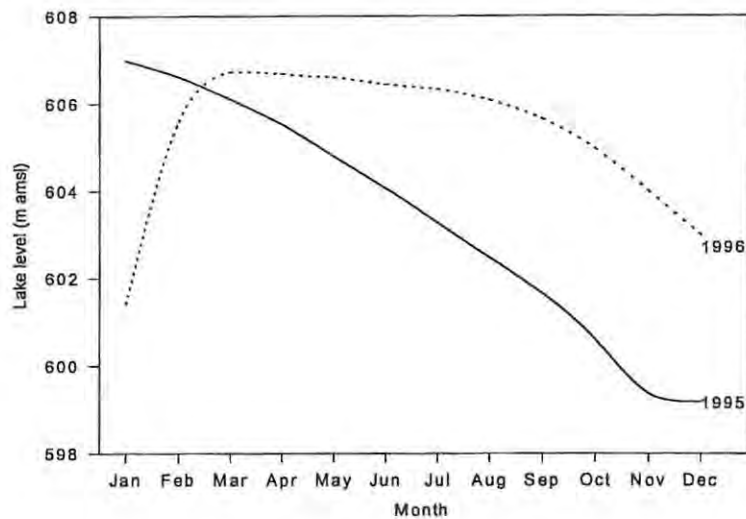


Figure 4.10. Lake level (m amsl) in Lake Chicamba during the 1995 (solid line) and 1996 (dotted line) calendar years.

Effects on feeding and predation

Zooplankton forms a major component in the diet of early juvenile *M. salmoides*, *T. rendalli* and *O. mossambicus* (Le Roux 1956, Munro 1967, Wagner & Rowe-Rowe 1972, Bruton & Bolt 1975, Caulton 1976, Whitfield & Blaber 1978, Bowen 1979, De Moor et al. 1986, Lazzaro 1991). After the early juvenile stage, *T. rendalli* is generally regarded as a macrophytic browser, yet, like many other cichlids it feeds opportunistically on a variety of food sources including aquatic insect larvae and zooplankton (Munro 1967, Wagner & Rowe-Rowe 1972, Caulton 1976, 1977 a & b, Chifamba 1990). Young *O. mossambicus* have been reported to feed mainly on diatoms in the detrital floc, periphyton and

zooplankton (Le Roux 1956, Bruton & Boltt 1975, Whitfield & Blaber 1978, Bowen 1979, De Moor et al. 1986), while adults feed mainly on detritus and filamentous algae (De Moor et al. 1986).

Man-made lakes become less fertile in time as initial nutrients are washed out or become fixed in the sediments, unless an external loading of nutrients is applied (Moss 1988). During flooding, rivers transport large quantities of nutrients into lakes. These direct inputs from inflowing rivers have been shown to increase zooplankton production in Lake Kariba (Marshall 1997). This increase in zooplankton production during flooding increases the food availability for juvenile cichlids and leads to an increased growth rate, which may result in increased survival and abundance. The importance of zooplankton for juvenile *M. salmoides* is negligible during flooding, because juveniles of this species no longer feed on zooplankton during this phase but tend towards piscivory (Chapter 3).

Work on Lake Kariba has shown that although the input of suspended solids into the lake can be considerable, the effect on lake nutrient levels can be highly localised (Lindmark 1997). Organic matter and fine silt material, rich in nitrogen and phosphorus, deposited in the lake sediments after flooding supports a large biomass of aquatic macrophytes (Machena 1989, 1997). These aquatic macrophytes play a vital role in sediment stabilisation and provide habitat diversity and shelter, substrata for periphyton and sites for abundant food production for invertebrates and fish (Wetzel & Hough 1973, Pelican et al. 1978, Ramberg et al. 1978, Howard-Williams 1981, Machena 1989 & 1997). However, in Lake Chicamba aquatic macrophytes are generally absent due to large fluctuations in lake

level and possibly the presence of the herbivorous *T. rendalli* (Junor 1969). However, during the drawdown phase, large areas of silt soils are exposed and colonised by terrestrial vegetation or are used for subsistence agriculture. Consequently, the inundation of these vegetated areas during flooding promotes interaction between the aquatic and terrestrial ecosystem (McLachlan 1974, Skarpe 1997) by increasing productivity, food availability and cover.

It has been calculated that vegetation with a mean dry biomass of $820 \pm 202 \text{ g m}^{-2}$ is submerged in Lake Chicamba during the flooding phase (see Chapter 2). From December 1995 to April 1996 the lake level rose by 7.6 m (Figure 4.10) inundating an area of 16.5 km² and a total dry plant biomass of approximately 13500 tons. These figures closely resemble the dry plant biomass estimate of 792 g. m⁻² in the drawdown zone of Lake Kariba (Skarpe 1997). Caulton (1977b) concluded from biomass estimates of *Panicum repens* in the flooded lake margins of Lake Kariba that a minimum of 222 kg. ha⁻² of *T. rendalli* could be supported by the annual flooding in Lake Kariba. Since no vegetation remains by the time drawdown occurs in Lake Chicamba (Chapter 2; Figure 2.2 a), food availability for *T. rendalli* may be severely limited during this phase. The direct effects of food availability as a consequence of flooding are illustrated by the increase in condition factor of *T. rendalli* during flooding from January to June and a decrease in condition factor from June to December (Figure 4.9). Thus, flooding events provide an immediate, though temporary, food supply for *T. rendalli*.

Decaying vegetation also provides a nutrient source to support increased primary productivity that leads to an increase in the availability of planktonic diatoms and periphyton for juveniles of both *T. rendalli* and *O. mossambicus*. In addition, the decaying vegetation enriches the detritus, which is used as a primary food source by *O. mossambicus* (De Moor et al. 1986). The persistence of detritus during the drawdown summer may in part explain the late response in the increase of the condition factor in *O. mossambicus* (Figure 4.9). The increase in the availability and quality of food leads to improved growth during flooding years (Figure 4.7), which may ultimately enhance survival through avoidance of predation and increased competitiveness. In the Kafue floodplain, Zambia, up to 75% of the expected first-year growth in *O. andersonii* and *O. macrochir* took place within six weeks following the peak flood (Dudley 1974, 1979).

The effect of submerged vegetation on prey evasion has been widely documented (Strange et al. 1975, Gotceitas & Colgan 1989, Savino & Stein 1989, Godinho & Ferreira 1994, Werner et al. 1983). In Lake Kariba, juvenile *T. rendalli* inhabit densely vegetated nursery areas in the littoral zone to avoid intense predation by the tigerfish *Hydrocynus vittatus* (Donnelly 1969). Similarly, the high spawning success of *O. mortimeri* during the initial flooding stages of Lake Kariba (1958/59) was attributed to increased survival as a consequence of an increase of available cover (Jackson 1961). In largemouth bass piscivory is mediated by the abundance of aquatic vegetation (Bettoli et al. 1992). For example, Heman et al. (1969) attributed a decrease in the density of *Lepomis macrochirus* fry after a reservoir drawdown to the elimination of vegetation cover and subsequent high predation rates by largemouth bass. In Lake Chicamba predation on juvenile cichlids by *M.*

salmoides during periods of reduced vegetation cover may partly explain the lower abundance of juvenile cichlids during the drawdown phase. As lake level recedes, the juvenile cichlids are forced out of the vegetated lake margins into deeper water where they become vulnerable to predation by largemouth bass. Although juvenile *M. salmoides* (70 – 120 mm FL) were the dominant prey item of bass (>300 mm FL) during the height of the 1995 drawdown (Chapter 3), it is possible that the low flood level during the beginning of 1995 caused a depletion of alternative cichlid prey earlier in the year.

Effects on growth

Growth rings on hard structures such as scales, otoliths and spines are formed as a response to one or more environmental variables that reduce metabolic rate and result in a slowing of the growth rate (Gauldie & Nelson, 1990). The period of annulus formation is highly variable in fishes in tropical and subtropical waters (Dudley 1974, Kapetsky 1974, Booth et al. 1995, Booth & Merron 1996, Garrod 1959, Bruton & Allanson 1974, Pannella 1974, Hecht 1980a, Le Roux 1961). In Lake Chicamba, the formation of a single opaque zone (observed under transmitted light) in the otoliths of *M. salmoides*, *T. rendalli* and *O. mossambicus* corresponded with the end of winter, when water temperatures are at their lowest and the lake is in its drawdown phase (Chapter 3, Figure 3.2). Therefore, the distance between annuli is indicative of the growth of the fish between winter periods. Since the relationship between fish length and otolith size is allometric (Table 4.2), the discussion on growth is based on annulus width.

Annulus width showed a trend in which the width between the first and second annuli was narrower in otoliths sampled from older *M. salmoides* and *O. mossambicus* than in those sampled from younger fish. This growth pattern is termed negative Lee's phenomenon (Lee 1912, Ricker 1969). Since only one flood and drawdown occurred within each growth increment, age and lake-level parameters cannot be separated in these two species. Negative Lee's phenomenon was also observed during growth studies undertaken on *O. machrochir* and *O. andersonii* in the Kafue Gorge dam, Zambia (Dudley 1979). However, the possibility that annulus width is correlated with flooding conditions should not be ignored.

The positive relationship between increased annulus width in *M. salmoides* otoliths and drawdown level may be a result of an increase in the availability of prey. Since drawdown concentrates the prey and limits cover, feeding conditions for *M. salmoides* may be enhanced during this phase. In its native range, increased feeding and growth rate of largemouth bass have been recorded during drawdown periods in reservoirs (Heman et al. 1969). Although severe drawdowns limit the abundance of juvenile cichlids, high prey abundance during drawdown is maintained by high rates of cannibalism when alternate prey is limiting (Chapter 3).

In *O. mossambicus*, the increased food availability as a consequence of submerged vegetation during flooding and a decrease in feeding area during the drawdown phase may be the principal determinants for increased growth. This is illustrated by a decrease in annulus width during years when drawdown was large and an increase in annulus width during periods of high lake level (Figure 4.9). Similar observations on growth rate were

made in Hartbeespoort dam, South Africa, where increased food availability after flooding led to increased growth in *O. mossambicus* (Cochrane 1985).

The reasons for an increase in annulus width timed with lake drawdown in otoliths of *T. rendalli* are not clear. Although *T. rendalli* feeds almost exclusively on aquatic macrophytes when these are available, it opportunistically feeds on a variety of food sources, including aquatic insect larvae and zooplankton (Munro 1967, Wagner & Rowe-Rowe 1972, Caulton 1976). In addition, this species may also become piscivorous in the absence of submerged vegetation (Junor 1969). The species may, therefore, overcome limitations in plant food during drawdowns by feeding on alternative food. In addition, the positive effects of flooding on *T. rendalli* annulus width may be masked by other effects such as sampling bias due to low sample sizes in older age groups, temperature regimes and the possibility that no further growth advantage is gained after a certain magnitude of flooding.

Although it was not possible to accurately determine the factors responsible for changes in growth rate with flooding and drawdown events in Lake Chicamba, the significant relationships between these factors and fish growth imply an increase in overall productivity of the lake during flooding years.

Conclusion

Although it was not possible to attribute the low juvenile cichlid abundance during periods of drawdown to any one factor, the increase in food availability and cover during flooding

coupled with the possibility of increased spawning success are likely to contribute towards an increase in recruitment during this period. It is interesting to note that the seine-net CPUE for *T. rendalli* and *O. mossambicus* during the 1996 and 1997 flooding summers did not differ significantly. Since the surface area of the lake's littoral zone was 5.1 km² in March 1996 and 9.7 km² in March 1997 and CPUE is an indirect measure of abundance, the total number of recruits in the lake as a whole was at least 1.9 times higher during 1997 than during 1996.

Since evidence was found that flooding of the lake margins might influence cichlid abundance in Lake Chicamba, the failure of flooding may lead to a reduction in recruitment. Although drawdowns have a negative effect on the success of spawning, they are a prerequisite for flooding and the negative effects of a 3-month drawdown during the spawning season of the cichlids from October to December are outweighed by the positive effects flooding has on recruitment. A time lag between the commencement of the rainy season and flooding is important in Lake Chicamba as the growth of terrestrial vegetation must take place before flooding.

CHAPTER 5

A quantitative assessment of the fishery.

5.1 INTRODUCTION

The first attempt to quantify fishing effort on Lake Chicamba was made in 1981 when an estimated 67 gill net fishers operated from a number of co-operative fishing ventures around the lake (Robelus & Vissers 1984). However, destabilisation activities by RENAMO and the ensuing civil war in Mozambique (1980-1992) caused large-scale migration of the rural population into safe areas such as the Beira corridor (Streck 1993). Lake Chicamba's northern shore falls within this 'safe area' and during 1993 the fishery was utilised by at least 600 fishers (Weyl 1994). These fishers are either concentrated in fishing villages or inhabit scattered households around the lake. While the fishers place little emphasis on any single target species, two cichlids, *Oreochromis mossambicus* and *Tilapia rendalli* and an introduced centrarchid, *Micropterus salmoides*, dominate the fishery (Weyl 1994).

Fishing takes place both from canoes and from the shore. Two canoe types, dugouts and barkhive canoes, are used on the lake. Dugout canoes are made from hollowed tree trunks and barkhive canoes are shaped from the bark of *Brachystegia boehmii* (Figure 5.1). Six gears are utilised by the fishers. These are hook and line fishing, long lines, traps, gill nets, beach seine net and cast net. While the canoe fishery utilises all gears, the shore fishers are limited to hook and line fishing, cast netting and small seine nets. In addition, line fishing and seine netting with 2-m to 5-m long lengths of shade cloth is practised by women and

children. The utilisation of all other gears is a male-dominated activity (Weyl 1994, Ainslie 1996).



Figure 5.1. (a) Dugout and (b) barkhiv canoes used by the subsistence fishers on Lake Chicamba.

Hook and line fishers use a bamboo rod (2 to 3 metres in length), an approximately equal length of monofilament fishing line and a hook ranging in size from #4 to #1 (Figure 5.2 a). The most commonly used baits are earthworms, cooked maize meal or small live fish. Hook and line fishing is only undertaken during daylight hours. Long lines are typically less than 50 m in length with hooks ranging in size from #2 to #1/0 attached at intervals of five metres. Longlines are baited with small live or dead fish. The longlines are set over-

night from canoes. Traps are small valve traps constructed from reeds and are funnel shaped (Figure 5.2 b). Traps are baited with cooked maize meal and set in shallow areas of the lake. Multifilament gill nets with stretched mesh sizes ranging from 70 to 100 millimetres are set over-night. The fishers use both surface-set and bottom-set gill nets and the gill nets are anchored to drowned trees in water seldom exceeding six metres in depth (Figure 5.2 c). Beach seines range in mesh size from mosquito netting and shade cloth (< 5 mm) to 70 millimetres and are from 3 to 100 metres in length. Smaller seine nets (3 - 5 m) are used from the shore while the larger seine nets are set with canoes and hauled towards the shore by two teams (Figure 5.2 d). Cast nets are cast either from the shore or from canoes (Figure 5.2 e). Commonly, cast net fishers bait areas with maize meal prior to fishing.

Muth *et al.* (1987) classified subsistence users as a group that: consume most of what they produce; sell little in the cash economy; use primitive technology for production and consumption; rely primarily on family labour; employ labour-intensive practices; maintain a limited economic standard of living; and often must consider individual, family, and group survival in decision making. Although most of the criteria for subsistence are met by the fishers on Lake Chicamba, all except hook and line and trap fishers, regularly sold at least part of their catch (Balarin & Weyl 1996). However, monetary gains from fishing with other gear are low and the whole fishery can generally be classed as a subsistence fishery.



Figure 5.2. (a) Hook and line fishing, (b) valve trap, (c) fisherman tending a gill net from a barkhive canoe, (d) seine netting, (e) cast netting from a dugout canoe in Lake Chicamba.

Present fisheries legislation in Mozambique requires all fishers, with the exception of subsistence fishers to be licensed (Anon 1990). The Provincial Directorate of Agriculture and Fisheries (DPAP) is responsible for the enforcement of management measures and licensing on Lake Chicamba (Ferraio 1997). Currently only line and trap fishers are exempt from licensing and minimum mesh sizes of 70 mm for gill-nets and 50 mm for seine-nets are prescribed (Alfredo Geronimo: DPAP Provincial Director, pers. comm.). However, due to budgetary and logistic constraints, there is no on-lake enforcement (Ferraio 1997). In addition, access into the fishery is not controlled by the local community (Ainslie 1996) and the fishery is therefore "open-access"(Cousins 1995).

The aim of this section of the study was to assess the sustainability of the Lake Chicamba fishery and to determine parameters for the future application of deterministic fisheries models. The main objectives were to: (1) assess the gear-selectivity and potential impact of each gear on three primary target species; (2) determine catch and effort for each gear; (3) determine the annual fishery yield and (4) determine the importance of each gear to the Lake Chicamba fishery.

5.2. MATERIALS AND METHODS

Catch composition

To describe gear use and utilisation patterns in the fishery, questionnaire and creel surveys were conducted at three major fish landing sites from July 1995 to March 1997 (Figure 2.1). Data were collected on five consecutive days per landing site per month. The date of each sampling period was randomised. All fishers at the landing site on the sampling day were interviewed and the gear type, effort and the total mass of each species component in

the catch was recorded. Subsequently, a sample of not less than 10% of each species component in the catch was measured for fork length (FL) or total length (TL) depending on species.

Initial analysis of catch data showed that cast nets and longlines were used by less than 5% of the fishers on the lake and are, therefore, not considered major components of the fishery. Thus, cast netting and longlines were excluded from further analysis.

Gear selectivity

In the seine-net fishery, individual seine nets were composed of stretched mesh sizes ranging from less than 10 mm (e.g. shade cloth) to 50 mm. Hook and line fishers used hook sizes ranging from #4 to #2/0. The stretched mesh size of the gill nets was never smaller than 70 mm; however, mesh sizes larger than 70 mm were used indiscriminately. In addition, the mending of damaged nets resulted in most gill nets being composed of a wide range of mesh sizes (70 mm to > 100 mm). Due to the complexity in assessing each individual gear, it was decided to determine the selectivity pattern of each fishery as a whole, rather than for individual mesh or hook sizes.

The determination of selectivity of the gill net, seine net and hook and line fishing sectors was based on converting the length-frequency distributions illustrated in Figure 5.3 to age-frequency (Figure 5.4) using the length-at-age keys presented in Chapter 3. In the seine-net and hook-and-line fisheries, the catch of all three species was dominated by 0+ year-old fish (Figure 5.4). The selectivity pattern of the seine-net and hook-and-line fisheries was

assumed to be both temporally invariant and could be adequately described by the logistic form:

$$S_a = \frac{1}{1 + e^{-(a-a_{50})/\delta}}, \quad (\text{Equation 5.1})$$

where S_a is the selectivity of the gear on a fish of age a , a_{50} is the age-at-50%-selectivity and δ is the parameter that determines the width of the age-specific selectivity function. In *M. salmoides*, age in months could be determined by the back-calculation procedure outlined in Chapter 3 and the logistic ogive was fitted to the ascending limb of the seine net and hook and line fishing age-frequency data. For all species, in the seine-net and hook-and-line fisheries, it was noted that the mode of the age-frequency distribution approximated 100%-selectivity. In the two cichlid species, the determination of age in months was not possible and the age-at-50%-selectivity (a_{50}) of each species, into the seine-net and hook-and-line fisheries, was presumed to be 'knife-edged' at an age of 0.5 years.

The determination of the selection pattern in the gill-net fishery was further complicated by the complexity of the gill nets used on the lake. The assumption was therefore made that all fish larger than the mode of the age-frequency distribution were retained by this fishery due to the wide range of mesh sizes in the fleets. For this reason, the selectivity pattern of the gill-net fishery was also assumed to be temporally invariant and normally distributed. For all species, in the gill-net fishery, it was noted that the mode of the age-frequency distribution approximated 50%-selectivity. Due to the dominance of age 0+ *M. salmoides* in the gill net catch (Figure 5.4), the logistic ogive was fitted to monthly age-frequency data

for this species. For the two cichlids, the logistic ogive was fitted to the age (years)-frequency distribution.

Catch rate

Procedures outlined by Pollock et al. (1994) were used to determine catch per unit effort (CPUE), total annual effort and annual yield for each gear used in the Lake Chicamba fishery. CPUE was determined for the subsistence gill net, seine net and hook and line fishing sectors. Effort units were standardised to 100m net night⁻¹ for gill nets, per haul for seine nets and hours fished per man for the hook and line fishers. Mean CPUE was then calculated using the equation:

$$\overline{CPUE} = \frac{\sum_{i=1}^n (C_i / E_i)}{n} \quad (\text{Equation 5.2})$$

where C_i is the catch on day i , and E_i is fishing effort on day i (Pollock et al. 1994).

Due to seasonal variation in catch rate, CPUE was calculated separately for four quarters in each year. Within each three-month period there were similar temperature and lake-level conditions. The four quarters represented the following months and lake conditions:

1st quarter (1Q): January to March; summer with rising lake level.

2nd quarter (2Q): April to June; beginning of winter with stable to slowly receding lake level.

3rd quarter (3Q): July to September; end of winter with rapidly receding lake level.

4th quarter (4Q): October to December; summer with rapidly receding lake level.

To compare seasonal CPUE data, the non-parametric Kruskal-Wallis one-way analysis of variance (ANOVA) on ranks was applied and Dunn's test (all-pairwise) was used for multiple comparison. A 95% confidence level was used in all tests.

The total yield for each gear in the fishery during each quarter was estimated for fishers operating from canoes and from the shore separately, using the following procedures. The proportional utilisation of fishing gear by 80 barkhive canoe and 58 dugout canoe owners was determined by means of a questionnaire (see Appendix I). Since all canoe owners interviewed were full-time fishers and fished for the whole year, the total effort of the gill-net, seine-net and canoe-based hook-and-line fishery could be estimated by means of a canoe count. The total number of canoes on the lake was determined by canoe counts. During July 1996, canoes were counted from a Cessna 180 aircraft on two occasions, one week apart. The flight path followed the shoreline at an altitude of approximately 200m and two observers counted the canoes independently. Further counts were conducted from a boat moving parallel to the shoreline around the whole lake at a slow speed and all canoes present on the lake were counted. During this boat-based canoe count it was found that fishers using barkhive canoes often sunk their canoes when not in use. This purposeful sinking of the canoes was performed for two reasons. Firstly, to prevent the canoes from drifting away during windy weather and secondly, to prevent the bark from drying out and cracking. Since these sunken canoes could not be counted during aerial surveys, the aerial canoe counts underestimated the total number of canoes. For this reason the results obtained by counting canoes from the boat were considered more accurate.

Weekly effort in days fished was determined during creel surveys. The mean weekly effort (wE) in days per canoe was then calculated using a modified version of the equation described by Pollock et al. (1994):

$$\overline{wE} = \frac{\sum_{i=1}^n wE_i}{n}, \quad (\text{Equation 5.3})$$

Weekly effort per fishery was scaled up for each of the quarters and multiplied by the mean CPUE for each quarter. The total annual yield was obtained from the summation of the yield from the four quarters.

The annual effort by the shore-based hook-and-line fishery was estimated through instantaneous activity counts. The lakeshore was divided into 10 sample areas of equal size (the area of each sampling area varied with lake level), and activity counts were performed at random times on 21 occasions per sample area from January 1996 to March 1997. Activity counts were conducted from a boat moving at high speed through the sampling area and fishers on the shore were counted. Since the activity count in each sampling area took no longer than 30 minutes it is assumed that no fishers immigrated or emigrated during the activity count.

Daily shore-based hook and line fishing effort in each sampling area was determined by scaling up the instantaneous counts to the total effort on the i th fishing day,

$$\hat{e}_i = I_i \times T, \quad (\text{Equation 5.4})$$

where e_i is the fishing effort for the i th day, I_i is the instantaneous count of the number of anglers in the i th-sampling unit and T is the total length (in hours) of the fishing day (Pollock et al. 1994). There was no significant difference in monthly effort (one-way ANOVA; $p > 0.05$) and, therefore, the total annual effort (aE) for the fishery could be calculated by the equation:

$$\hat{aE} = \sum_{i=1}^n \left(\hat{e}_i / p_i \right), \quad (\text{Equation 5.5})$$

where p_i is the total probability that fishing period i is included in the sample (Pollock et al. 1994). The CPUE for the shore fishing sector was determined by creel surveys conducted on random fishers in each sampling area. These creel surveys were identical to those conducted at the access points. Annual effort was then multiplied by the mean CPUE to obtain total annual yield for the shore-based hook-and-line fishery.

5.3 RESULTS

Species composition of the catch

Table 5.1 shows the contribution of 12 species in Lake Chicamba to the gill-net, seine-net cast-net, longline and shore- and canoe-based hook-and-line fisheries as a percentage of the entire sampled catch from August 1995 to March 1997. Three species, *O. mossambicus*, *T.*

rendalli and *M. salmoides* dominate the fishery. *O. mossambicus* was the mainstay of the gill net catch (72.6%), and made up over 30% of the catch in the seine-net, cast-net and shore-based hook-and-line fisheries. *T. rendalli* was the largest component in the seine-net (48.3%), cast-net (61.4%) and shore-based hook-and-line fisheries (46.6%). *M. salmoides* made up 51.1% of the canoe-based hook and line catch and 74.2% of the longline catch. The contribution of all other species to the total catch was less than 10% in all fishery sectors. The exception was *C. gariepinus*, which contributed 21.9% to the longline catch. Cast nets and longlines were used by less than 5% of the fishers on the lake and were excluded from further analysis.

Table 5.1. The percent catch composition in the gill-net, seine-net, cast-net, longline and the shore- and canoe-based hook-and-line (H&L) fisheries. Species composition was determined by the proportional weight of each species in the total catch sampled from August 1995 to March 1997. The contribution of three *Barbus* species *B. paludinosus*, *B. radiatus* and *B. trimaculatus*, to the total catch was combined (n = number of fishers sampled).

Species	Gill net (n=622)	Seine net (n= 173)	Cast net (n=26)	Shore H&L (n=336)	Canoe H&L (n=278)	Long line (n=72)
<i>Anguilla</i> sp.	0	0%	0	0	0	3.5
<i>Labeo cylindricus</i>	0.2	3.7	1.8	0.1	0.1	0
<i>Barbus</i> sp.	0	0.9	0.2	0.4	0.4	0
<i>Cyprinus carpio</i>	0.4	1.4	0	1.1	0	0
<i>Oreochromis mossambicus</i>	72.6	31.4	30.7	32.1	14.9	0.4
<i>Oreochromis niloticus</i>	6.4	0.7	0.9	8.1	2.3	0
<i>Tilapia rendalli</i>	6.5	48.3	61.4	46.6	28.1	0
<i>Pseudocrenilabrus philander</i>	0	0	0	0.4	0	0
<i>Micropterus salmoides</i>	4.7	9.4	2.3	10.0	51.1	74.2
<i>Clarias gariepinus</i>	9.2	4.2	2.7	1.2	3.1	21.9

Gear selectivity

The length- and age-frequencies of *M. salmoides*, *O. mossambicus* and *T. rendalli* in the gill-net, seine-net and hook-and-line fisheries are illustrated in Figure 5.3 and Figure 5.4, respectively. The age-at-50%-selectivity (a_{50}) of each species into each of these fisheries is summarised in Table 5.2. All three species were selected into the seine-net and hook-and-line fisheries as juveniles, while 50%-selectivity into the gill-net fishery occurred at lengths and ages close to maturity (Figure 5.3, Figure 5.4 & Table 5.2).

Table 5.2. Age-at-50%-selectivity (a_{50}) and the width of the logistic selectivity ogive (δ) of *M. salmoides*, *O. mossambicus* and *T. rendalli* into the gill-net, seine-net and hook-and-line fisheries.

Species	Gill net		Seine net		Hook & line	
	a_{50}	δ	a_{50}	δ	a_{50}	δ
<i>M. salmoides</i>	0.74	0.18	0.29	0.04	0.20	0.03
<i>O. mossambicus</i>	2.96	0.92	0.50	0.01	0.5	0.01
<i>T. rendalli</i>	3.26	2.02	0.50	0.01	0.5	0.01

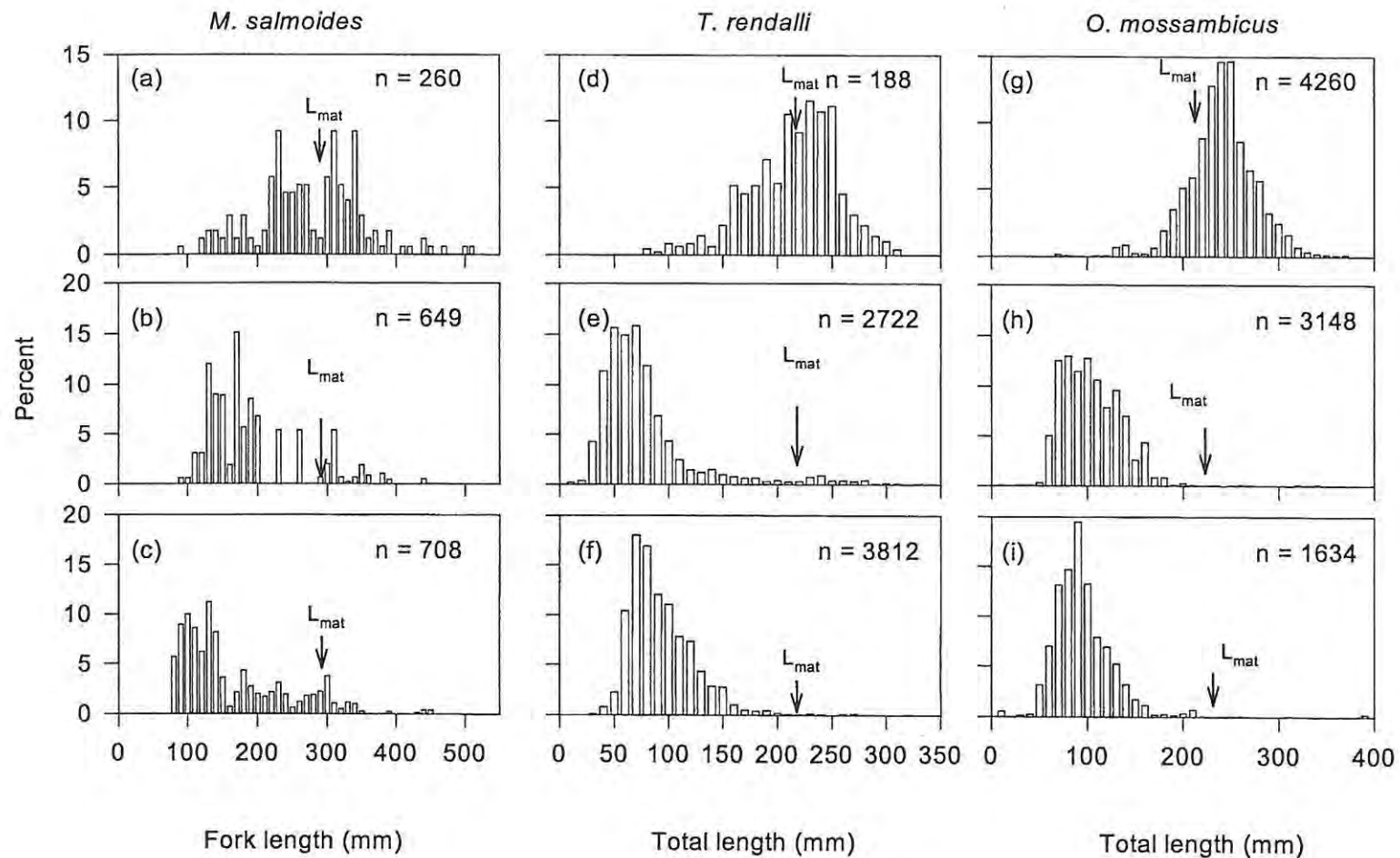


Figure 5.3. Length frequency distribution of *Micropterus salmoides* in the (a) gill-net, (b) seine-net and (c) hook-and-line fishery; *Tilapia rendalli* in (d) gill-net, (e) seine-net and (f) hook-and-line fishery and *Oreochromis mossambicus* in the (g) gill-net, (h) seine-net and (i) hook-and-line fishery; in Lake Chicamba, Mozambique. (L_{mat} denotes the length-at-50%- maturity).

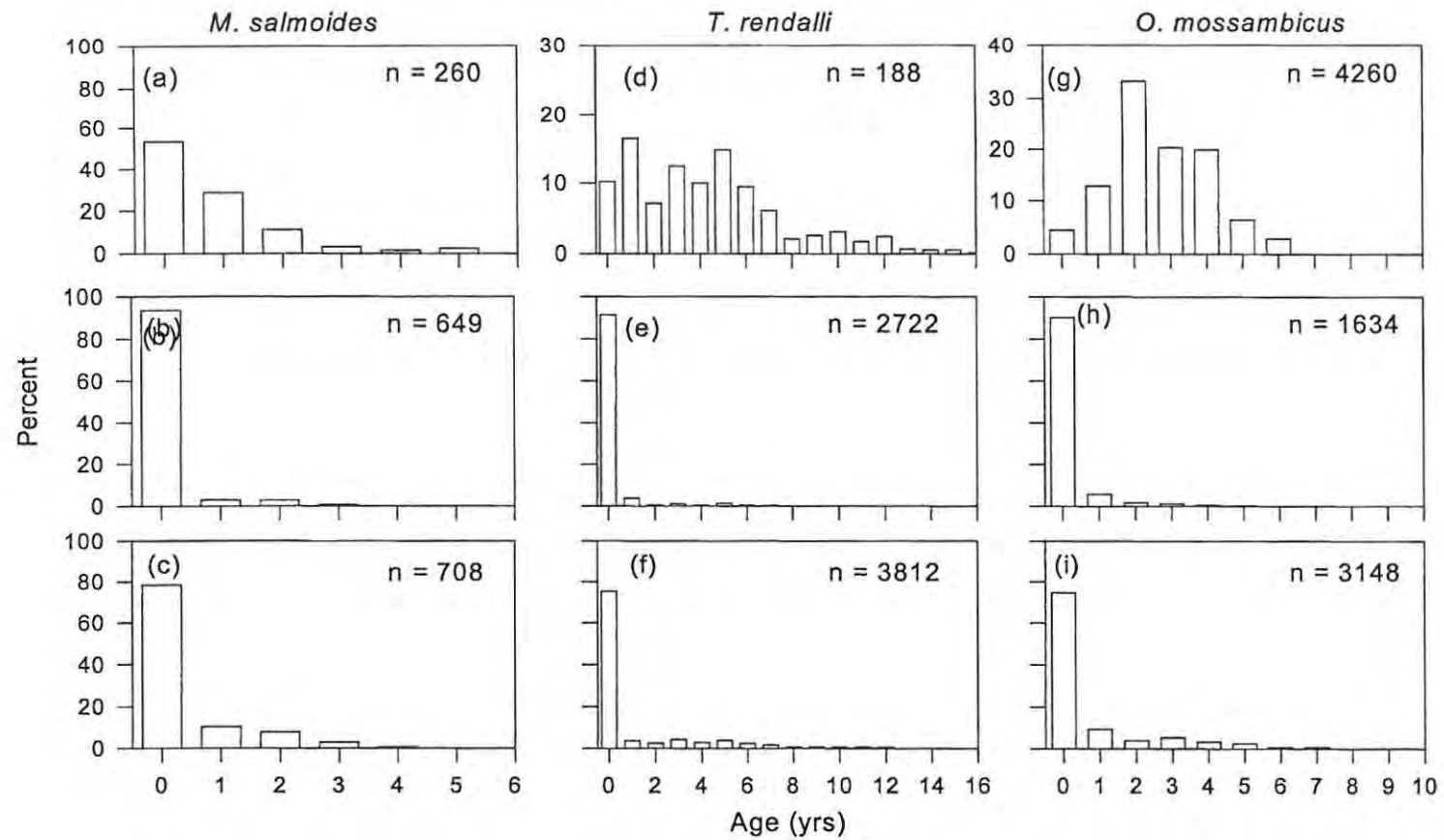


Figure 5.4. Age-frequency distribution of *Micropterus salmoides* in the (a) gill-net, (b) seine-net and (c) hook-and-line fishery; *Tilapia rendalli* in the (d) gill-net, (e) seine-net and (f) hook-and-line fishery and *Oreochromis mossambicus* in the (g) gill-net, (h) seine-net and (i) hook-and-line fishery; in Lake Chicamba, Mozambique.

Catch rate

In the gill-net, seine-net and shore- and canoe-based hook-and-line fisheries, the individual catch per unit effort (CPUE) for *M. salmoides*, *O. mossambicus* and *T. rendalli* varied considerably between quarters. The CPUE for each quarter period in the shore-based hook-and-line fishery, canoe-based hook-and-line fishery, gill-net fishery and seine-net fishery are shown in Figures 5.5, 5.6, 5.7 and 5.8, respectively.

With the exception of the shore-based hook-and-line fishery, where there were no inter-quarter variations in total CPUE (Figure 5.5), the total CPUE for canoe-based hook and line fishing, gill netting and seine netting showed a significant dependence on quarter period (Figures 5.6, 5.7, 5.8). The highest total CPUE was attained during the 2nd and 3rd quarters of 1996 in the canoe-based hook-and-line fishery (Figure 5.6), the 3rd and 4th quarters of 1995 in the gill-net fishery (Figure 5.7) and during the 3rd quarter of 1995 in the seine-net fishery (Figure 5.8).

The CPUE of the individual species was significantly dependent ($p < 0.05$) on the quarter periods in all four fisheries tested. The CPUE of *M. salmoides* for shore-based hook and line fishing and seine netting was highest during the 1st quarter of 1996 (Figure 5.5 & 5.8), while canoe-based hook and line fishing and gill net CPUE was highest during the 2nd quarter of 1996 (Figure 5.6 & 5.7). *O. mossambicus* CPUE was highest during the 1st and 2nd 1996 quarters in the shore-based hook-and-line fishery (Figure 5.5), the 3rd 1995 quarter in the canoe-based hook-and-line fishery (Figure 5.6), the 3rd and 4th 1995 quarters in the gill-net fishery (Figure 5.7) and during the 3rd and 4th 1995 quarters and the 1st 1996 quarter in the seine-net fishery (Figures 5.8). *T. rendalli* CPUE was highest during the 2nd and 3rd

quarter of 1996 in the shore-based hook-and-line fishery (Figure 5.5), the 3rd 1996 quarter in the canoe-based hook-and-line fishery (Figure 5.6) and during the 3rd and 4th 1995 quarters in the gill-net and seine-net fisheries (Figure 5.7 & 5.8).

Total effort was constant throughout the year for the canoe fishery. Gill net fishers set a mean length of 137 m of net on 5.1 ± 2.3 nights a week. Seine net fishers fished on 3.4 ± 1.9 days a week, with an average of 5.4 net hauls per day. Line fishers fished on 2.9 ± 1.9 days per week with a mean daily effort of 2.6 hours. There was no significant difference between areas nor in the number of line fishers operating from the shore from month to month and an average of 1.9 ± 2.7 fishers were recorded per area. Total yield could, therefore, be calculated directly from the seasonal CPUE data and estimated effort data. The number of operators determined from canoe counts and total annual effort for each sector and species is shown in Table 5.3. The yield for each of the three species as well as the estimated total yield in the gill-net, seine-net, shore-based hook-and-line and canoe-based hook-and-line fishery in each quarter is shown in Table 5.4. A summary of the 1996 catch of each species by each gear is shown in Table 5.5.

Table 5.3. Number of fishers determined from canoe counts and total annual effort in the gill-net fishery, seine-net fishery, canoe-based hook-and-line (H&L) fishery and shore-based hook-and-line fishery on Lake Chicamba.

	Gill net	Seine net	H&L (canoe)	H&L(shore)
Number of fishers	258	80	130	Undefined
Annual effort	80731 net nights. yr ⁻¹ .	76377 hauls. yr ⁻¹	35794 hours. yr ⁻¹ .	84680 hours. yr ⁻¹ .

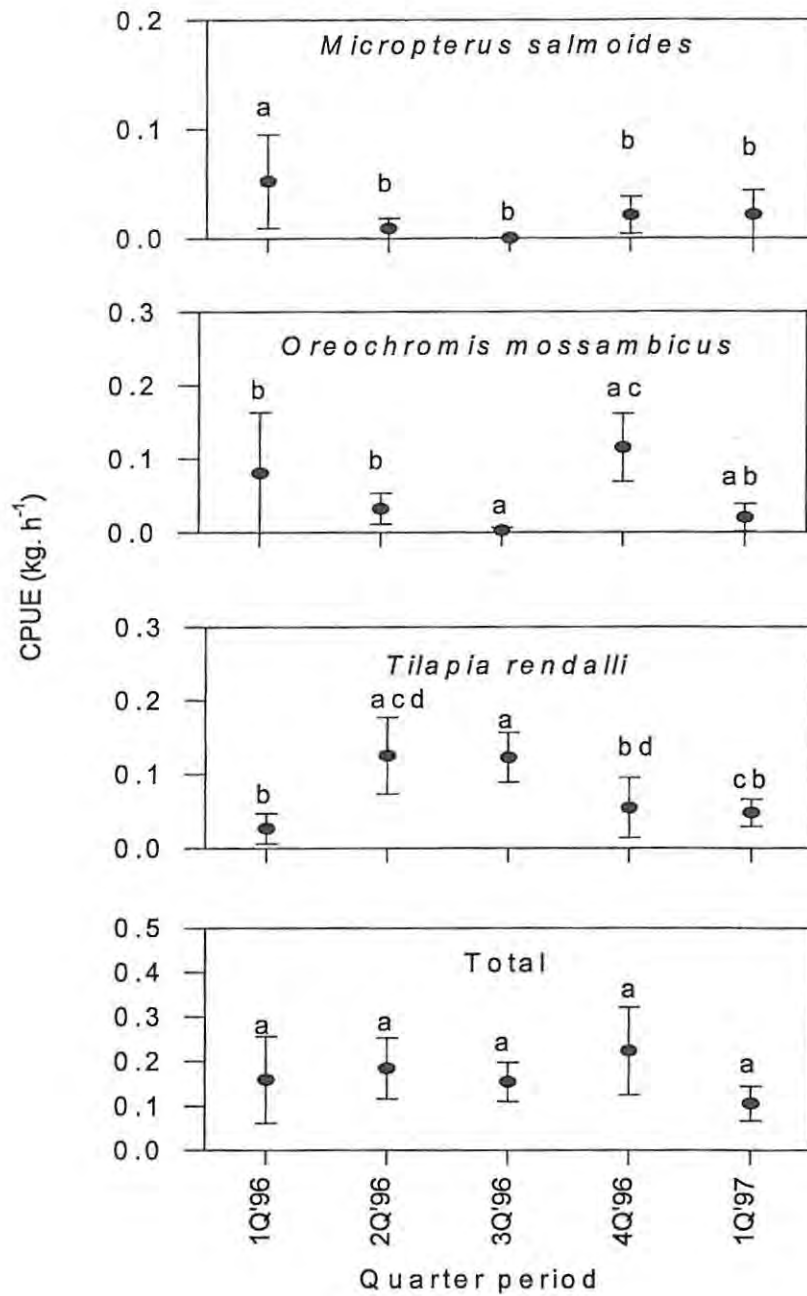


Figure 5.5. The catch per unit effort (CPUE) for *M. salmoides*, *O. mossambicus*, *T. rendalli* and the total CPUE \pm 95% confidence intervals for the shore-based hook-and-line fishery in Lake Chicamba for five quarter (Q) periods from January 1996 to March 1997. Different letters denote significant differences at the $p < 0.05$ level (Kruskal-Wallis one-way ANOVA on ranks; Dunn's test for all-pairwise multiple comparison).

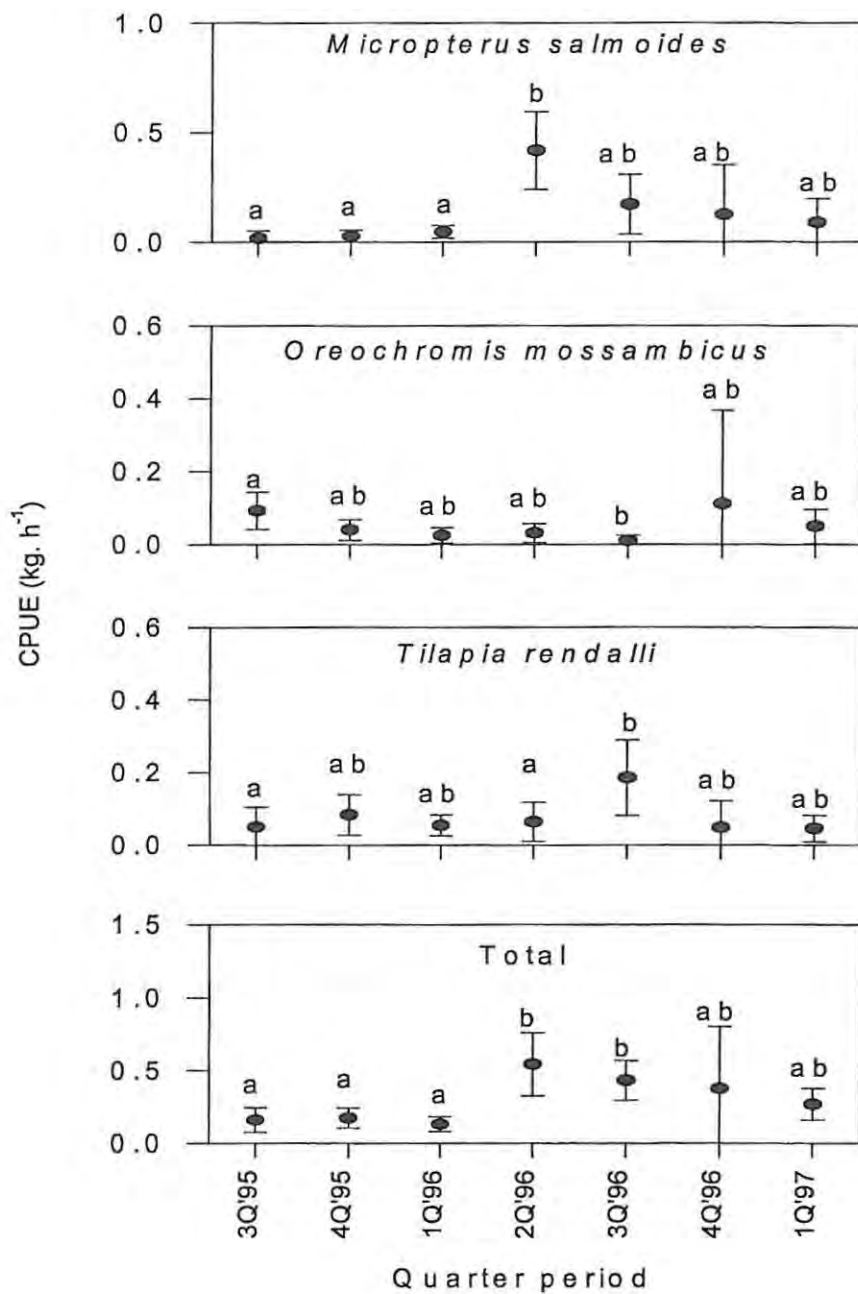


Figure 5.6. The catch per unit effort (CPUE) for *M. salmoides*, *O. mossambicus*, *T. rendalli* and the total CPUE \pm 95 % confidence intervals for the canoe-based hook-and-line fishery in Lake Chicamba for seven quarter (Q) periods from July 1995 to March 1997. Different letters denote significant differences at the $p < 0.05$ level (Kruskal-Wallis one-way ANOVA on ranks; Dunn's test for all-pairwise multiple comparison).

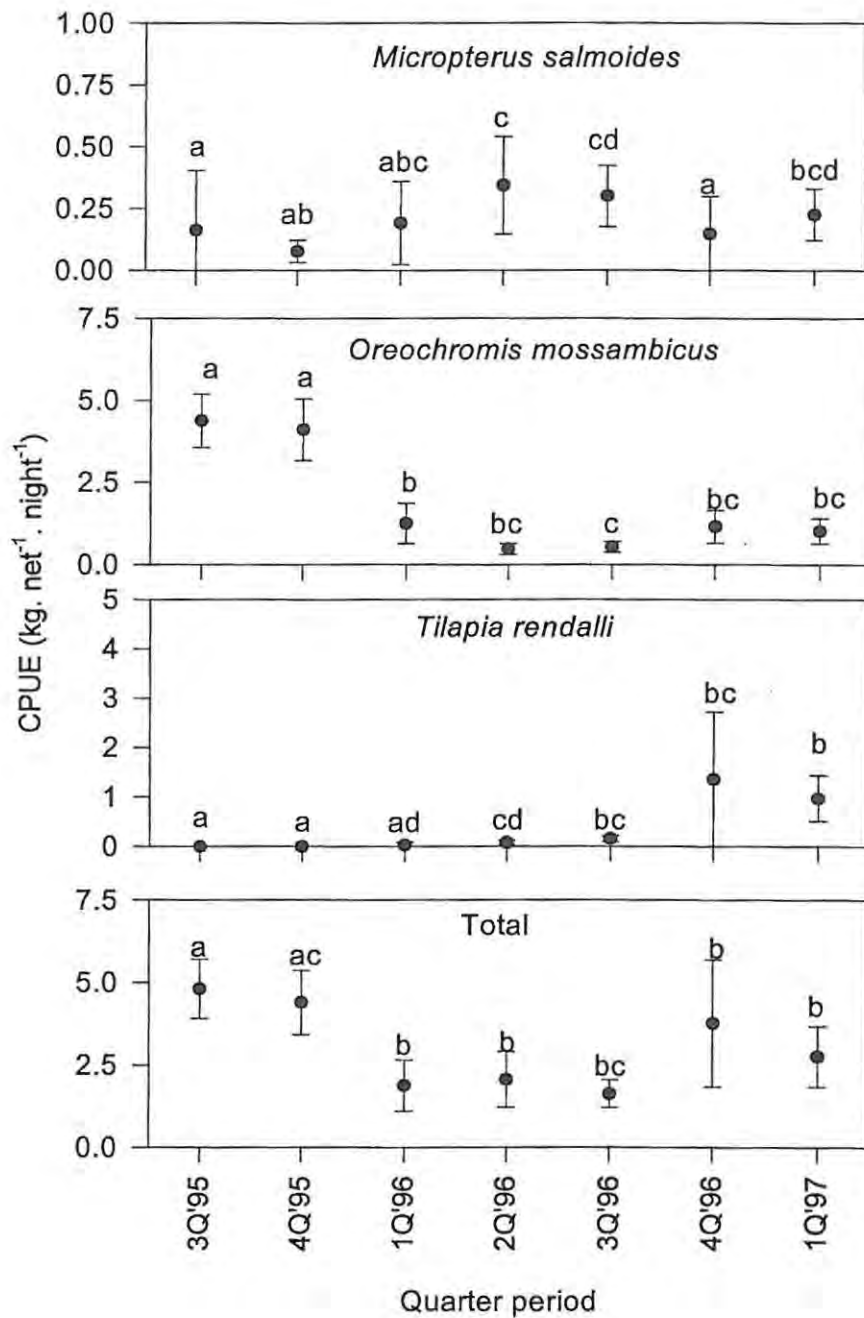


Figure 5.7. The catch per unit effort (CPUE) for *M. salmoides*, *O. mossambicus*, *T. rendalli* and the total CPUE \pm 95% confidence intervals for the gill-net fishery in Lake Chicamba for seven quarter (Q) periods from July 1995 to March 1997. Different letters denote significant differences (Kruskal-Wallis one-way ANOVA on ranks; Dunn's test for all-pairwise multiple comparison).

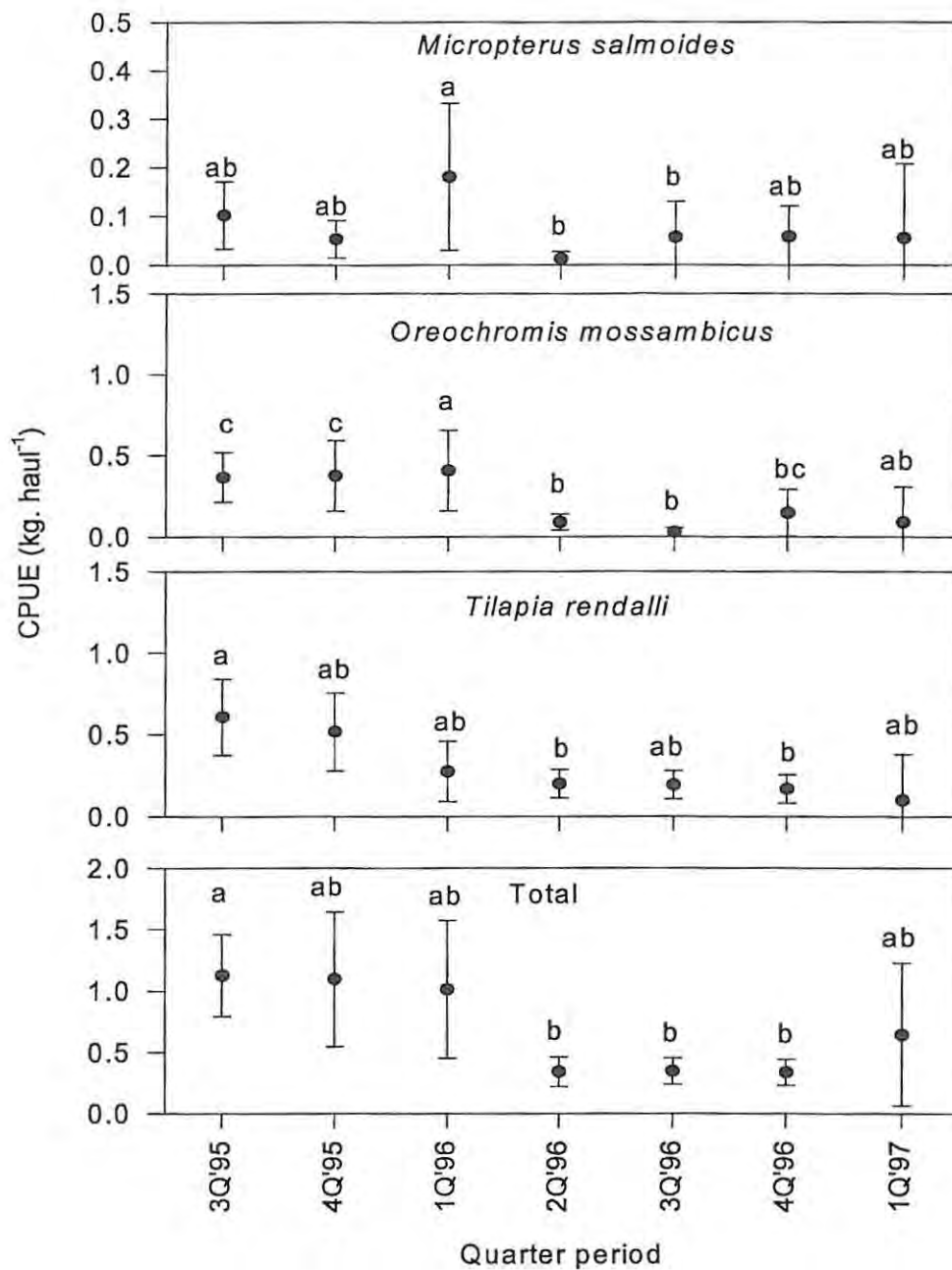


Figure 5.8. The catch per unit effort (CPUE) of *M. salmoides*, *O. mossambicus*, *T. rendalli* and the total CPUE \pm 95 % confidence intervals for the seine-net fishery in Lake Chicamba for seven quarter (Q) periods from July 1995 to March 1997. Different letters denote significant differences at the $p < 0.05$ level (Kruskal-Wallis one-way ANOVA on ranks; Dunn's test for all-pairwise multiple comparison).

Table 5.4. Total catch (kg) of *M. salmoides*, *O. mossambicus*, *T. rendalli* and the total catch in Lake Chicamba for seven quarter (Q) periods from July 1995 to March 1997 for the gill-net, seine-net, shore-based hook-and-line (H&L) and canoe-based hook-and-line fisheries (nd = no data).

	<i>M. salmoides</i>					<i>O. mossambicus</i>				
	Gill	Seine	H&L (shore)	H&L (canoe)	Total	Gill	Seine	H&L (shore)	H&L (canoe)	Total
3Q '95	2153	1222	nd	100	3475	58934	4374	nd	549	63857
4Q '95	1615	953	nd	235	2803	82951	6741	nd	353	90045
1Q '96	3835	3253	1046	419	8553	25228	7298	1612	216	34354
2Q '96	6862	234	179	3732	11007	9486	1618	641	274	12019
3Q '96	6055	1007	0	1536	8598	10697	521	46	90	11354
4Q '96	3027	1043	420	1124	5614	23210	2642	2293	994	29139
1Q '97	4642	989	428	796	6855	20586	1618	399	436	23039

	<i>T. rendalli</i>					Total catch				
	Gill	Seine	H&L (shore)	H&L (canoe)	Total	Gill	Seine	H&L (shore)	H&L (canoe)	Total
3Q '95	0	7250	nd	291	7541	96906	20178	nd	1432	118516
4Q '95	0	9275	nd	741	10016	88639	19684	nd	1557	109880
1Q '96	605	4925	526	480	6536	37732	18171	3184	1179	60266
2Q '96	1615	3577	2503	570	8265	56302	6115	3685	4869	70701
3Q '96	3229	3451	2449	1655	10784	32737	6225	3082	3874	45918
4Q '96	2725	3020	1084	428	7257	75873	6036	4472	3371	89752
1Q '97	19779	1797	951	402	22929	55694	11563	2115	2400	71773

Table 5.5. Species specific catch (kg) by gill nets, seine nets, shore based hook and line fishing (HL) and canoe based hook and line fishing during the 1996 calendar year in Lake Chicamba.

	Gill	Seine	H&L (shore)	H&L (canoe)	Total
<i>M. salmoides</i>	19779	5537	1645	6811	33772
<i>O. mossambicus</i>	68621	12079	4592	1574	86866
<i>T. rendalli</i>	8174	14973	6562	3133	32842

The total catch per quarter per hectare as a function of total lake surface area is shown in Figure 5.9. The data were adequately described by the linear regression model:

$$\text{Total catch (kg. ha}^{-1}\text{.quarter}^{-1}\text{.)} = 82.4 - 0.0185 \times \text{surface area (ha)}; (r^2 = 0.96; p < 0.001)$$

Although the total number of data points was low ($n = 6$), the power of the regression was adequate (power with $\alpha = 0.05$: 0.986).

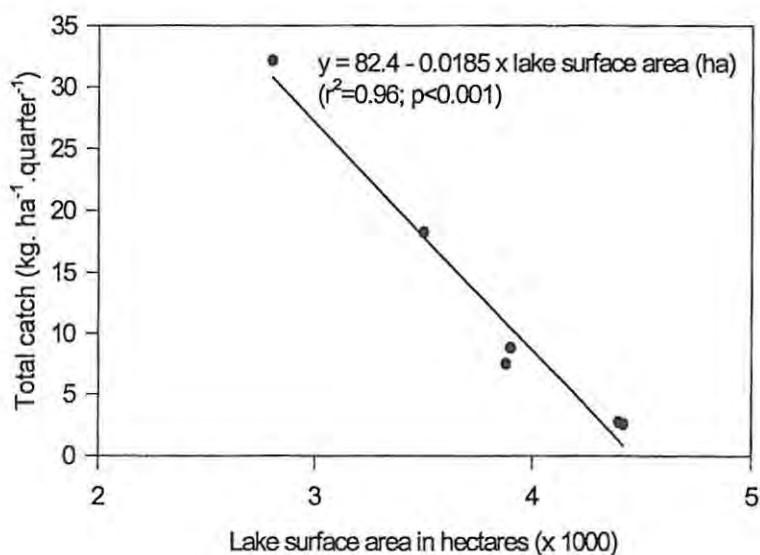


Figure 5.9. Total quarterly catch (kg. ha⁻¹) as a function of lake surface area. The quarterly catches were estimated from data collected between 1995 and 1996.

5.4 DISCUSSION

The Lake Chicamba fishery is similar to those in many other African reservoirs. The definition of a target species is vague as all fish caught are utilised by the fishers. Target species are therefore defined not by the preference of the fishers, but rather by the selectivity of the gear. *M. salmoides*, *O. mossambicus* and *T. rendalli* form the backbone of the fishery. Although gill nets, seine nets and hook and line fishing were species selective to a certain degree, none of the gears excluded any of the three species (Table 5.1). Additionally, the age-at-selectivity into the various fisheries also varied considerably (Figure 5.4, Table 5.2). Juveniles dominated the seine-net and hook-and-line fishery catches, while the gill-net fishery caught mainly adults of the three species (Figure 5.3 & 5.4, Table 5.2). These selectivity patterns can in part be explained by habitat utilisation of the three species. *O. mossambicus* dominate the gill-net fishery, as they tend to inhabit open water as adults (Pet & Piet 1993). *T. rendalli* prefers shallower water making it more vulnerable to the seine-net and shore-based hook-and-line fisheries. Adult *M. salmoides* prefer dense stands of drowned trees due to its “hide and wait” feeding strategy (Savino & Stein 1982), thereby avoiding seine and gill nets to some degree. The prevalence of juveniles of all three species in the seine net and hook and line catches can be attributed to their preference for the littoral zone as a nursery area (Caulton 1977a, Bowen & Allanson 1982, Meals & Miranda 1991, Pet & Piet 1993). The multi-gear nature of the fishery leads to a situation in which all age classes of the stocks are caught. Therefore, the fishery as a whole may tend towards both growth overfishing (where recruits are caught before they can significantly contribute to the biomass) and recruitment overfishing (where spawner stock levels are depleted to levels below which the stock cannot replenish itself) (Sparre & Venema 1992).

The seine-net fishery is relatively small, with 80 operators, and only contributed 37.8 t to the total catch of 223 tons in 1996. However, this fishery primarily targets the juveniles of the three dominant species, which may lead towards recruitment as well as growth overfishing. In addition, given that all three species are nest builders in the shallow areas of the lake, seine netting must inevitably disrupt spawning activity by destroying nests, capturing guarding parents and disrupting mating behaviour. The magnitude of this disruption can be estimated given the following assumptions: (1) approximately 60% of Lake Chicamba's shoreline is accessible to seine nets and this area is fished randomly; (2) spawning sites are randomly distributed in the lake's littoral zone in areas less than 2 m deep; and (3) spawning is only successful if nesting sites remain undisturbed for at least 22 days for *T. rendalli* (Fryer & Iles 1972), 10 days for *M. salmoides* (De Moor & Bruton 1988) and 3 days for *O. mossambicus* (Caulton 1975). Since the modal length of seine nets was 50 m, and assuming the net was set in a half circle, the surface area covered by each haul was 796 m² and, therefore, the entire seine net fishery (222 hauls per day) disrupts between 5.4 and 8.3 % of the surface area available for seine netting, per day. The chance that seine netting disrupts each spawning fish is therefore between 3% and 5% per day. When one considers the time period that these fish require for successful spawning (3 to 22 days), the probability of brood failure as a consequence of disruption by seine nets is approximately 66% for *T. rendalli*, 30% for *M. salmoides* and 9% for *O. mossambicus*.

While juveniles of the three species also dominate the hook and line catch, the impact of this fishery on spawning areas and spawning activity of the target species is limited. In addition, hook and line fishing is vital for food security in a large number of subsistence

households and access control is not feasible since the Department of Fisheries lacks the resources necessary for the effective enforcement of regulations. Subsequently, limitations in the hook and line fishing sector are not feasible.

Of these two fisheries, the seine-net fishery is seen as the more destructive fishery. The low age-at-50% selectivity, destruction of spawning areas and disruption of spawning activity associated with the seine-net fishery determines that its removal from the fishery is of vital importance for the sustainability of the stocks. The gill-net fishery, is seen as sustainable since this passive gear does not target nesting fish and the selection pattern for this fishery tends towards mature fish (Figure 5.3 & 5.4).

When the quarterly yield from the entire fishery is considered, it becomes evident that the highest recorded catches were during 1995, with a total of 228 tons caught during the 3rd and 4th quarters alone. The quarterly catch declined sharply during 1996. This is considered to be a consequence of rising lake level and the resultant dilution effect consequently reducing CPUE, rather than due to seasonal variations in catch rate (Figure 5.9). Although rising water level had a significant effect on the total catch in the fishery, these effects are likely to be short term as good recruitment and growth rates during periods of rising water level are likely to increase future catch rates (see Chapter 4).

Since the sampling period only covered one full calendar year (1996), and fluctuating water levels affected the catch, with lower catches after flooding (Figure 5.9), an estimate for the total annual yield was determined by the summation of the yield of 4 consecutive quarter periods (Table 5.6). The total annual yield for Lake Chicamba therefore ranged from 58

kg. ha⁻¹ to 98 kg. ha⁻¹. The highest estimates were obtained when the 1995 data were included in the estimate. Relationships between the morphoedaphic index and fish yield were first developed for tropical African lakes by Henderson & Welcomme (1974) and an improved relationship for southern African impoundments was described by Marshall (1984). Estimates using 1996 and 1997 data only, were similar to yields of 68 kg. ha⁻¹ derived from the Marshall (1984) morphoedaphic model (Table 5.6). Since morphoedaphic relationships are based upon the hypothesis that the fishing intensity is sufficient to produce maximum yield, which in turn is based on the carrying capacity of the ecosystem, the similarity between direct estimates of annual yield and the estimates derived from morphoedaphic models implies that the fishery is fully exploited.

Although the morphoedaphic model (Marshall 1984) predicted an annual yield for Lake Chicamba that closely matched estimates of annual catch made during this study, the application of this model in the development of a management strategy for the fishery is limited as it does not consider important biological characteristics of the fish stock. A direct comparison between the length/age-at-50% selectivity of the three species into the various fisheries and the length/age-at-maturity of these species gives an indication of the sustainability of each gear in the fishery as a whole. However, models that allow for the evaluation of the species-specific response of yield and spawner-biomass to changes in exploitation rate are essential for the development of management strategies.

Table 5.6. Total annualised yield estimates, obtained by the summation of four different periods of quarterly catch during the July 1995 – March 1997 sampling period, and yield estimates using empirical relationships between the morphoedaphic index and yield described for southern African reservoirs by Marshall (1984) and for tropical African lakes by Henderson & Welcomme (1974). Due to variable lake level, the yield estimates based on morphoedaphic models were calculated for each quarter period separately and averaged.

Period	Total annual yield	Marshall (1984) Model	Henderson & Welcomme(1974) Model
Jul'95- Jun'96	98 kg. ha ⁻¹	69 kg. ha ⁻¹	45 kg. ha ⁻¹
Oct'95–Sep'96	75 kg. ha ⁻¹	69 kg. ha ⁻¹	44 kg. ha ⁻¹
Jan'96-Dec'96	62 kg. ha ⁻¹	68 kg. ha ⁻¹	44 kg. ha ⁻¹
Apr'96-Mar'97	58 kg. ha ⁻¹	66 kg. ha ⁻¹	43 kg. ha ⁻¹
Average	73 kg. ha ⁻¹ y ⁻¹	68 kg. ha ⁻¹ y ⁻¹	44 kg. ha ⁻¹ y ⁻¹

The short sampling period and the paucity of historical data pertaining to the Lake Chicamba fishery negates the use of more data-intensive models (e.g. Butterworth & Andrew 1984, Deriso et al. 1985, Pope & Shepherd 1985, Butterworth et al. 1990, Sparre 1991, Booth 1997) in determining the status of the fishery. However, the estimation of catch and effort presented here are a crucial first step in the development of a long-term database for the Lake Chicamba fishery and the estimation of parameters upon which to base more data-intensive stock assessment methods (Pope & Shepherd 1985, Butterworth et al. 1990, Deriso et al 1985, Booth 1997) (Chapter 6).

CHAPTER 6

Assessment and management of *M. salmoides*, *O. mossambicus* and *T. rendalli* using traditional per-recruit analysis and new multi-species\multi-fishery-per-recruit analysis.

6.1 INTRODUCTION

The paucity or complete lack of directed catch and effort data often constrains the assessment of lacustrine fisheries in developing countries. In addition, there are often insufficient length- or age-based catch data and other biological data pertinent to the application of age-based models. When available, data are often imprecise and temporally disjunct and subsequently of little quantitative value. Therefore, stock assessment methods such as the surplus production model (Schaefer 1954, 1957, Butterworth & Andrew 1984), *ad hoc* tuned Virtual Population Analysis (Pope & Shepherd 1985, Butterworth et al. 1990, Punt 1993a), integrated analysis (Deriso et al. 1985) and age-structured production models (Booth 1997) cannot be applied. For these reasons, fisheries managers in developing countries have focused on the application of the yield-per-recruit model, which is an abbreviation of the full dynamic-pool model (Beverton & Holt 1956, 1957), in the management of both marine and lacustrine fisheries (Cochrane 1985, Amarasinghe & De Silva 1992, Blay & Asabere-Ameyaw 1993, Manyala et al. 1995, Thompson & Allison 1997). These 'traditional' yield-per-recruit models allow for the evaluation of the response of the yield-per-recruit of a single species to changes in fishing mortality and age-at-50%-selectivity in a single fishery. However, management advice based on the assessment of a fishery in isolation is inadequate when there are a number of fisheries harvesting the stock

at differing ages-at-50%-selectivity (Djama & Pitcher 1997). In addition, it has long been recognised that when a common gear harvests a number of species, it is impossible to manage each species at its optimum level (Beverton & Holt 1957, Anderson 1975, Pope 1979, Mitchell 1982, Pikitch 1987). For these very valid reasons, studies in the past have focused on the development of yield-per-recruit models which account for the interaction of different species captured by similar gear (Murawski 1984, Pikitch 1987), or for different gears harvesting the same species at different selectivities (Murawski 1984, Djama & Pitcher 1997).

In an attempt to define optimum fishing mortality from a per-recruit perspective the use of target reference points (TRPs) has become common practice in fisheries management (Clarke 1991, Punt 1993b, Punt & Butterworth 1993, Caddy & Mahon 1995, Booth 1997, Griffiths 1997). The yield-per-recruit approach allows for the determination of at least two commonly used TRPs: firstly, the fishing mortality which corresponds to the maximum of the yield-per-recruit curve (F_{max}) and secondly, the marginal yield or $F_{0.1}$ strategy (Gulland & Boerema 1973, Deriso 1987), which is the rate of fishing mortality at which the slope of the yield-per-recruit curve falls to 10% of its value at the origin.

This yield-per-recruit approach assumes that recruitment is constant and independent of spawner biomass. In most marine fish, the stock-recruitment relationship is density dependent, but data are typically so few or so variable that the form of the relationship has not been determined objectively (Shepherd 1982, Sissenwine & Shepherd 1987). Models that have been used to describe the stock-recruitment relationship suggest either that recruitment approaches an asymptote at high stock densities (Beverton & Holt 1957) or that

recruitment reaches a maximum before decreasing at higher levels of stock abundance (Ricker 1954, 1975). Although no spawner biomass-recruit relationships have been determined for fish species in African reservoirs, many of the target species in these fisheries exhibit reproductive behaviours, which imply that a strong density dependent spawner biomass-recruitment relationship exists (e.g. nest guarding and mouthbrooding in cichlids). The use of TRPs that ignore the density dependence between spawner biomass and recruitment should therefore be avoided. The F_{max} strategy maximises yield-per-recruit without regard to whether sufficient spawner biomass is conserved to ensure sufficient recruitment in the future (Deriso 1987, Sissenwine & Shepherd 1987, Clarke 1991). While the $F_{0.1}$ strategy is more conservative than the F_{max} strategy it also does not take into account the effects of fishing on the spawning stock and subsequent recruitment (Clarke 1991, Punt 1993b).

Due to the dependence of recruitment on spawner stock, scientists concerned with the management of marine species have tended to base their TRP recommendations on the results of spawner biomass-per-recruit models (Butterworth et al. 1989, Smale & Punt 1991, Booth 1997, Griffiths 1997). The definition of a spawner-biomass TRP ($F_{SB(x)}$) involves setting the fishing mortality to a level at which spawner biomass-per-recruit is reduced to x% of its pristine level. Although there is no conventional $F_{SB(x)}$ TRP, spawner biomass-per-recruit recommendations lie between 25% and 50% of unexploited levels (Deriso 1987, Sissenwine & Shepherd 1987, Butterworth et al. 1989, Smale & Punt 1991, Gabriel et al. 1989, Quinn et al. 1990, Clark 1991, Punt 1993b, Mace 1994, Booth & Buxton 1997). In the absence of information on the surplus production function or the spawner biomass-recruitment relationship, the $F_{SB(x)}$ TRPs are currently considered the most

robust, allowing for the determination of a fishing mortality rate that will provide relatively high yields at lower risks (Clarke 1991, Punt 1993b).

A spawner biomass-per-recruit approach has never been extended to include multi-species or multi-gear effects. The Lake Chicamba fishery, like many other African reservoir fisheries, is a multi-species fishery with a number of sectors actively targeting the fish stocks with different gear types, each varying considerably in species- and size-selectivity (Chapter 5). Since there is no existing spawner biomass-per-recruit model that allows for the definition of $F_{SB(x)}$ TRPs in multi-species and multi-gear fisheries, the development of such a model was considered to be vital for the future sustainable management of these fisheries. For this reason an attempt was made to develop a multi-species/multi-fishery spawner biomass-per-recruit model to complement the multi-species/multi-fishery yield-per-recruit model of Murawski (1984). This would allow for the assessment of the response of yield- and spawner biomass-per-recruit in the three target species in Lake Chicamba, to changes in effort in the gill-net, seine-net and hook-and-line fisheries simultaneously. The results obtained from the multi-species/multi-fishery per-recruit models could then be compared to findings based on the traditional yield- and spawner biomass-per-recruit approach in order to develop a management strategy for the lake.

6.2. The development of a new multi-species/multi-fishery spawner biomass-per-recruit model.

All multi-species/multi-fishery per-recruit models are based on an extension of the traditional per-recruit models. It was therefore necessary to provide a concise review of

these traditional models before showing the specific points of departure from this traditional approach.

The fundamental assumption of all per-recruit analyses is that the parameters for recruitment, growth and mortality are constant from one year to the next and, therefore, the stock is in a steady state. The selectivity of each gear is assumed to be time invariant, having the logistic form described in Equation 5.1 (Chapter 5). In the gill net fishery the selectivity pattern was assumed to be of a logistic form due to the wide range of mesh sizes used in the fishery. Under these assumptions the composition of the stock is then calculated by considering a cohort during its lifespan (Beverton & Holt 1957). Therefore, the relative proportion of fish at age a (\tilde{N}_a), is defined recursively as:

$$\tilde{N}_a = \begin{cases} 1 & \text{if } a = 0 \\ \tilde{N}_{a-1} e^{-(M+S_{a-1}F)} & \text{if } 1 \leq a < \text{max} \\ \tilde{N}_{\text{max}-1} e^{-(M+S_{\text{max}-1}F)} / (1 - e^{-(M+S_{\text{max}-1}F)}) & \text{if } a = \text{max} \end{cases} \quad (\text{Equation 6.1})$$

where S_a is selectivity at age a , F is the instantaneous rate of fishing mortality on fully recruited cohorts, M is the instantaneous rate of natural mortality and max is the maximum recorded age.

In all per-recruit models the weight-at-age is described by:

$$W_a = \alpha (l_a)^\beta \quad (\text{Equation 6.2})$$

where l_a is the length-at-age determined by the von Bertalanffy growth equation (Equation 3.1; Chapter 3) and α and β are parameters describing the length-weight relationship.

Yield-per-recruit (YPR) and spawner-biomass-per-recruit (SBR) as a function of fishing mortality (F) were determined by:

$$YPR_F = \sum_{a=0}^{\max} w_a S_a F \tilde{N}_a \left[1 - e^{-(M+S_a F)} \right] / (M + S_a F) \Delta a \quad (\text{Equation 6.3})$$

$$SBR_F = \sum_{a=0}^{\max} \psi_a w_a \tilde{N}_a \Delta a \quad (\text{Equation 6.4})$$

and biomass-per-recruit (BR) as function of age was determined as:

$$BR_a = w_a \tilde{N}_a \quad (\text{Equation 6.5})$$

where ψ_a is the proportion of mature fish at age a . All summations were conducted with a step size (Δa) of 0.10 of a year.

In a multi-gear fishery, the number of fish at age a is determined by the relative fishing mortality rate of each gear and its inherent selectivity. To illustrate this, Figure 6.1 represents the number of fish-at-age in a population harvested by two gears. The first gear selects fish of 3 years and older while the second gear selects fish of 6 years and older. Subsequently, the total mortality rate (Z) is increased with each gear due to the additive effect that each gear has on the total fishing mortality rate (F) such that for j fisheries:

$$Z = M + \sum_j F_j \quad (\text{Equation 6.6})$$

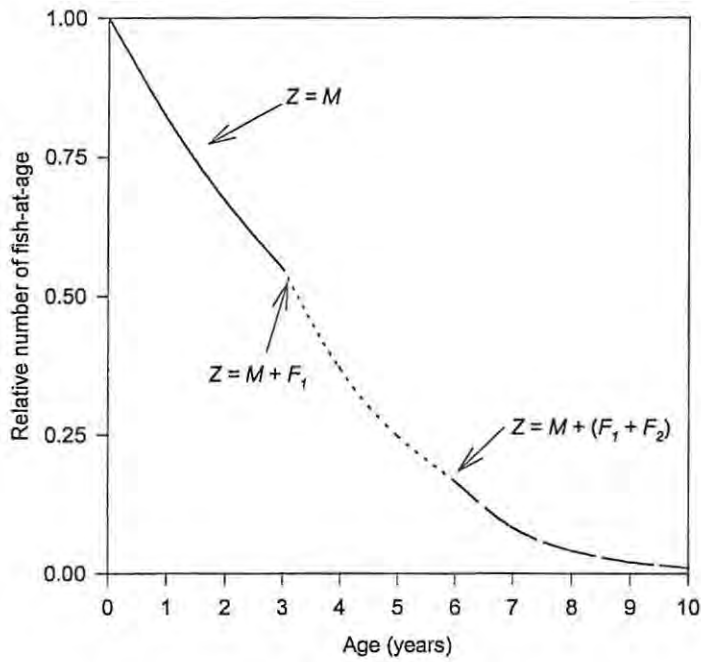


Figure 6.1. Multi-gear effects on the relative number of fish-at-age. In an unfished population the total mortality rate (Z) = the natural mortality rate (M). When one fishing gear is used: $Z = M + F_1$ (F_1 = fishing mortality) and when two fishing gears are used: $Z = M + F_1 + F_2$.

For example, when three fisheries, 1, 2 and 3, are active the relative number-at-age of species i (\tilde{N}_{ia}), is described as:

$$\tilde{N}_{ia} = \begin{cases} 1 & \text{if } a = 0 \\ \tilde{N}_{i,a-1} \exp(-(M + (S_{a1}F_{a1} + S_{a2}F_{a2} + S_{a3}F_{a3}))) & \text{otherwise} \end{cases} \quad \text{(Equation 6.7)}$$

where M is the rate of natural mortality, S_a , S_{a2} and S_{a3} are the selectivities for age class a of the three fisheries under consideration and F_{a1} , F_{a2} and F_{a3} are the proportional fishing mortality rates (yr^{-1}) for each of the three fisheries.

Since the fishery targets each species, the coefficients of proportionality between fishing effort and fishing mortality (i.e. the catchability coefficients) will vary between species due to differences in their availability and vulnerability to the various gear (Murawski 1984). Therefore, at any given level of effort, the F for each species in a multi-species fishery will be different. Catchability coefficients were estimated using the linear relationship:

$$F_{ij} = q_i \times f_j \quad (\text{Equation 6.8})$$

where q_i is the vector of catchability coefficients of species i , and f_j is the vector of standardised effort in fishery j . Although alternative forms of Equation 6.8 have been suggested for various species (Peterman & Steer 1981), in this study the relationship between f and F is assumed to be linear for all species. The fishing mortality of species i in each fishery j (F_{ij}) could be determined by the proportional contribution of the catch (kg) of species i by each gear to the total catch of that species in all gears.

The spawner-biomass-per-recruit for each species i (SBR_i) in a multi-gear fishery was then determined by:

$$SBR_i = \sum_{a=0}^{\max} \psi_{ia} w_{ia} \tilde{N}_{ia} \Delta a \quad (\text{Equation 6.9})$$

and yield-per-recruit for species i (YPR_i) in a multi-species fishery was determined by the model described by Murawski (1984):

$$YPR_i = \sum_{a=0}^{\max} \left[(w_{ia} \tilde{N}_{ia} (1 - \exp(-(M_i + \sum_j S_{iaj} F_{ij})))) \frac{\sum_j S_{iaj} F_{ij}}{M_i + \sum_j S_{iaj} F_{ij}} \right] \Delta a \quad (\text{Equation 6.10})$$

where w_{ia} is the mass of species i at age a , S_{iaj} is the selectivity for age class a of species i by fishery j , F_{ij} is the instantaneous rate of fishing mortality rate (yr^{-1}) for species i for all fisheries j under consideration, M_i is the rate of natural mortality of species i , and \max is the maximum recorded age for species i . All summations were conducted with a step size (Δa) of 0.10 of a year.

The annual yield of each species i in all fisheries (Y_i) can be estimated by the equation:

$$Y_i = YPR_i \times R_i \quad (\text{Equation 6.11})$$

where YPR_i is the yield-per-recruit of species i and R_i is the number of recruits of species i at equilibrium level.

The yield of all species in the fishery j (Y_j) was calculated by:

$$Y_j = \sum_i Y_i \quad (\text{Equation 6.12})$$

and to obtain the total yield from all fisheries, all individual fishery yields were summed as:

$$Y_{total} = \sum_j Y_j \quad \text{(Equation 6.13)}$$

6.3 Application of traditional and multi-species/multi-fishery per-recruit analysis to Lake Chicamba.

The traditional per-recruit models, the Murawski (1984) multi-gear/multi-species yield-per-recruit model and the newly developed multi-species/multi-gear spawner biomass-per-recruit model were applied to the Lake Chicamba fishery using the parameters summarised in Table 6.2.

Growth and mortality parameters were obtained from data presented in Chapter 3 and gear selectivity estimates were obtained from data presented in Chapter 5. Due to the low maximum recorded age of *M. salmoides* (5 years), a lumped plus group of 6 years was used to define the parameter for maximum age (*max*), as it was possible that fish exist in the population of an older age than that recorded in age estimates (Butterworth et al. 1989). This specification had little effect on the analysis. The maximum recorded ages for *O. mossambicus* (10 years) and *T. rendalli* (16 years) were considered to be an accurate representation of *max*.

The proportional contribution of the gill-net ($F_{\text{gill net}}$), seine-net ($F_{\text{seine net}}$) and hook-and-line ($F_{\text{hook \& line}}$) fisheries to the estimated instantaneous rate of fishing mortality (F) for *M. salmoides*, *O. mossambicus* and *T. rendalli* was estimated using Equation 6.8. Fishing effort was standardised to the effort exerted by one gill net fisher (using a net 137 m long \times 3 m deep) or seine net fisher (using the modal net length of 50 m) per year. The selectivity scenarios were identical but CPUE differed for the shore- and canoe-based hook-and-line fishers (Chapter 5). It was therefore necessary to standardise hook and line fishing effort to a proportion of the annual effort in both sectors (i.e. 130 canoe-based hook-and-line fishers + 84680 shore hook-and-line fishing hours). The fishing mortality of each species in each fishery could then be determined by the proportional contribution of the catch (kg) of each species in each gear to the total 1996 catch of that species in all gears (Chapter 5).

A first approximation of recruitment (R_i) was obtained by three methods. The mean density of juvenile cichlids and *M. salmoides* in the lake's shallow littoral areas was estimated using a fry seine-net and a 10-mm mesh size, 30-m long seine net as described in Chapters 2 and 4. The mean density of juveniles of each species was extrapolated to the total calculated nursery size. The nursery size was taken as the surface area of lakeshore areas less than 0.5 m deep for fry seine-net samples, and less than 2-m deep for 10-mm seine-net samples, during the period January to April 1996. The effective depth sampled by each gear (Chapter 4) set these limits. In addition, a further estimate of recruitment was obtained by dividing the total catch of each species (Y_i) during the 1996 calendar year by the total yield-per-recruit (YPR_i) from all fisheries determined using Equation 6.11 with 'base case' fishing and natural mortality scenarios.

Recruitment estimates derived from fry seine-net samples, 10-mm seine-net samples and from Equation 6.11 are summarised in Table 6.2. Although the estimate from Equation 6.12 was less conservative than the 10-mm seine-net estimate, it was the most conservative recruitment estimate for both *T. rendalli* and *M. salmoides*. In addition, 10-mm seine-net samples are likely to be negatively biased due to gear avoidance. Since juvenile cichlids in fry seine-net samples could not be identified to species level (Chapter 4), total cichlid recruitment is given for all three methods. In addition, no juvenile *M. salmoides* were captured using the fry seine-net. Overall, the estimates derived from Equation 6.11 were the most conservative for the cichlids. Recruitment estimates derived from Equation 6.11 were therefore taken to represent a first approximation of recruitment (R_i) for the three species.

Table 6.1. Recruitment estimates for *O. mossambicus*, *T. rendalli* and *M. salmoides* in Lake Chicamba using abundance estimates derived from fry seine-net and 10-mm mesh size (30-m long) seine-net samples and from Equation 6.12, (nd = not determined because of the difficulty in identifying cichlids to species level and no juvenile *M. salmoides* were caught in the fry seine net).

Method	Recruitment			
	<i>O. mossambicus</i>	<i>T. rendalli</i>	Total cichlid	<i>M. salmoides</i>
10-mm seine-net	1985791	2142251	4128042	319148
Fry seine-net	nd	nd	3651132	nd
Equation 6.11	267745	443980	3121125	172524

Table 6.2. Parameter estimates used in the per-recruit analysis for *Micropterus salmoides*, *Oreochromis mossambicus* and *Tilapia rendalli* in Lake Chicamba.

Parameter	Description	<i>M. salmoides</i>	<i>O. mossambicus</i>	<i>T. rendalli</i>	Source
L_{∞}	Predicted asymptotic length	465.51 mm (FL)	266.06 mm (TL)	238.74 mm (TL)	Chapter 3
K	Brody growth coefficient	1.175	-0.790	-0.636	"
T_0	Age at 'zero' length	-0.009 years	-0.269 years	-0.905 years	"
α	Parameter for length/weight equation	0.000013	0.000021	0.000012	"
β	"	3.043	2.984	3.136	"
M	Natural mortality rate	0.73 yr ⁻¹	0.38 yr ⁻¹	0.20 yr ⁻¹	"
F	Fishing mortality rate	0.54 yr ⁻¹	0.24 yr ⁻¹	0.12 yr ⁻¹	"
Max	Maximum age	6 years	10 years	16 years	"
a_m	Age-at-50%-maturity	0.9 years	2.83 years	2.89 years	"
δ_m	Width of maturity logistic ogive	0.001 years	0.31 years	0.29 years	"
a_{50} : gill net	Age-at-50%-selectivity	0.74 years	2.96 years	3.26 years	Chapter 5
δ_{50} : gill net	Width of the selectivity logistic ogive	0.18 years	0.92 years	2.02 years	"
a_{50} : seine net		0.29 years	0.50 years	0.50 years	"
δ_{50} : seine net		0.035 years	0.01 years	0.01 years	"
a_{50} : hook & line		0.2 years	0.50 years	0.50 years	"
δ_{50} : hook & line		0.025 years	0.01 years	0.01 years	"
$F_{gill\ net}$	Gear-specific fishing mortality rate	0.316 yr ⁻¹	0.190 yr ⁻¹	0.030 yr ⁻¹	Chapter 6
$Q_{gill\ net}$	Catchability coefficient	0.001225	0.000736	0.000116	"
F_{seine}		0.089 yr ⁻¹	0.033 yr ⁻¹	0.055 yr ⁻¹	"
$Q_{seine\ net}$		0.001113	0.000413	0.000688	"
$F_{hook\ \&\ line}$		0.135 yr ⁻¹	0.017 yr ⁻¹	0.035 yr ⁻¹	"
$Q_{hook\ \&\ line}$		0.00135	0.00017	0.00035	"
R_i	First estimate of recruitment	172524	2677145	443980	"

Per-recruit analysis

Isopleth diagrams, generated using traditional yield-per-recruit models, describing the response of yield-per-recruit to different values of fishing mortality (F) and age-at-50%-selectivity for *O. mossambicus*, *T. rendalli* and *M. salmoides* are shown in Figure 6.2. The response isopleths showed that, in all three species, yield-per-recruit increased rapidly at low values of F over most of the age range of a_{50} . Maximum yield-per-recruit was attainable at values of a_{50} between 0.3 and 1 years in *M. salmoides* and at values of a_{50} between 1 and 3 years in *O. mossambicus* and *T. rendalli*. Asymptotic yield-per-recruit was attained at low values of F when the age-at- 50%-selectivity was greater than 3 years in *O. mossambicus* and *T. rendalli* and greater than 2 years in *M. salmoides*.

Biomass-per-recruit as a function of age as well as yield- and spawner biomass-per-recruit as a function of fishing mortality (F) are illustrated in Figures 6.3, 6.4 and 6.5 for *M. salmoides*, *O. mossambicus* and *T. rendalli* respectively. Since the age-at-50%-selectivity in the seine-net and hook-and-line fisheries was similar, only the seine-net fishery and the gill-net fishery exploitation scenarios are shown in Figures 6.3, 6.4 and 6.5. In all scenarios the biomass-per-recruit of fish surviving past the age-at-50%-selectivity decreased rapidly. In all three species higher yield-per-recruit was obtained at higher rates of F in the gill-net fishery than in the seine-net and hook-and-line fisheries (Figure 6.3b, 6.4b, 6.5b). Similarly, spawner biomass depletion rates were lower and higher effort levels were required to reduce spawner biomass-per-recruit to 50% of pristine levels in the gill-net fishery than in the seine-net and hook-and-line fisheries (Figures 6.3c, 6.4c, 6.5c).

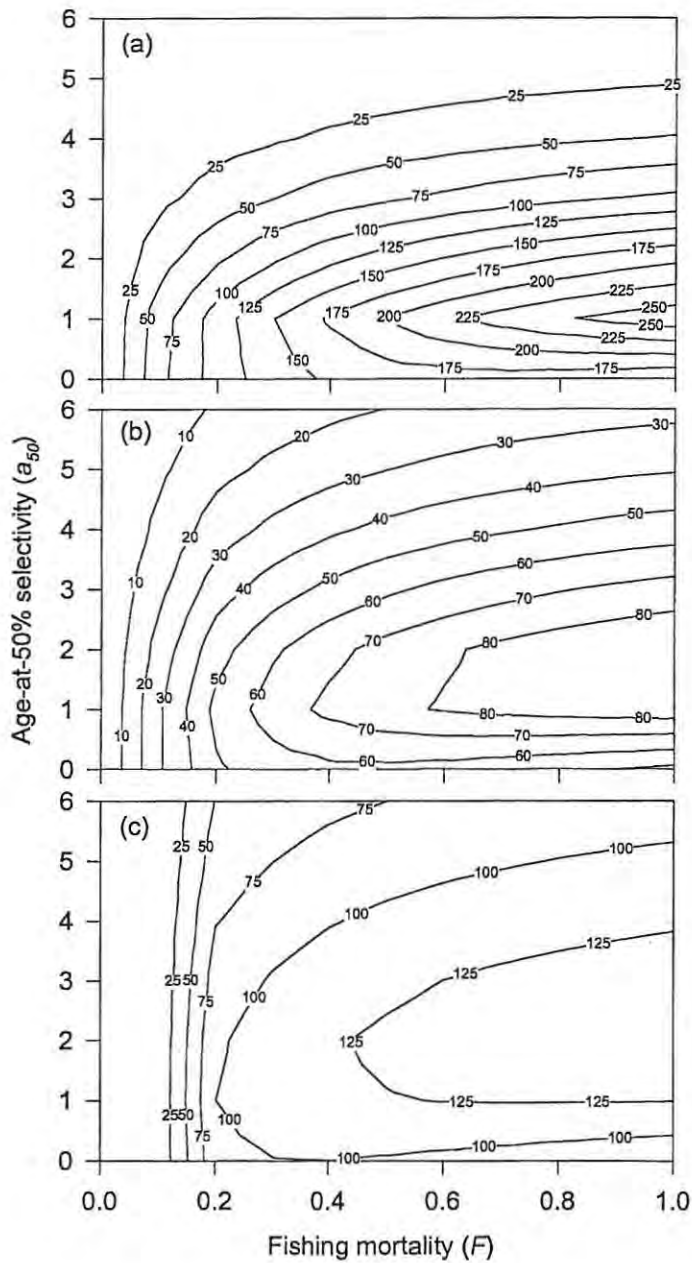


Figure 6.2. Isopleth diagrams describing the response of yield-per-recruit to different combinations of fishing mortality and age-at-50%-selectivity in Lake Chicamba for (a) *Micropterus salmoides*, (b) *Oreochromis mossambicus* and (c) *Tilapia rendalli*. Analysis was conducted using the 'traditional' single-species models with the 'base case' scenario where $M = 0.73$, 0.38 and 0.20 for *M. salmoides*, *O. mossambicus* and *T. rendalli*, respectively. The selectivity function was 'knife edge' ($\delta = 0.01$) in all scenarios.

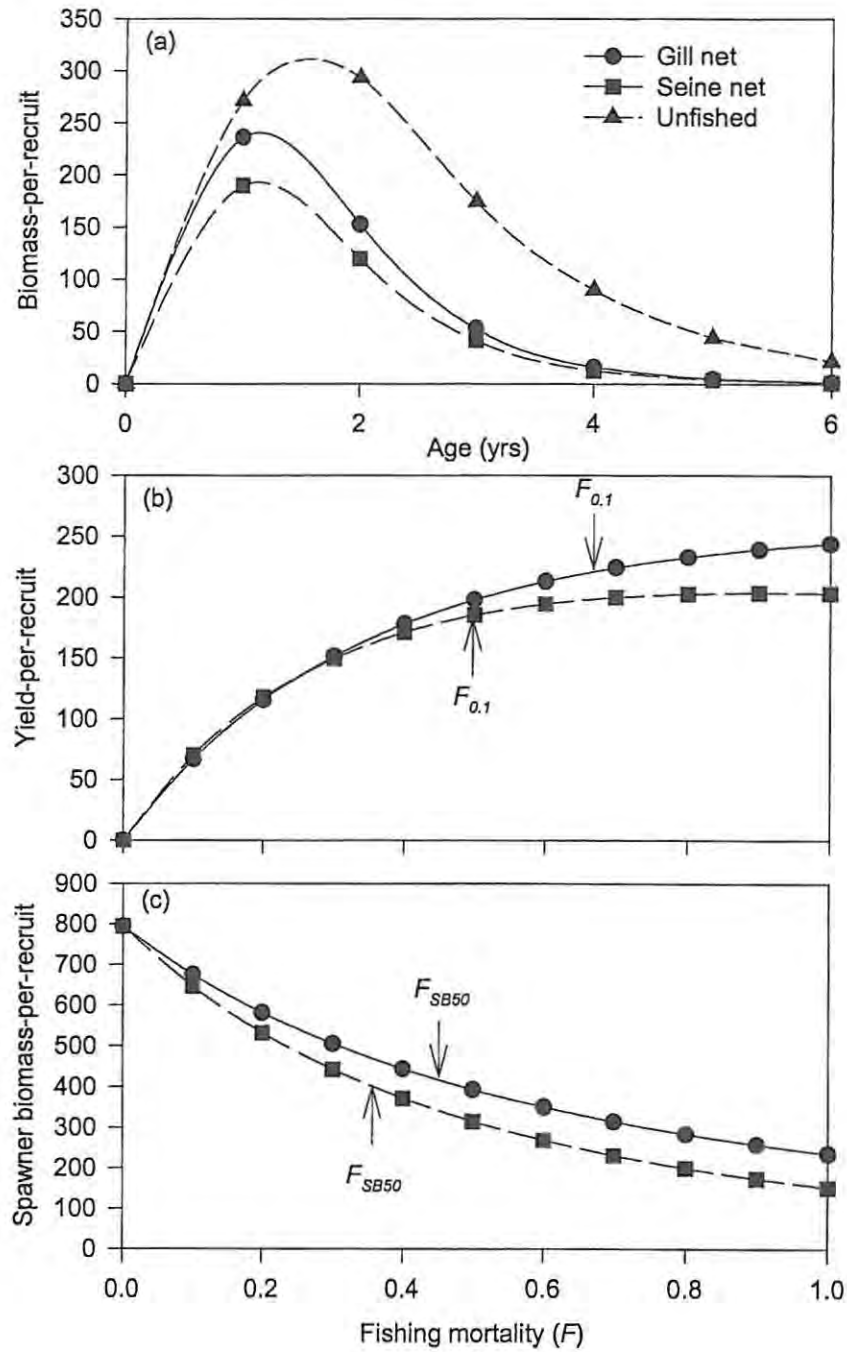


Figure 6.3. *M. salmoides*: (a) biomass-per-recruit as a function of age comparing an unfished population with two exploited 'base case' scenarios, (gill net and seine net fishing), (b) yield-per-recruit with 'base case' gill net and seine net fishing and (c) spawner-biomass-per-recruit with 'base case' gill net and seine net fishing. Analyses were conducted using the 'traditional' single-species models. 'Base case' scenario parameters were $M = 0.73$; $F = 0.54$; gill net $a_{50} = 0.74$ and $\delta = 0.18$; seine-net $a_{50} = 0.29$ and $\delta = 0.04$.

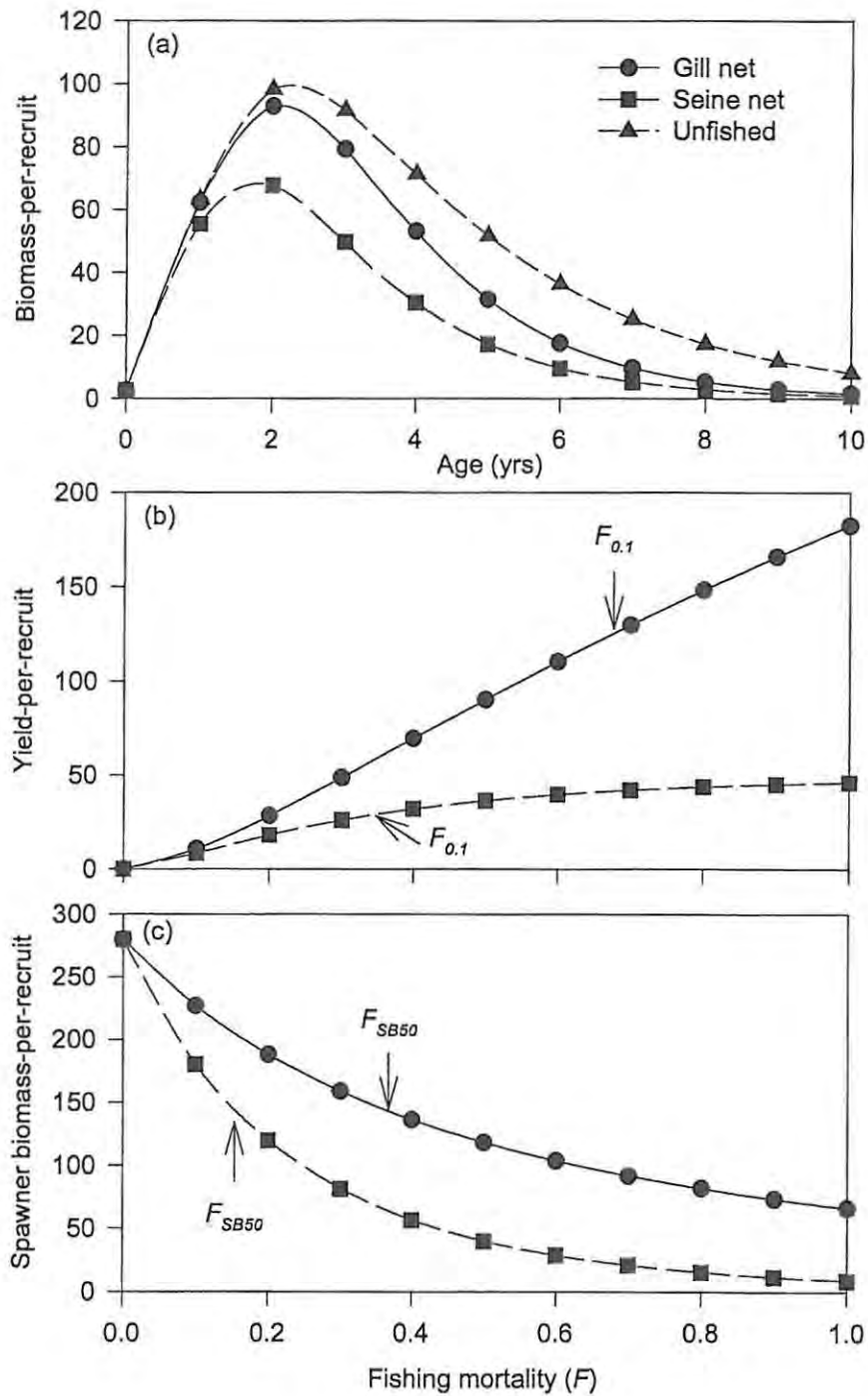


Figure 6.4. *O. mossambicus*: (a) biomass-per-recruit as a function of age comparing an unfished population with two exploited 'base case' scenarios, (gill net and seine net fishing), (b) yield-per-recruit with 'base case' gill net and seine net fishing and (c) spawner-biomass-per-recruit with 'base case' gill net and seine net fishing. Analyses were conducted using the 'traditional' single-species models. 'Base case' scenario parameters were $M = 0.38$; $F = 0.24$; gill net $a_{50} = 2.96$ and $\delta = 0.92$; seine-net $a_{50} = 0.5$ and $\delta = 0.01$.

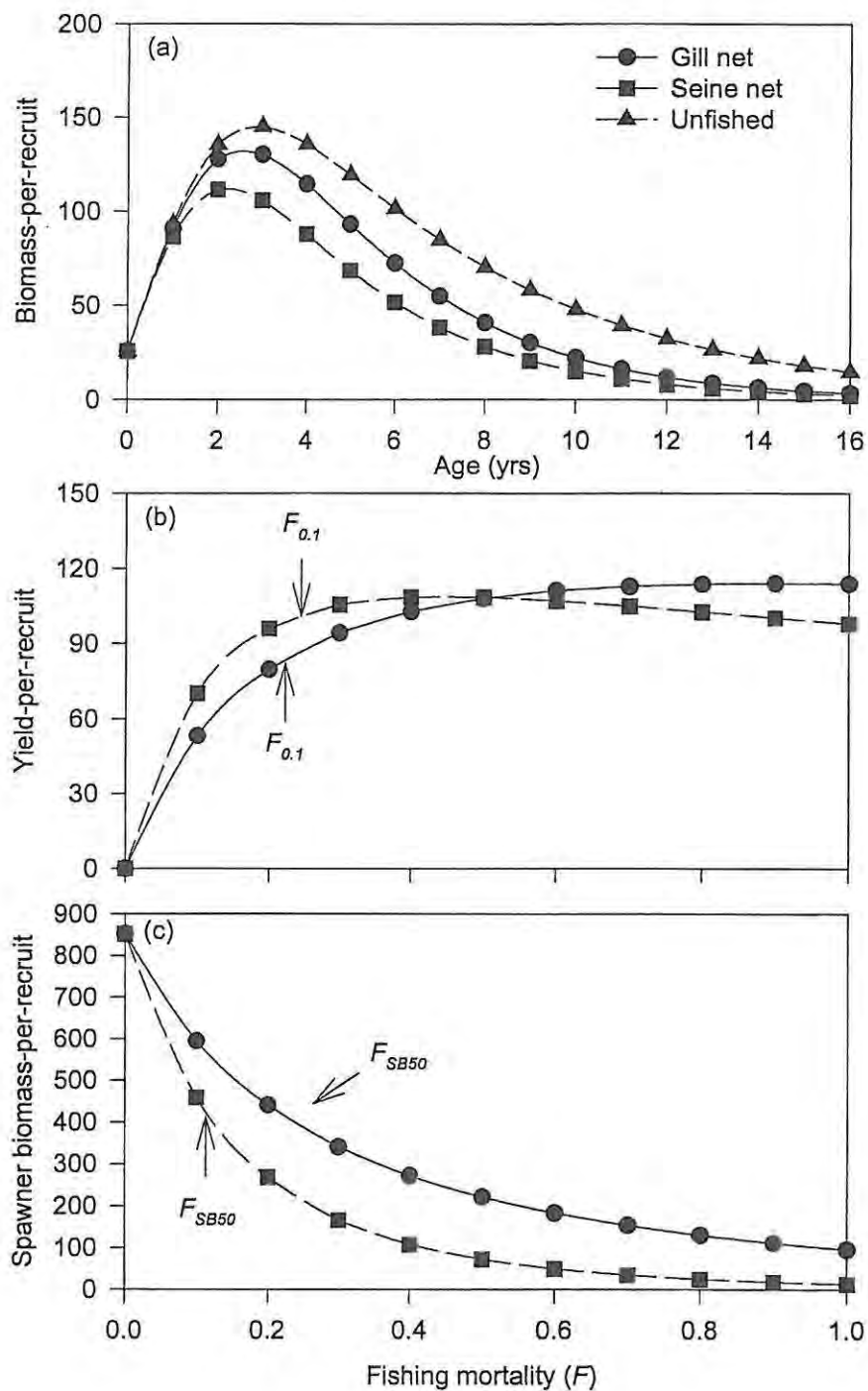


Figure 6.5. *T. rendalli* : (a) biomass-per-recruit as a function of age comparing an unfished population with two exploited 'base case' scenarios, (gill net and seine net fishing), (b) yield-per-recruit with 'base case' gill net and seine net fishing and (c) spawner-biomass-per-recruit with 'base case' gill net and seine net fishing. Analyses were conducted using the 'traditional' single-species models. 'Base case' scenario parameters were $M = 0.20$; $F=0.12$; gill-net $a_{50} = 3.26$ and $\delta = 2.02$; seine-net fishery $a_{50} = 0.5$ and $\delta=0.01$.

Four target reference points (TRPs) were investigated for the traditional yield-per-recruit and spawner biomass-per-recruit curves. These were, F_{max} the fishing mortality which corresponds to the maximum of the yield-per-recruit curve, $F_{0.1}$ or marginal yield value (Gulland & Boerema 1973) where the slope of the yield-per-recruit curve is 10% of that at the origin and F_{SB50} and F_{SB40} which are the fishing mortalities that correspond to a reduction in the spawner biomass-per-recruit curve to 50% and 40% of its unexploited equilibrium level, respectively. The F_{SB40} and F_{SB50} TRPs were chosen because all three species exhibited reproductive behaviour (i.e. nest guarding and mouthbrooding) that implied a strong dependence of recruitment on spawner stock levels.

Due to the inherent difficulty in the estimation of the instantaneous rate of natural mortality (M) the sensitivity of the yield-per-recruit and spawner biomass-per-recruit models to changes in the rate of natural mortality (M) was assessed. A Monte-Carlo (Buckland 1984) estimation procedure was used to estimate the standard error and confidence intervals of the TRP \hat{F} using uniformly distributed natural mortality scenarios with upper and lower limits 25 % higher or lower than 'base case' M estimates. 'Base case' estimates for natural mortality were 0.73 yr^{-1} for *M. salmoides*, 0.38 yr^{-1} for *O. mossambicus* and 0.20 yr^{-1} for *T. rendalli*. In the procedure a large number (in this case 500) (U_{500}) of random mortality samples ($M_U: U=1,2,\dots,U_{500}$) were generated with a uniformly distributed mortality error structure, and a corresponding set of ($\hat{F}^1, \hat{F}^2, \dots, \hat{F}^{U_{500}}$) TRPs computed.

The variance of \hat{F} was estimated by:

$$Var(\hat{F}) = \frac{1}{U_{500} - 1} \sum_{U=1}^{U_{500}} [\hat{F}^U - \bar{F}]^2 \quad (\text{Equation 6.14})$$

where \bar{F} is the mean of the \hat{F} vector.

The standard error for the TRP \hat{F} was estimated as:

$$SE^{\hat{F}} = \frac{Var(\hat{F})}{\sqrt{500}} \quad (\text{Equation 6.15})$$

The percentile method was used to estimate 95% confidence intervals, where the 2.5% and 97.5% quartiles from the sorted \hat{F} vector were chosen to represent the upper and lower 95% confidence intervals respectively (Buckland, 1984).

The F_{max} , $F_{0.1}$, F_{SB50} and F_{SB40} TRP fishing mortalities, 95% confidence intervals and yield at each TRP for *M. salmoides*, *O. mossambicus* and *T. rendalli* are presented for the gill net, seine net and hook and line fishing scenarios, respectively, in Table 6.3.

In all scenarios, a marginal-yield fishing strategy ($F_{0.1}$) was obtained at higher fishing mortalities in the gill-net fishery where a_{50} occurred at or after the age-at-50% maturity. In all scenarios, higher fishing pressure was necessary to obtain the marginal yield ($F_{0.1}$) than the F_{SB40} TRP. The Monte-Carlo estimation procedure illustrated that of all the TRPs

considered the F_{SB50} TRP showed the least variation. This target reference point was therefore considered the most robust in setting effort limits for the Lake Chicamba fishery.

Table 6.3. Target reference points (TRP), upper and lower 95% Monte-Carlo confidence intervals (in parenthesis) and estimated annual yield in tons (Y) at these TRPs for *Micropterus salmoides*, *Oreochromis mossambicus* and *Tilapia rendalli* in Lake Chicamba.

	<i>M. salmoides</i>		<i>O. mossambicus</i>		<i>T. rendalli</i>	
	TRP	Y	TRP	Y	TRP	Y
Gill net	$a_{50} = 0.74$ yrs; $\delta = 0.18$		$a_{50} = 2.96$ yrs; $\delta = 0.92$		$a_{50} = 3.26$ yrs; $\delta = 2.02$	
F_{max}	1.14 (0.94,1.34)	43	1.86 (1.39,2.39)	790	0.48 (0.39,0.56)	48
$F_{0.1}$	0.67 (0.56,0.78)	38	0.69 (0.54,0.86)	342	0.25 (0.21,0.29)	39
F_{SB50}	0.46 (0.40,0.53)	33	0.37 (0.32,0.42)	169	0.21 (0.20,0.22)	36
F_{SB40}	0.64 (0.55,0.73)	38	0.52 (0.45,0.59)	253	0.23 (0.6,0.18)	35
Seine net	$a_{50} = 0.29$ yrs; $\delta = 0.04$		$a_{50} = 0.50$ yrs; $\delta = 0.01$		$a_{50} = 0.50$ yrs; $\delta = 0.01$	
F_{max}	0.76 (0.65,0.86)	35	0.53 (0.45,0.61)	117	0.42 (0.35,0.49)	48
$F_{0.1}$	0.50 (0.43,0.57)	32	0.33 (0.28,0.38)	82	0.23 (0.20,0.27)	44
F_{SB50}	0.35 (0.31,0.38)	28	0.16 (0.15,0.17)	39	0.12 (0.11,0.13)	34
F_{SB40}	0.47 (0.42,0.52)	31	0.22 (0.20,0.23)	56	0.16 (0.15,0.17)	39
Hook & line	$a_{50} = 0.2$ yrs; $\delta = 0.03$		$a_{50} = 0.5$ yrs; $\delta = 0.01$		$a_{50} = 0.5$ yrs; $\delta = 0.01$	
F_{max}	0.69 (0.60,0.78)	33	0.53 (0.45,0.61)	95	0.42 (0.35,0.49)	50
$F_{0.1}$	0.47 (0.41,0.53)	30	0.33 (0.28,0.38)	72	0.23 (0.20,0.27)	45
F_{SB50}	0.33 (0.30,0.36)	26	0.16 (0.15,0.17)	38	0.12 (0.11,0.13)	35
F_{SB40}	0.45 (0.40,0.49)	30	0.22 (0.20,0.23)	50	0.16 (0.15,0.17)	17

However, since the traditional yield- and spawner biomass-per recruit models treat each fishery in isolation, the combined effect of all fisheries on the fish populations cannot be determined. The various TRPs considered here are, therefore, only valid if two of the three fisheries are closed. The closure of two fisheries is not considered a viable management

option for this fishery. Thus the fishery was assessed using multi-species/multi-gear yield- and spawner biomass-per-recruit models. Since traditional per-recruit analysis indicated that the $F_{SB(x)}$ TRP approach was the most robust and this approach is widely accepted as a low risk management strategy (Clarke 1991, Punt 1993b), only $F_{SB(x)}$ TRPs are considered in the multi-species/multi fishery simulations.

Using the multi-species/multi-fishery per-recruit models it was possible to assess the response of *M. salmoides*, *O. mossambicus* and *T. rendalli* yield-per-recruit and spawner-biomass-per-recruit to different combinations of F in the gill-net, hook-and-line and seine-net fisheries (Figures 6.6, 6.7 & 6.8). It was determined that in *M. salmoides* and *T. rendalli* higher levels of F in the gill-net and hook-and-line fishery were required to maximise yield-per-recruit and attain the F_{SB50} TRP after the theoretical closure of the seine-net fishery (Figure 6.6, 6.8). In *O. mossambicus*, the closure of the seine-net fishery had little effect on yield-per-recruit but resulted in higher levels of F in the gill-net and hook-and-line fishery before the F_{SB50} TRP was reached (Figure 6.7).

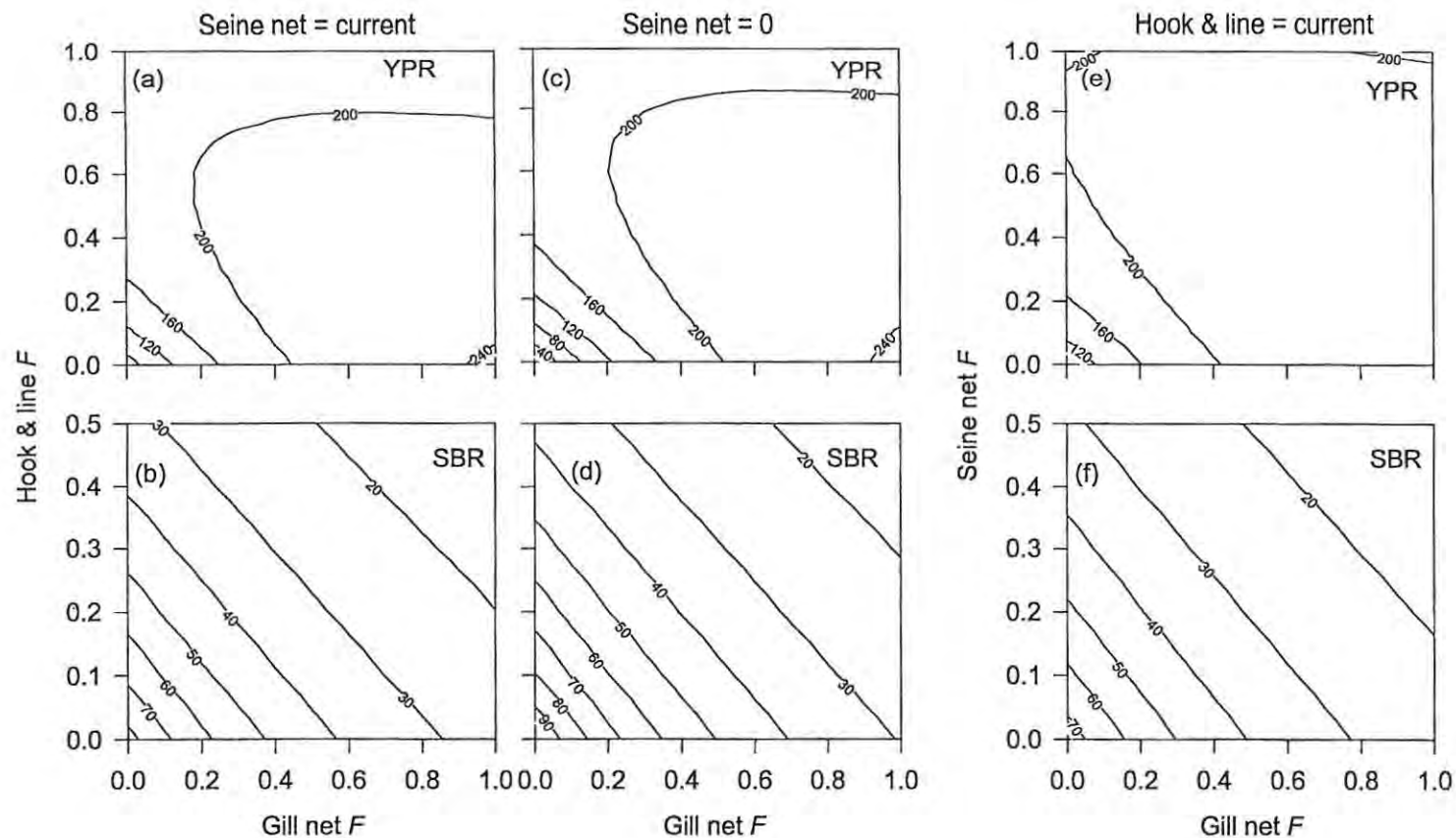


Figure 6.6. Isopleth diagrams showing the response of *M. salmoides* yield-per-recruit (YPR) to changes in fishing mortality (F) in the gill-net, seine-net and hook-and-line fishery in the following scenarios (a) seine net fishing at current levels, (c) seine-net fishery closed ($F = 0$) and (e) hook-and-line fishery at 'base case' levels and the response of spawner biomass-per-recruit (SBR), as a percentage of pristine levels, to changes in F in the gill-net, seine-net and hook-and-line fishery with fishing mortality in the following scenarios (b) seine-net fishing at current levels, (d) seine-net fishery closed ($F = 0$) and (f) hook-and-line fishery at 'base case' levels. Analyses were conducted using the multi-species/multi-fishery models.

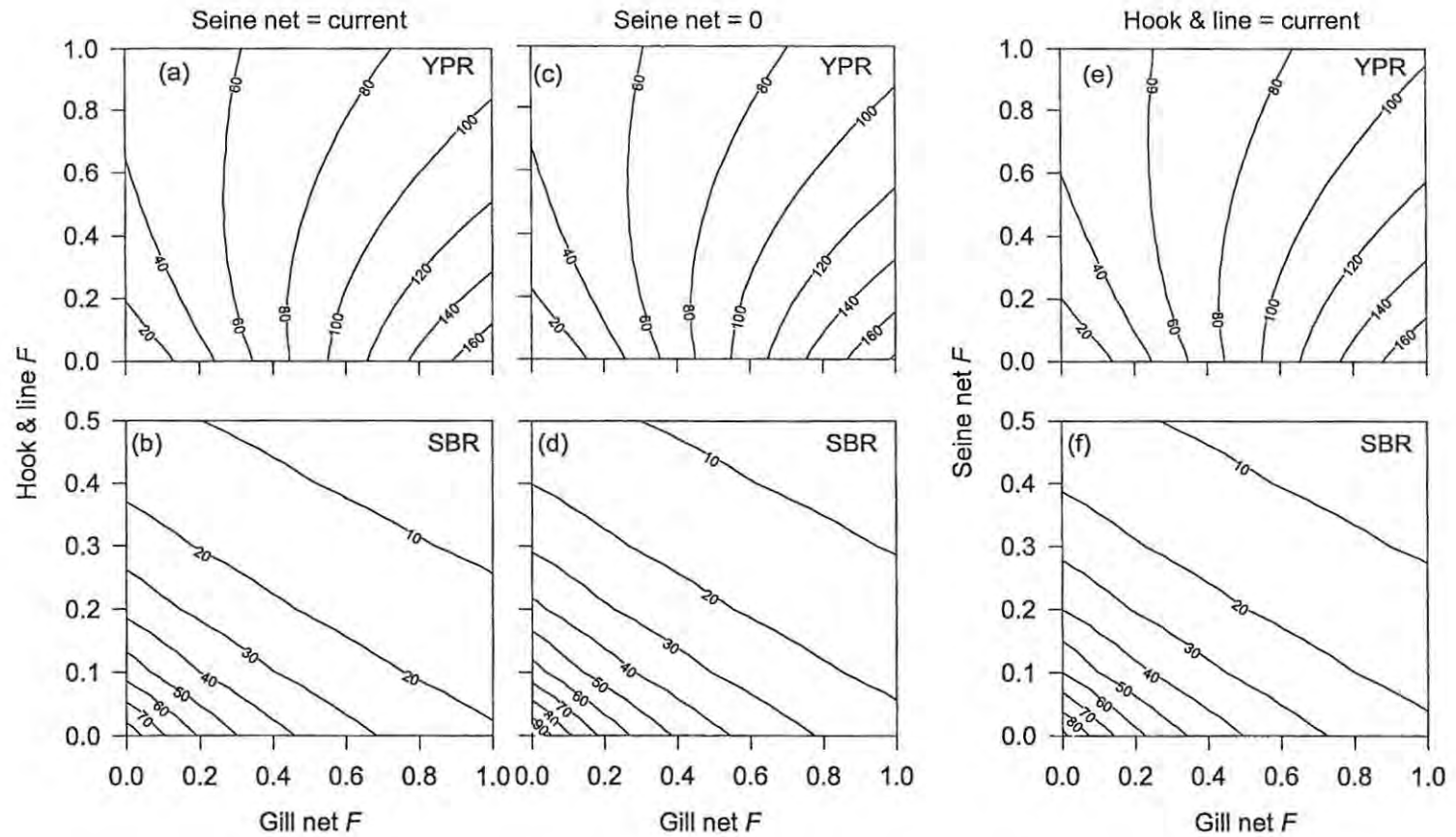


Figure 6.7. Isopleth diagrams showing the response of *O. mossambicus* yield-per-recruit (YPR) to changes in fishing mortality (F) in the gill-net, seine-net and hook-and-line fishery in the following scenarios (a) seine net fishing at current levels, (c) seine-net fishery closed ($F = 0$) and (e) hook-and-line fishery at 'base case' levels and the response of spawner biomass-per-recruit (SBR), as a percentage of pristine levels, to changes in F in the gill-net, seine-net and hook-and-line fishery with fishing mortality in the following scenarios (b) seine-net fishing at current levels, (d) seine-net fishery closed ($F = 0$) and (f) hook-and-line fishery at 'base case' levels. Analyses were conducted using the multi-species/multi-fishery models.

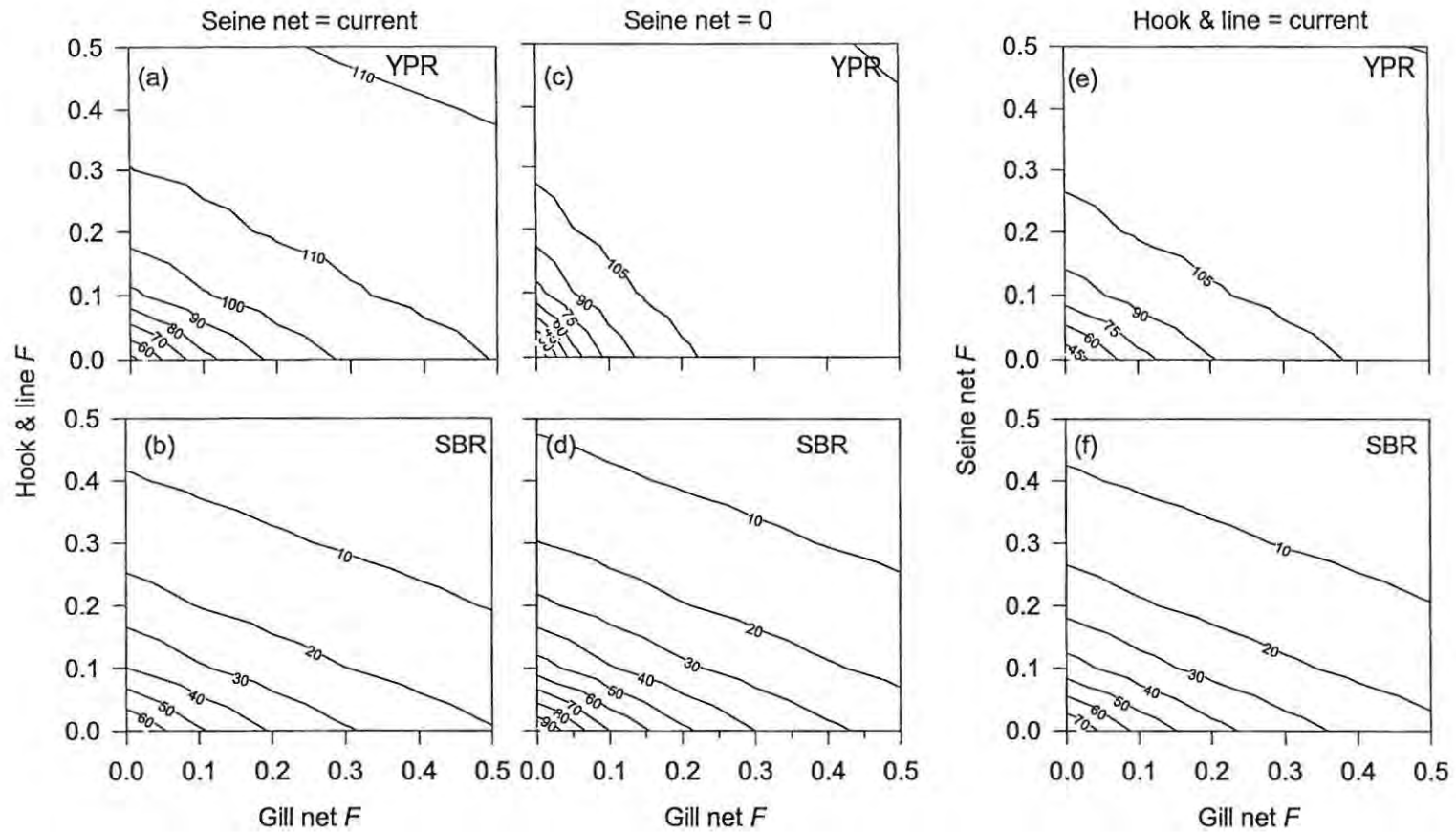


Figure 6.8. Isopleth diagrams showing the response of *T. rendalli* yield-per-recruit (YPR) to changes in fishing mortality (F) in the gill-net, seine-net and hook-and-line fishery in the following scenarios (a) seine net fishing at current levels, (c) seine-net fishery closed ($F = 0$) and (e) hook-and-line fishery at 'base case' levels and the response of spawner biomass-per-recruit (SBR), as a percentage of pristine levels, to changes in F in the gill-net, seine-net and hook-and-line fishery with fishing mortality in the following scenarios (b) seine net fishing at current levels, (d) seine-net fishery closed ($F = 0$) and (f) hook-and-line fishery at 'base case' levels. Analyses were conducted using the multi-species/multi-fishery models.

Since there are a large number of possible combinations of gill net, seine net and hook and line fishing mortality rates, the determination of a TRP, such as F_{SB50} , in any one fishery is dependent on the effort levels in the other two fisheries. For this reason, the multi-species/multi-fishery per-recruit models were used to assess the effect of the following management scenarios on the yield-per-recruit and spawner biomass-per-recruit of *M. salmoides*, *O. mossambicus* and *T. rendalli*:

Scenario:

- 1- A 10%, 20% and 30% increase in current fishing effort with all four fisheries active.
- 2- The closure of the seine net fishery without the integration of these fishers into other fisheries.
- 3- The closure of the seine net fishery and the integration of these fishers into the gill net fishery and a subsequent increase of a 10%, 20% and 30 % in fishing effort in the gill and hook and line fishery.
- 4- The effect of a 30 % increase in hook and line fishing effort with effort levels in the gill net fishery set at a maximum of 338 fishers (338 gill net fishers allows the 80 seine net fishers access into the 258 fisher gill net fishery after the closure of the seine net fishery).

The results of proportional increases in current fishing effort in the gill-net, seine-net and hook-and-line fisheries on the yield and spawner-biomass-per-recruit are shown in Table 6.4. These results are point estimates obtained from using the input parameters presented in Table 6.2 and their accuracy is dependent on the precision of these parameter estimates. At current fishing effort levels, spawner biomass levels were estimated to range between 40

and 50% of unexploited levels for *M. salmoides* and between 50 and 60 % of unexploited levels for *O. mossambicus* and *T. rendalli*.

Table 6.4. The response of the percentage spawner-biomass-per-recruit, yield (Y) and total fishery yield (TY) to the following management scenarios: (1) No change in gear and increase (Δ) in current fishing effort; (2) Closure of the seine-net fishery; (3) the integration of the seine net fishers into the gill net fishery with subsequent increase in effort; and (4) a ceiling level of 338 gill net fishers with a 30% increase in hook and line fishing.

Scenario + Δ	<i>M. salmoides</i>		<i>O. mossambicus</i>		<i>T. rendalli</i>		Total TY(tons)	
	SBR (%)	Y(tons)	SBR (%)	Y(tons)	SBR (%)	Y(tons)		
1	0 %	42.2	33.8	55.9	86.5	52.1	32.8	153.1
	10 %	39.2	34.8	53.1	97.2	49.1	34.5	166.5
	20 %	36.6	35.7	50.5	107.8	46.3	36.0	179.5
	30 %	34.1	36.3	48.1	118.3	43.8	37.4	192.1
2		48.7	31.8	63.7	76.5	71.7	20.9	129.2
3	0 %	40.4	35.1	56.4	108.6	65.2	25.3	169.0
	10 %	37.6	36.0	53.7	122.3	62.6	27.0	185.3
	20 %	34.9	36.8	51.1	136.0	60.2	28.5	201.4
	30 %	32.6	37.5	48.8	149.7	58.0	29.9	217.1
4		40.1	35.1	56.2	108.7	64.6	25.7	169.5

An increase of 10% in current fishing effort in each sector resulted in an estimated increase of 13 tons in yield. However, this increase in yield resulted in a calculated decrease in the spawner biomass-per-recruit of *M. salmoides* and *T. rendalli* to below 40 and 50 % of pristine levels, respectively. The closure of the seine-net fishery with no increase in either gill net fishing or hook and line fishing resulted in a slight recovery of the spawner biomass-per-recruit in *M. salmoides* once equilibrium has been attained. However, this increase was negligible and failed to increase spawner biomass-per-recruit to above 50 % of pristine. The integration of the 80 seine net fishers into the gill-net fishery after

theoretical closure of the seine-net fishery, resulted in an immediate increase of 31% in gill-net effort and an estimated increase of 16 tons in annual yield for the entire fishery. After this increase in gill-net effort, *M. salmoides* spawner biomass could not be maintained at the F_{SB40} TRP with a further 10% increase in effort in both the gill-net and hook-and-line fisheries. When effort levels in the gill-net fishery were set at 338 fishers (the sum of existing gill net fishers and 80 seine net fishers) an increase in hook and line fishing effort of 30% was possible before *M. salmoides* spawner biomass dropped to below 40% of pristine levels. This fishing scenario corresponded to an estimated yield of 170 tons for the entire fishery.

6.4 DISCUSSION

Low natural mortality rates, long lifespan, late maturity and extended parental care imply a relatively low maximum yield-per-recruit for the two cichlid species (Adams 1980). Subsequently, maximum equilibrium yield occurs at later ages of entry into the fishery and at low fishing mortality rates (Figure 6.2b, 6.2c). These populations are likely to have relatively stable population sizes and, therefore, catch levels (Adams 1980). However, once the fishery becomes overfished, it would require a relatively long period (depending on the extent of overfishing) for the stock to rebuild due to the longevity, slow growth and low natural mortality inherent to the stocks. Conversely, *M. salmoides* is fast growing with a high rate of natural mortality (Chapter 3). Typically these traits lead to a more productive fishery where fish can be harvested at younger ages (Figure 6.1a). However, these fisheries are likely to be of a “boom and bust” nature (Adams 1980), characterised by high initial stock sizes, and the potential for both growth and recruitment overfishing.

Peak yield-per-recruit is attained if an infinite fishing mortality is applied when the biomass of a cohort is at its maximum (Pereiro 1992). If this maximum is maintained after the age-at-50%-maturity, the risk of spawning failure is reduced. However, if the age-at-50%-maturity is less than or equal to the age-at-50 % selectivity there could be an overfishing situation where the spawner biomass-per-recruit would rapidly reach levels where spawning and recruitment would fail. Thus, the maintenance of the spawner stock at levels where it can replace itself is vital. Typically, spawner biomass-per-recruit recommendations lie between 25% and 50% of unexploited levels (Deriso 1987, Sissenwine & Shepherd 1987, Gabriel et al. 1989, Quinn et al. 1990, Clark 1991, Punt 1993b, Mace 1994, Booth & Buxton 1997). Reproductive behaviour such as nest guarding by *M. salmoides* and *T. rendalli*, and mouthbrooding by *O. mossambicus* implies that recruitment is strongly dependent on spawner stock levels. Management of these species should therefore focus on the maintenance of spawner biomass at 50% of unexploited levels (F_{SB50}). Although the F_{SB50} strategy is the most conservative strategy (Table 5.3), the relationship between spawner stock size and recruitment is at present unknown and any increase in effort must be viewed with caution.

In Lake Chicamba, the existence of a fishery in which a number of gear types collectively target all age classes of the stocks, indicates that the fishery as a whole is vulnerable to both growth overfishing (where recruits are caught before they can significantly contribute to the biomass) and recruitment overfishing (where spawner stock levels are depleted to levels below which the stock cannot replenish itself). Of primary concern are the seine net and hook and line fishing sectors of the fishery. These sectors target primarily juveniles, which may lead towards recruitment as well as growth overfishing. Of these two fisheries, the

seine-net fishery is seen as the more destructive fishery due to its disruptive effects on spawning (Chapter 5).

'Traditional' per-recruit analysis showed that both the seine-net and hook-and-line fisheries harvested all three species at ages well below the age-at-50% maturity and this led to rapid decreases in spawner biomass with small increases in fishing effort (Figure 6.3c, 6.4c & 6.5c). Conversely, the gill-net fishery harvested both *O. mossambicus* and *T. rendalli* above the age-at-50%-maturity and *M. salmoides* just below the age-at-50%-maturity. Gill net fishing is therefore more sustainable and relatively large increases in fishing mortality only result in a marginal drop in spawner biomass-per-recruit (Figure 6.3c, 6.4c & 6.5c).

In an attempt to define optimum fishing mortality from a per-recruit perspective the use of target reference points (TRPs) has become common practice in fisheries management (Clarke 1991, Punt 1993b, Caddy & Mahon 1995, Booth 1997). Of the different TRPs chosen, the F_{max} strategy consistently produced the highest estimates for optimum fishing mortality and always at severe spawner biomass-per-recruit reduction. Punt (1993b) recommends that the F_{max} strategy should be avoided unless there is strong evidence that suggests that recruitment is unrelated to spawner biomass and that the marginal yield ($F_{0.1}$) strategy is the most stable and could be used with a minimum risk of stock collapse. However, an $F_{0.1}$ strategy for the Lake Chicamba fish stocks also fared poorly from a resource conservation perspective, with the fishing mortality required to reduce the spawner-biomass to 50% of pristine levels being consistently lower than the fishing mortality required for marginal yield ($F_{0.1}$) (Table 6.3). In addition, the F_{SB50} TRP was estimated with greatest precision and is considered to be the most robust to changes in the

estimate of natural mortality rate (Table 6.3). Although current fishing mortality estimates were found to be considerably lower than maximum yield (F_{max}) and marginal yield ($F_{0.1}$) TRPs for each species, the current fishing mortality rate exceeded the F_{SB50} TRP in the seine-net and hook-and-line fisheries for all species, and in the gill-net fishery for *M. salmoides*. However, since these models treat each fishery in isolation, the combined effect of all fisheries on the fish populations could not be determined. The definition of TRPs using a single-species/fishery-per-recruit model was therefore of limited value in developing a management strategy for this multi-gear fishery.

Since the relationship between fishing effort and fishing mortality varies among species due to differences in availability and vulnerability to the gear (Murawski 1984), the determination of catchability coefficients for each species in each fishery allowed for the determination of effort levels required for the attainment of the F_{SB40} and F_{SB50} TRPs. This is illustrated in Table 6.5, where differences in the catchability of each species account for large differences in effort levels at the F_{SB50} TRP.

Although the estimation of catchability coefficients may aid in determining the least resilient species for each gear type, and subsequently allow for the setting of effort limits that protect this species from overexploitation, its application is limited to fisheries where management excludes all but one fishery. Since the exclusion of two of the existing three fisheries on Lake Chicamba is not a viable management option, the development of models which can determine TRPs in a fishery where multiple gears exploit a mixed-species assemblage is vital in the development of an operational management procedure.

Table 6.5. Spawner biomass-50% (F_{SB50}) target reference points (TRP) for *M. salmoides*, *O. mossambicus* and *T. rendalli*, catchability coefficients (q) and effort levels required to attain the F_{SB50} TRP in the Lake Chicamba gill-net, seine-net and hook-and-line fisheries. Effort levels in the hook-and-line fishery are given as a percentage of current fishing effort (current fishing effort = 100%).

	<i>M. salmoides</i>	<i>O. mossambicus</i>	<i>T. rendalli</i>
Gill net			
F_{SB50}	0.46 yr ⁻¹	0.37 yr ⁻¹	0.21 yr ⁻¹
Q	0.001225	0.000736	0.000116
Effort	376 fishers	503 fishers	1810 fishers
Seine net			
F_{SB50}	0.35 yr ⁻¹	0.16 yr ⁻¹	0.12 yr ⁻¹
Q	0.001113	0.000413	0.000688
Effort	314 fishers	387 fishers	174 fishers
Hook and line			
F_{SB50}	0.33 yr ⁻¹	0.16 yr ⁻¹	0.12 yr ⁻¹
Q	0.00135	0.00017	0.00035
Effort (current $F = 100\%$)	244 %	941 %	343 %

When the Lake Chicamba fishery was modelled using the new multi-species/multi-fishery spawner biomass-per-recruit approach, it was estimated that the spawner biomass-per-recruit at current levels of fishing mortality for both *O. mossambicus* and *T. rendalli* were in excess of 50% (Table 6.4). At current exploitation levels the *M. salmoides* spawner biomass was at 42% of its pristine levels (Table 6.4). This implies that at current exploitation levels the fishery is not over-utilised. However, the reduction of *M. salmoides* and *T. rendalli* spawner biomass levels to below 40% and 50% of pristine levels, respectively, with an increase of only 10 % in current effort levels, was cause for concern (Table 6.4).

Since the seine-net fishery is seen as the most destructive fishery (Chapter 5), the effect of its removal on yield and spawner-biomass was modelled. Using multi-species/multi-fishery-yield-per-recruit simulations, the closure of the seine-net fishery produced an increase in yield-per-recruit for all three species at lower values of F in the gill-net and hook-and-line fisheries (Figure 6.6, 6.7 & 6.8). In addition, the F_{SB50} TRP was attained at higher values of F in the gill-net and hook-and-line fisheries after the closure of the seine-net fishery (Figure 6.6, 6.7 & 6.8).

Since the seine-net fishery harvests a large proportion of the *T. rendalli* caught in the fishery, the closure of the seine-net fishery led to a decrease in total yield for this species even after the integration of the seine net fishers into the gill-net fishery (Table 6.4). In addition, the closure of the seine-net fishery was insufficient to produce a harvesting strategy where *M. salmoides* spawner biomass-per-recruit would recover to 50% of pristine levels. However, in this species high fishing mortality rates are seen as responsible for the elimination of intra-specific competition and subsequent promotion of high growth rates (Chapter 3). Subsequently, the maintenance of this stock at spawner-biomass levels of 40% of pristine levels was not considered destructive. In addition, it was hypothesised that the closure of the seine-net fishery would lead to increased recruitment due to a reduction in nest destruction and disruption of spawning activity (Chapter 5).

It is recognised that not all species can be managed at optimum levels, and therefore, a management strategy should focus on the least resilient species. Since catchability coefficients vary considerably for each species and fishery, the effects of increased effort in

the gill-net and hook-and-line fishery after the theoretical closure of the seine-net fishery are best illustrated when F is standardised (Figure 6.9).

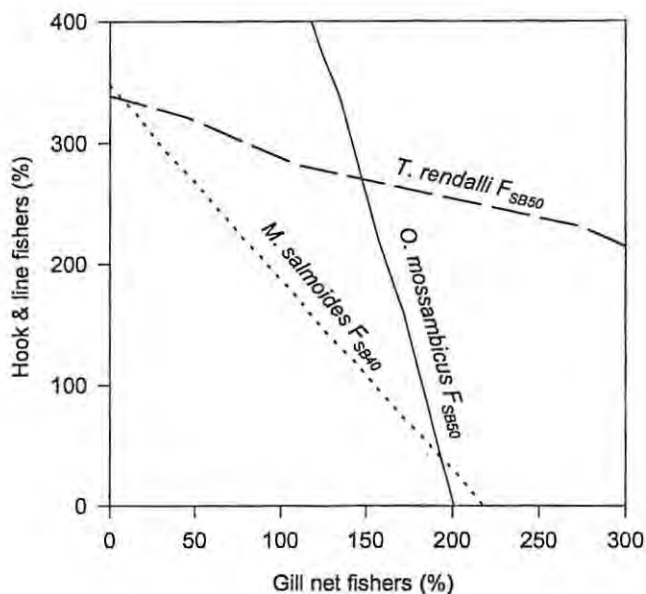


Figure 6.9. Isopleth diagram showing the effort levels (as a percentage of current F) required in the gill-net and hook-and-line fisheries to attain the F_{SB40} target reference point (TRP) for *M. salmoides* and the F_{SB50} TRP for *O. mossambicus* and *T. rendalli* (current $F = 100\%$).

In the Lake Chicamba fishery, the low age-at-50%-selectivity of *M. salmoides* in both the gill-net and hook-and-line fisheries and the high proportion of this species in the hook and line fishing catch make this species the most vulnerable to increases in gill net and hook and line fishing effort (Figure 6.9). Since the gill-net fishery harvests *O. mossambicus* and *T. rendalli* at ages older than the age-at-50%-maturity, large increases of effort are necessary before spawner biomass is decreased to below 50% of pristine levels (Figure

6.9). Management recommendations should therefore focus on the maintenance of the F_{SB40} TRP for the *M. salmoides* stock.

The Lake Chicamba fishery is primarily of a subsistence nature and an effective management strategy must be able to compensate fishers that loose their seine nets if this fishery were to be closed. These fishers must therefore be allowed access into the gill-net fishery. When gill net fishing effort is set at 338 fishers (which incorporates the 80 seine net fishers into this sector) using the current mean net length of 130 m, hook and line fishing effort could be allowed to increase by over 30% before *M. salmoides* spawner biomass dropped to below 40% of pristine levels (Table 6.4). At this effort level, *O. mossambicus* and *T. rendalli* spawner biomass would be in excess of 50% (Table 6.4, Figure 6.9). Given that hook and line fishing is undertaken primarily for subsistence, effort in this fishery is likely to increase as a response to population growth rather than to the migration of new fishers into the fishery. Since spawner biomass TRPs are not exceeded with a theoretical effort increase of 30% in hook and line fishing the proposed effort limits are considered safe.

Given the lack of historical data pertaining to the Lake Chicamba fishery, per-recruit models allow for the highest resolution in the determination of a management procedure. However, in this fishery, the use of multiple gears and the mixed-species nature of the catch in the fishery limits the application of the traditional per-recruit models, which focus on each fishery in isolation and ignore the interaction of different fisheries. For this reason, the development of multi-species/multi-fishery per-recruit models that take the dynamic nature

of the fishery into account was a vital contribution towards the sustainable utilisation of this fishery.

It must be considered that all parameter values used within the models discussed in this thesis are point estimates. Since these parameter estimates have associated variability, it has been attempted to address these issues in the Monte-Carlo simulations and sensitivity analysis. Addressing the effect of variability in multi-species and multi-gear per-recruit simulations is a vital step in the development of a comprehensive assessment model. However, this falls beyond the scope of the thesis.

The multi-species and multi-fishery characteristics of the Lake Chicamba fishery are shared by many riverine, lacustrine and marine fisheries (Welcomme 1978, Van der Waal 1991, Merron et al. 1993, Kapetski 1986, Balogun & Ibeun 1994, Bramiah 1994, Machena 1994, Marshall & Maes 1994, Rashid 1994, Van Der Knaap 1994, Japp et al. 1994, Beckley & Fennessy 1996, Kyle & Robertson 1997). The 'traditional' single-species-per-recruit models, which ignore important species and gear interactions, are not suitable assessment tools for these fisheries. However, the lack of historical data negates the use of more comprehensive methods such as multi-species Virtual Population Analysis (Sparre 1991, Magnusson 1995) in most fisheries. Therefore, the multi-species/multi-fishery per-recruit approach is the most comprehensive management tool available for these fisheries, until such time when relevant long-term directed catch-at-age or catch-at-length data are available. It is recognised that the per-recruit approach has limitations, such as its assumption of constant recruitment (Perreiro 1992), and, therefore, its use as a predictive tool is limited to short-term predictions. It is crucial that relevant long-term directed catch-

at-age or –length data are collected, in all fisheries, to allow for the combination of the per-recruit data with other age-structured models in order to provide more accurate, comprehensive and sustainable strategies for long-term management.

CHAPTER 7

General discussion with management considerations for the multi-species/multi-gear fishery in Lake Chicamba.

A management protocol for African reservoir fisheries

The use of multiple gears and the mixed species catch in African reservoir fisheries is the rule rather than the exception. The formulation of a management procedure that takes this dynamic nature of the fishery into account is, therefore, of vital importance for the sustainable management of these fisheries. In African fisheries the application of data-intensive models (Schaefer 1954, 1957, Beverton & Holt 1956, 1957, Deriso et al. 1985, Pope & Shepherd 1985, Schnute 1987, Lewy 1988, Butterworth et al. 1989, Schnute et al. 1989, Punt 1993a, 1993b, 1994) has often been hindered by the high cost associated with the collection of data (Lae 1997).

Since it is unrealistic to assume unlimited budgets in the assessment of a fishery, management advice must be based on the best possible scientific information that can be obtained within the given constraints of time and budget. Therefore, a management protocol must be flexible enough to allow management advice to be obtained (albeit with varying levels of resolution) from each stage in the protocol. The flowchart presented in Figure 7.1 represents a management protocol that prioritises research activity according to the management information that can be obtained from each level of the protocol.

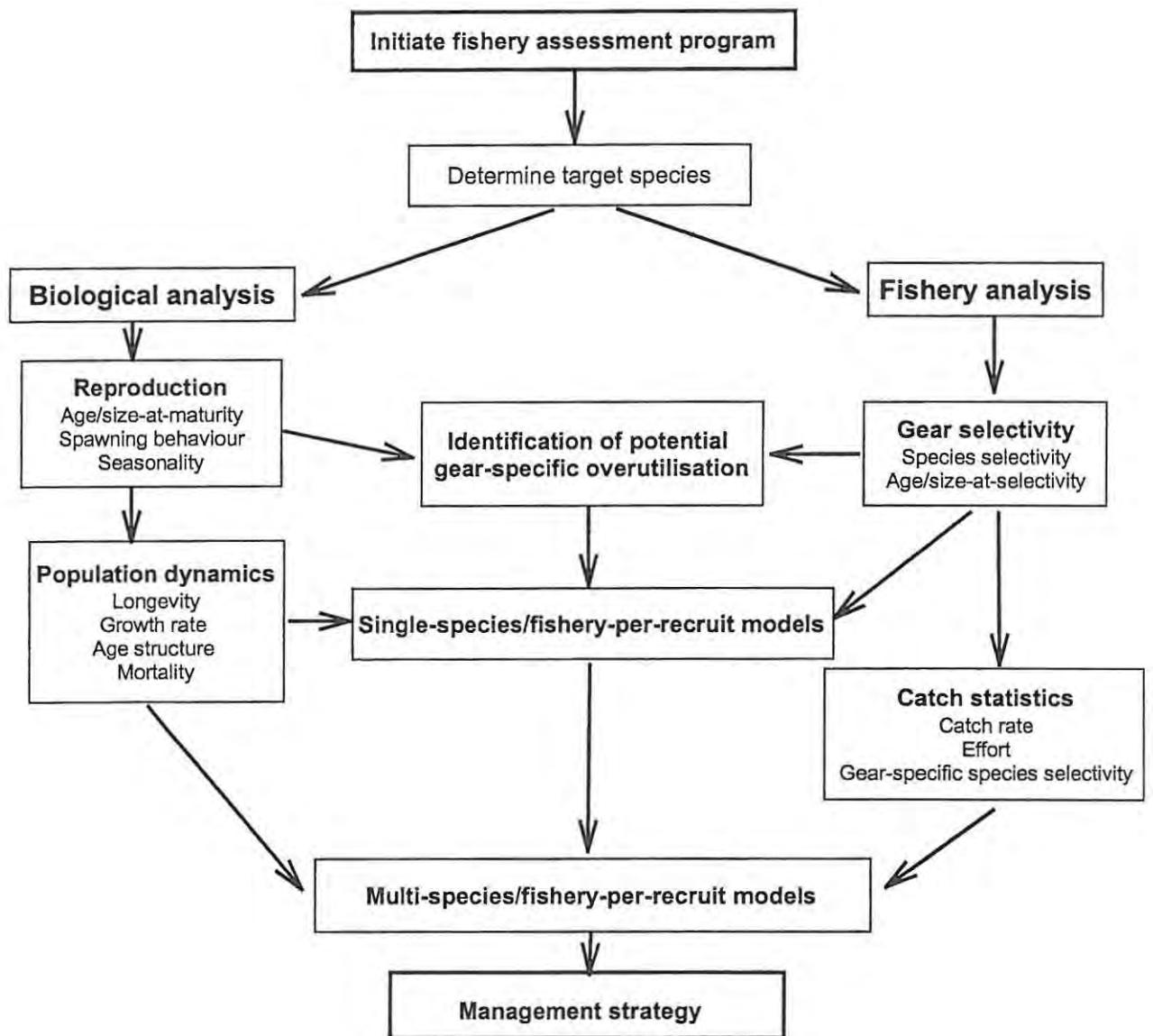


Figure 7.1. Flowchart of a proposed management strategy for data poor African reservoir fisheries.

The first priority in fisheries assessments should be to determine the target species and the selectivity of each harvesting gear. Subsequently the biological parameters pertinent for

the application of analytic models should be investigated for each of the target species. Growth and maturity parameters in freshwater fishes are locality specific (Chapter 3) and the determination of these parameters forms the basis for management in each particular water body. Since the harvesting of a fish stock after the attainment of 50%-maturity reduces the risk of spawning failure (Chapter 6), the determination of the size-at-50% maturity should be the first priority. By comparing the size-at-selectivity of each species harvested in each fishery to the age-at-maturity, the sustainability of each fishery can be assessed. For example, in Lake Chicamba both the seine-net and hook and line fisheries were considered potentially destructive as they selected juveniles of the three target species (Chapter 5). The knowledge that all three target species were nest spawners, and given that seine netting must inevitably disrupt spawning activity, allowed for the determination that the seine-net fishery was the more destructive of the two fisheries (Chapter 5).

The subsequent determination of age and growth, using sectioned otoliths (Chapter 3), allows for an increase in resolution of management advice. The determination of fish length-at-age allows for the determination of mortality rates, which together with growth parameters can then be used to apply 'traditional' per-recruit models. The traditional per-recruit models are capable of assessments for one species in one fishery (Chapter 6). These models increase the resolution in management advice as they allow for the assessment of different management strategies, such as the effect of an increase or decrease in the selectivity or effort in a fishery. In the absence of an active fishery or if the fishery is composed of a single gear harvesting a single species, these 'traditional' per-recruit models are adequate. However, fisheries which target one species with one gear are rare, and it is

therefore imperative that management advice be based on models that account for gear and species interactions.

Few African reservoirs have the historical data upon which models such as multi-species virtual population analysis (Sparre 1991) can be based. In addition, the development of a long-term data base is unrealistic given limited budgets and the fact that management of African reservoir fisheries is often an immediate rather than a future concern. The development of multi-species/multi-fishery-per-recruit models is therefore a valuable step in managing these fisheries. The input parameters for these models require that the fishery be quantified in terms of species-specific catch coefficients for each gear type. In addition, the quantification of catch data may also contribute towards the application of more data-intensive models in the future. This study has resulted in the development of a multi-species model, which assesses the response of spawner biomass-per-recruit to different management strategies (e.g., gear and/or effort changes).

Although the per-recruit approach is highly applicable in African fisheries, the models assume that age-specific maturity, age-specific selectivity, the growth equation, natural mortality and the current rate of fishing mortality can be estimated without error, there is no recruitment variability and that it is possible to impose a specified fishing mortality (Punt 1993b). Therefore, it is vital that the sampling regime uses the most robust available methods in the calculation of the input parameters. Peer review is also seen as an important process in the determination of the input parameters since this allows for the critical assessment of the methodology employed in the calculation of these parameters. This approach was employed in this study. Biological parameter estimates which were

subjected to peer review have subsequently been accepted for publication (Weyl & Hecht in press a, in press b). Since certain estimates such as natural mortality and recruitment are difficult to assess accurately, the risk associated in using the per-recruit models can be minimised by calculating error terms for target reference points (Chapter 6). In addition, since recruitment is highly variable and affected by lake level in Lake Chicamba (Chapter 4), conservative estimates for recruitment should be used. Although the per-recruit models have a number of constraints resulting from the assumptions outlined above, they have the highest resolution for management advice given current constraints in available historic data.

Management considerations for the Lake Chicamba fishery

The guarding and mouthbrooding reproductive behaviour of the three target species was considered to be the most important factor in adopting target reference points for these species. The reduction of spawner-biomass to 50% of pristine levels in the two cichlids *O. mossambicus* and *T. rendalli* and a reduction to 40% of pristine levels of *M. salmoides* was seen as acceptable in ensuring the future sustainability of the fish stocks (Chapter 6). Although current exploitation rates did not reduce spawner-biomass to levels below these target reference points, the reduction of spawner biomass to below target reference point levels in two of the three species with a 10% increase in fishing effort, emphasised the need for management (Chapter 6).

The success of a management strategy is primarily determined by how well it compliments the current fishery. Therefore, management advice must take into account not only the biological and technological aspects of the fishery but also the socio-economic influences

on the fishery. The management of the fish stocks in Lake Chicamba is complicated by the subsistence nature of the fishery. In this subsistence fishery little emphasis is placed on the size of the fish caught but rather the combined weight of the catch. The fish caught are not selected by personal preference but rather are determined by the gear available to the fisher. Secondly, since a subsistence existence implies that the primary objective is to meet household consumption, the introduction of new harvesting strategies are likely to be met with resistance if the risk of failure associated with a new gear seems unacceptable to the fishers. Thirdly, the fishers have a very limited knowledge of the biology of the fish in the lake. This was shown during a questionnaire survey designed to test the resource awareness of the fishers. Over 85% of the respondents underestimated the size-at-maturity of the two cichlids and *M. salmoides* and only 5% knew that the cichlids spawned in summer (Weyl 1997).

Although the overall results from the analysis undertaken suggest that the stocks have not been badly depleted (Table 6.4), all respondents that had fished on the lake for more than 2 years agreed that there had been a general decline in the fishery. The reasons given by the fishers, for this decline and their perceived solutions are summarised in Table 7.1. However, the perceived decline in the fishery may be little more than short term catch fluctuations caused by the concentration or dilution effect of fluctuating lake levels (Figure 5.9). Alternatively, the decline may be a result of a long-term decrease in overall lake productivity common in man-made reservoirs (Wood 1951, Jackson 1961). Unfortunately, there is no long-term catch data available for comparison.

Table 7.1. Reasons given by fishers (n = 37) for the general decline in catches and their suggested solutions (after Weyl 1997).

Reason for decline	%
Small-meshed nets (e.g. seine nets) overfish the juvenile stock.	51.3
Too many fishers on the lake.	35.1
Fluctuations in water levels leading to less efficient gear use.	35.1
Don't know.	18.9
Multi-gear nature of the fishery targeting all the fish.	5.4
Solutions	
Removal of small-meshed nets (e.g. sack seine nets) from the fishery.	45.9
Stocking programme to introduce more fish and new fish species.	35.1
Don't know.	32.4
Provision of suitable equipment (e.g. gill nets).	21.6
Halt fishing activity until stocks recover.	16.2
Establish closed areas.	2.7

All fishermen interviewed expressed a need for management on Lake Chicamba. The use of seine nets was of special concern to the fishers not currently using this gear (Table 7.1). However, no community pressure is put on the operators of these gears (Ainslie 1996) and the fishers expressed an eagerness for the government to set up a management framework for the fishery.

The best management option in the maximisation of both yield and spawner biomass would entail setting the age-at-selectivity of each species into the Lake Chicamba fishery near the age-at-maturity. Although the Lake Chicamba gill-net fishery approximates this scenario, a management strategy based entirely on the gill-net fishery with the exclusion of the hook-and-line and seine-net fisheries is not viable, given the current status of the fishery. Since hook and line fishing is undertaken primarily for subsistence and only a small percentage of the current catch is at the size-at-maturity (Chapter 5), a size limit in this sector is not seen as feasible. In addition, effort limitations in this sector would be impossible to enforce given the open access nature of this resource. In addition, the importance of the hook-and-

line fishery in the provision of food security for the rural population in the area makes this fishery the most important fishery on the lake. Management must therefore focus on the gill-net and seine-net fisheries.

The destructive effects of seine netting on spawning success of the target species (Chapter 5) was the primary determinant for the decision that this gear should be excluded from the fishery. In addition, the seine-net fishery, with 80 fishers (Chapter 5) is currently the smallest active fishery on the lake. When this factor is considered together with the attitude of gill net and hook and line fishers that the seine net sector is responsible for the decrease in catches, the closure of the seine-net fishery would be met with the least resistance by the fishery as a whole. The integration of these fishers into the gill-net fishery will also aid in the success of this management option.

Although gill net fishing is considered acceptable from both a biological perspective and by the fishers, effort limitations in this sector are necessary to ensure the harvesting of all three species within the limits of the target reference points. The proposed management strategy in which the gill-net fishery is set at 338 fishers (each using the current mean net length of 137 m), would allow for an increase of 30% in hook and line fishing before spawner biomass would be depleted to target reference point levels in the three species. For management purposes the gill-net fishery should be limited to 340 fishers. This limit of 340 gill-net fishers is seen as socially acceptable since it allows for the integration of the seine net fishers into the gill-net sector. Although, this management plan under-utilises the two cichlid species (Chapter 6), an increase in yield of 16.4 tons is predicted for the three

species. However, the implementation of this management strategy relies on an effective licensing scheme for the fishery.

Licensing

Presently, a licensing structure exists and all fishers, with the exception of hook and line fishers, require a mandatory license. Yet, the current scenario is that less than 10% of the fishers are fishing legitimately. This is an area of concern as it implies that there is no mechanism for controlling entry into the fishery and therefore further increases in effort are likely. Present factors that may cause increases in the number of fishers are:

- The fishery approximates an open-access system with little control exerted by the community on new entrants. Therefore, there is no extant system for effort limitation.
- The subsistence nature of the community surrounding the lake and a high reliance on farming for household survival implies an increase in fishing effort during drought years when the income from farming decreases.
- There is a large pool of potential fishers in the areas surrounding the lake.

It appears essential that a licensing scheme be effectively implemented in an attempt to control increasing effort in the fishery. However, Ainslie (1996) recommended that: "No illusions should be harboured about the ability of these rural communities to collectively manage their common fishing resources independent of outside assistance". The reasoning for this view was that the fishermen were a highly independent group, who were able to fish singly for food and income. This independence is likely to be a major stumbling block

for collective action. The state, therefore, should play a role in setting management guidelines, as well as administering and enforcing the management system.

Concluding remarks

The limitations of historical data pertaining to the Lake Chicamba fishery coupled with the dynamic multi-species and multi-user nature of the fishery resulted in the development of a new per-recruit approach that integrates the biological and technological interactions of the different fishery sectors. Since the nature of the Lake Chicamba fishery is not unique to this locality, the results presented in this thesis contribute not only towards the sustainable management of the Lake Chicamba fishery but also to the assessment of other fisheries. A management procedure, which prioritised the relevant data to be collected, was therefore formulated.

A comprehensive life history study of the three major target species in the Lake Chicamba fishery, *M. salmoides*, *O. mossambicus* and *T. rendalli* was undertaken and those life history parameters necessary for describing the population dynamics of the population were estimated. Growth analysis based on sectioned otoliths revealed that the three species differed considerably in growth rate and natural mortality. The two cichlids were relatively long lived and late maturing with low rates of natural mortality, while *M. salmoides* was relatively short lived with a high rate of natural mortality. However, all species displayed highly precocial reproductive behaviour and consequently a high reliance of recruitment on spawner biomass was hypothesised. In addition, it was shown that lake-level fluctuations in Lake Chicamba affected both recruitment and growth of the three species.

Information on the fishery was obtained with respect to catch rate and selectivity. It was shown that low ages at selectivity into the seine-net and hook-and-line fishery were areas of concern. Subsequently, management options were developed based on the application of existing and newly developed per-recruit models, and the sustainability of various catch scenarios was analysed. These investigations showed that although the current exploitation trends were not over-utilising the fishery an increase in fishing pressure would lead to an over utilisation of the stocks.

The analysis of current fishing methods and the attitude of the fishers led to the recommendation for the closure of the seine-net fishery. With the closure of the seine-net fishery an increase in gill net fishing and hook and line fishing was possible before the spawner-biomass of the three species attained target reference point levels. Although the multi-species nature of the fishery led to a scenario where not all species were utilised at optimum levels, the management scenario presented here was seen as the best possible strategy given the known species and gear interactions in the fishery.

Although the new multi-species/multi-fishery models presented in this work are confined by the assumptions of traditional per-recruit models, they allow for the highest resolution in stock assessment given the lack of historic data. Therefore, the Lake Chicamba fishery should be harvested at effort levels set by these new models until an adequate database is established upon which further and more data-intensive stock assessment methods can be employed.

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APPENDIX 1

Questionnaires used to ascertain gear use, utilisation patterns and resource awareness among fishers

1: Questionnaire used to assess gear utilisation and effort in the Lake Chicamba

Ref #		Date		Location	
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Canoe or shore fishing?

If canoe fishing, dugout or barkhive?

Gear Type:

	Mesh size/ Hook size	Gear dimension
Gill net		(metres)
Seine net		(metres)
Cast net		(diameter)
Hook and Line		(Number of hooks)
Long line		(Number of hooks)

How many hours did you fish today?

How many days did you fish in the last week?

Do you sell your catch?

Yes	No

How often do you sell your catch?

	Days per week
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2: Questionnaire to assess resource awareness among fishers

What is your primary source of income?

Fishing	
Farming	
Other	

Did you learn to fish on Lake Chicamba?

Yes	No

If no where did you learn to fish?

Location:	Province:
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How many years have you been fishing on Lake Chicamba?

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Do you think that your catches have changed over the time that you have been fishing on the lake?

Yes	No

Why do you think you are catching less fish now than in the past?

- Too many other fishers
- Small meshed nets used by other fishers
- Water levels
- Less equipment
- Other reasons

What would you consider as possible solutions?

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Why do you think you are catching more fish now than in the past?

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At what size do the following fish mature?

Species	10 cm	20 cm	30 cm	40 cm
Redbreast tilapia				
Mozambique tilapia				
Bass				
Do not know				

When do these fish breed?

Species	Summer	winter	All year
Redbreast tilapia			
Mozambique tilapia			
Bass			
Do not know			

